

Vegetation ecology of a woodland-savanna mosaic in central Benin (West Africa):
Ecosystem analysis with a focus on the impact of selective logging

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1 Introduction

Worldwide, mankind is facing the negative repercussions of global change (Walker *et al.* 1999, IPCC 2000, WBGU 2000). A main consequence of global change is an increasing shortage of natural resources, especially the resource freshwater, but also a threat to biodiversity (Cosgrove & Rijsberman 2000, Wolters *et al.* 2000, Lambin *et al.* 2003, Thomas *et al.* 2004). In the semiarid and subhumid zones of West Africa, abnormal drought occurred in the last decades affecting the socio-economy of the local population (IUCN 2004). Variations in the sea surface temperatures of the tropical Atlantic and changes of the land surface (e.g. vegetation cover) are generally considered to be a major cause of interannual to multidecadal rainfall variability across tropical West Africa (Nicholson 2000, Giannini *et al.* 2003, Paeth & Hense 2004). Therefore, it is important to understand how land use change influences precipitation patterns due to soil-vegetation-precipitation feedback mechanisms and conversely, how seasonal rainfall variations affect vegetation dynamics (IUCN 2004, Paeth & Hense 2004).

In the Guinean and Congolian Rain Forest zone of West Africa, land use change was strongly enhanced by timber logging and the conversion of former dense forests into plantations and arable land starting with the beginning of the last century (e.g. Chatelain *et al.* 1996a, Chatelain *et al.* 1996b, Fairhead & Leach 1998, FAO 2001, Poorter *et al.* 2004). In the Sudanian zone, land use change was strongly accelerated during the last 30 years due to an improvement of infrastructure and an increase in population. The latter is a result of an elevated population growth rate, but in particular a consequence of migration from northern regions. There the above mentioned climatic change in combination with the overuse of natural resources and the degradation of soils caused people to migrate (compare Williams 2003, Albert *et al.* 2004). The most drastic and directly obvious land use change is the conversion of forests, woodlands, and savannas to arable land and settlements (FAO 2001). The forest-savanna mosaic, however, can also be strongly influenced by an increase of less destructive land use forms, above all grazing and selective logging of valuable tree species (Bassett *et al.* 2003). Consequences of an increase of the latter two land use forms, however, occur more gradually within longer time spans.

For any modelling approach in the context of global change, data on land cover and land use, and in particular their change over time are highly demanded. In order to set up land cover and vegetation maps, knowledge on spatial distribution and characteristics of land cover and vegetation classes is needed. When land use maps are of interest, complex information on the relation between land cover and land use as well as on the properties of each class is additionally required (Innes & Koch 1998, de Bie 2000). However, compared to other regions

in the world, such knowledge is relatively sparse for tropical regions in general and particularly for West Africa. Therefore, studies that address both general properties of ecosystems and effects of land use on ecosystems are urgently needed.

IMPETUS framework

Shortage of fresh water is expected to be a central problem of the 21th century that may even lead to social and political instability. Cosgrove & Rijsberman (2000) predict that in 2025 about half of the human population will live in countries with high water stress due to increased use of fresh water, also caused by population growth, and in particular due to the impact of global change on the hydrological cycle (UNESCO 2003). Fresh water supply could become problematic especially in West Africa, where droughts have been observed since the last three decades. In this context, the German Federal Ministry of Education and Research (BMBF) founded the research program GLOWA (Globaler Wandel des Wasserkreislaufes) to study the water cycle of different climatic zones and to develop integrative strategies for the sustainable use of fresh water. GLOWA comprises five projects, one of which is IMPETUS (Integratives Management Projekt für den effizienten und tragfähigen Umgang mit der Ressource Süßwasser) – an integrated approach to the efficient management of scarce water resources in West Africa. IMPETUS is a cooperative, interdisciplinary and integrative project located in Morocco (sub-tropical Northwest Africa) and Benin (tropical West Africa).

The aim of IMPETUS, with a project duration of eight years, is to offer concrete ways of translating scientific results into action through scientifically based strategies. In the first three-year phase, the project's focus was set on the identification and analysis of factors influencing different aspects of the water budget. In this context, the present thesis on vegetation ecology, located in central Benin, is embedded in the IMPETUS sub-project A3-2 (Analysis and modelling of spatio-temporal vegetation dynamic in the Upper Ouémé Valley in dependence of climatic and anthropogenic factors) to provide an ecosystem analysis of dominant vegetation types with low human impact that play a central role within the hydrological cycle controlling fresh water availability. In the second three-year phase, methods will be developed to predict changes during the coming decades based on the results of the first phase. In the final two years, the collected insights of all disciplines will be coupled in order to assess management options and to install operative tools for decision-making process (IMPETUS 1999, 2002, 2003).

Aims of the present thesis

The present thesis comprises two main topics. The first topic deals with the ecosystem analysis of the woodland-savanna mosaic of the Upper Aguima catchment in central Benin (Chapter 4.1 – 4.4 and 5.1 – 5.3). The ecosystem analysis is subdivided in three sub-topics that focus on the analyses of vegetation composition and their classification (Chapter 4.1 and 5.1), structural parameters (Chapter 4.2 and 5.2), and the relation of environment and vegetation (Chapter 4.3 – 4.4 and 5.3).

The second topic addresses the impact of selective logging on woodlands dominated by *Isobertia doka* (Chapter 4.5 – 4.6 and 5.4). Here, the logging history and intensity, the impact of gap creation on environmental parameters and floristic composition, and the recruitment of woody species in gaps are treated.

The aims of these topics are introduced separately in the following two sub-chapters (Chapter 1.1 and 1.2).

1.1 Ecosystem analysis

1.1.1 Vegetation composition and classification

In West Africa, most fundamental for the classification of vegetation was the accord of the Yangambi conference (CSA 1956) that has been extended by diverse notes of several authors (e.g. Keay 1956, Aubréville 1957, Trochain 1957, Monod 1963, Aubréville 1965). This approach is mainly based on physiognomic aspects of vegetation (compare Table 3.1). Additional criteria for particular categories are part of the Yangambi classification, e.g. ecological, physiological, dynamic, floristic, and physiographic ones (Menaut 1983). This has been criticized by Lawesson (1994) as inappropriate combination of criteria. However, for savannas and woodland, the Yangambi categories refer only to physiognomic criteria. The importance of the Yangambi classification is its applicability to wide regions of West Africa (Lawesson 1994) due to descriptive definitions without orders of magnitude for the considered parameters. Sanford & Isichei (1986) elaborated a classification for West African savannas based on physiognomic and structural characteristics giving detailed values for stem density and girth distribution of the tree layer. The applicability of the latter approach for larger regions, however, has not yet been tested.

Phytosociological approaches in West Africa are sparse (Hall & Jenik 1968, Hall & Swaine 1981, Hahn-Hadjal 1998). On local and regional scale, some studies used floristic data for classification (e.g. Emberger *et al.* 1950, Mangenot 1955, Adjanohoun 1964, Schmidt 1973, Jenik & Hall 1976, Sinsin 1993, Hahn 1996, Devineau *et al.* 1997, Sokpon *et al.* 2001,

Sieglstetter 2002). Some approaches for phytosociological classification of particular vegetation classes in West Africa were undertaken, e.g. by Sinsin (1993) for savannas in northern Benin. Nevertheless, an overall integrative classification system as it exists for other regions, e.g. Europe (Willner 2002) and Japan (Miyawaki 1980), is missing for West Africa. Schmitz (1988) developed a floristic classification system for Rwanda, Burundi and Zaïre. West African studies often refer to this classification system, but its direct transferability is questionable and would be worthwhile to be tested and discussed by integrative studies.

In botanical as well as applied studies (e.g. pastoral or forestry), the Yangambi approach is one that is most frequently used for vegetation classification. This is not exclusively a result of its applicability to wide regions (Lawesson 1994), but its current importance has been extended by the widespread access to remote sensing techniques (e.g. CENATEL 2002, Mayaux *et al.* 2002). Remotely sensed data, especially from satellite images, are related to the photosynthetic active surface, being often expressed as NDVI (Normalized Difference Vegetation Index), and therefore to the density of vegetation cover and its physiognomic characteristics (Jensen 1996). Thus, the Yangambi categories appear to be reasonable to set up a classification scheme for analyses of remote sensing data. Unfortunately, this often led to an uncritical utilization of the physiognomic vegetation types. The classified physiognomic types are often intermingled with further information such as land use properties and floristic composition (e.g. CENATEL 2002). From a botanical point of view, it can not be expected that the physiognomic vegetation types can be translated directly into land use classes or to floristic composition (compare Mueller-Dombois & Ellenberg 1974, Dierschke 1994, Crawley 1997). Nevertheless, there is some evidence that for specific regions, physiognomic vegetation types can be related to floristic characteristics (Poilecot *et al.* 1991, César 1992, Reiff 1998).

The objective of this sub-topic is to describe floristic characteristics of the vegetation of the study area in central Benin in order to establish to which extent physiognomic but ecological meaningful classes can be related to phytosociological classes. In order to identify their limits and feasibility, two classification approaches are compared by means of tabular comparison and multivariate ordination. The first approach is based on the physiognomic categories of Yangambi (CSA 1956) in combination with a separation of zonal and azonal sites and a further subdivision of woodlands according to dominant tree species. In the second approach, vegetation data are classified according to phytosociological criteria.

1.1.2 Vegetation structure

Knowledge on structural characteristics of vegetation is highly demanded both globally and locally. On the global scale, more detailed and standardized data on biomass and vegetation structure of vegetation units are needed (Brown & Gaston 1996, FAO 2001) in order to parameterise global vegetation maps (e.g. Loveland *et al.* 1999), and in particular to be

implemented into climatic and hydrological modelling approaches (IPCC 2000). For example, with regards to biogeochemical cycles, tree layers represent an important carbon stock and are one of the most important variables that influences the magnitude of the terrestrial carbon flux. Annual burning of the herb layer on the other hand, is of high relevance for the emission of reactive and greenhouse gases (Delmas *et al.* 1991, Cahoon *et al.* 1992, Isichei *et al.* 1995, Lacaux *et al.* 1995, Brown & Gaston 1996).

On the local scale, knowledge on structural characteristics of vegetation as well as standardized inventories of these properties are strongly required for the compilation of silvicultural and pastoral management plans (Brown & Gaston 1996, PAMF 1996, CENATEL 2002). In West Africa and in particular in the study region, local forest, pasture and fire management options are needed since both population density and land-use pressure on these recourses have dramatically increased in recent years (Sayer & Green 1992, Sodeik 1999, Doevenspeck 2004). In addition, structural vegetation data may help to understand ecosystem processes and the historical development of vegetation units.

With regard to the herb layer, many studies can be found in the literature from the Sahel to the Sudanian zone (compare Le Houérou 1989), and also in the studied region, several studies have been conducted (Sinsin 1993, Houinato 1996, Agonyissa & Sinsin 1998, Yayi 1998, Biauou 1999, Hunhyet 2000). However, as the economic value of the closed forest stands in the coastal region of West Africa is much higher than that of woodlands and savannas, little attention was given to the structure of the tree layer of woodlands and savannas (Brown & Gaston 1996). Thus, the aims of this sub-topic are firstly to give detailed structural descriptions of both the tree and the herb layer with respect to the stratified vegetation types, and secondly, to compare the vegetation types in terms of structural parameters.

1.1.3 Environmental parameters and vegetation

The savanna biome covers about 20% of the global land surface, and about half of the area of Africa (Huntley & Walker 1982, Scholes & Walker 1993, Scholes & Archer 1997). Savannas can be found over a broad range of climatic conditions with annual rainfall of less than 300 mm to more than 1,500 mm and are generally characterized by the coexistences of trees and grasses (Huntley & Walker 1982, Solbrig *et al.* 1996, Mistry 2000a). To explain the coexistence of trees and grasses in savanna systems, Walter (1971) focused in his hypothesis of the separation of rooting niches on the competition for soil moisture in different soil horizons. According to Walter (1971), trees have access to water in deeper soil horizons, whereas grasses are superior competitors for water in the upper horizons (see also Walker & Noy-Meir 1982). Detailed field studies led to the rejection of the Walter hypothesis as the singular explanation for tree-grass coexistence (e.g. studies in West Africa: Le Roux *et al.* 1995, Seghieri 1995, Mordelet *et al.* 1997, Le Roux & Bariac 1998). Beside soil moisture, several other environmental parameters have been discussed to be important for the

maintenance of savannas such as nutrient availability, fire, grazing and browsing, geology and geomorphology, soil, cultivation history, and termites (e.g. Frost *et al.* 1986, Furley *et al.* 1992, Abbadie *et al.* 1996, Furley 1997, Scholes & Archer 1997, van Langevelde *et al.* 2003). However, the interaction of environmental parameters in savannas leading to the coexistence of grasses and trees is complex (see review in Scholes & Archer 1997, Sankaran *et al.* 2004) and may vary between different savanna types (Jeltsch *et al.* 2000). Recently, Jeltsch *et al.* (2000) proposed in a unifying concept of tree-grass coexistence to focus on ecological buffering mechanisms which prevent the savanna system from crossing the boundaries to other vegetation systems, i.e. pure grassland and closed forest.

In contrast to abundant studies and theories on the coexistence of trees and grasses in savannas, studies linking species composition to environmental parameters are sparse for West African savanna systems (e.g. Schmidt 1973, Sinsin 1993, Hahn 1996, Devineau 2001). Such knowledge, is however required in order to expand the understanding of ecosystem processes, to relate vegetation maps to ecological properties, and as a basis for modelling approaches.

Therefore, the first aim of this sub-topic is to characterize the stratified vegetation types with regards to environmental parameters. In a second step, the environmental parameters will be correlated with the species composition of herb and tree layer and their significance to explain species composition will be examined. Third, the power of environmental parameters selected in respective models and the power of single key parameters that are supposed to integrate various environmental gradients will be compared with each other in order to explain floristic variability.

1.2 Impact of selective logging on the woodland-savanna mosaic

In the woodland-savanna mosaic of Benin selective logging was introduced in the 1950ies (PAMF 1996, Sodeik 1999). It is the most frequent form of forest exploitation, apart from which only a few teak plantations are found in the country (Sayer & Green 1992). Selective logging of single tree individuals of valuable timber wood leads to disturbance in form of more or less evenly distributed gaps in the woodland-savanna mosaic. According to Pickett & White (1985), disturbance comprises “any relatively discrete event in time that disrupts ecosystems community or population structure, and changes resources, substrate availability of the physical environment”. Gaps are defined as fine scale disturbances, i.e. disturbances of low intensity from <100 to 1000 m² size. Such disturbances do not kill or remove all organisms in the gap (Runkle 1985, Denslow 1987, Connell 1989, Spies & Franklin 1989, Veblen 1989). Natural disturbances transform about 1-2% of the forest area into a canopy gap each year in tropical rain forests as well as in temperate forests (e.g. Brokaw & Scheiner 1989, Connell 1989, Schupp *et al.* 1989, Hartshorn 1990, Jans *et al.* 1993, van der Meer &

Bongers 1996). Gaps are often interpreted as one phase of forest cycles that consists of three phases: gap (open), building (growth) and mature (closed), whereby the influence of the gap phase on the species composition is widely discussed (e.g. Brokaw & Scheiner 1989, Whitmore 1989). However, with respect to successional processes within a gap, multiple successional pathways are conceivable (McCook 1994, Gibson 1996, Perry 2002). Nevertheless, forest composition has often been related to size and frequency of treefall gaps (see review in Veblen 1989). Important characteristics of gaps are their episodic nature, within-gap environmental heterogeneity such as microtopographic variation or presence of woody debris, interference from understorey plants, and changes in microenvironment (Veblen 1989). Especially the microenvironmental parameters light, water and nutrient availability can be expected to change after gap creation (compare Bongers & Popma 1988, Whitmore 1996).

Since the 1980ies gaps in closed forest formations in the tropics and temperate zones have been studied widely (e.g. special feature in *Ecology* 70(3), 1989). Studies on gaps in woodland and savanna systems are however absent from the literature, both for gaps created by natural disturbance and by humans. This is also true in Benin, although selective logging has been a frequent process in woodlands and savannas since the 1950ies with an unknown impact on the ecosystem. Therefore, the incorporation of ecological gap research into plans for silvicultural management of woodlands and savannas is highly needed as already recommended by Hartshorn (1989) for forest formations.

With respect to gaps created by selective logging in the studied woodland-savanna mosaic, this topic aims at clarifying two aspects. Firstly, the logging history of the study area is described and the logging intensity examined for an intensely logged area. Secondly, it is assessed how gaps created by selective logging in an *Isoberlinia* woodland differ from undisturbed vegetation types concerning environmental parameters, species composition of the herb layer, and composition of seedling and sapling of woody species.

2 Study site

The study was carried out in a woodland-savanna mosaic in the Upper Aguima catchment with an extension of about 3 km² located near the village Doguè in central Benin (9°13'N, 1°91'W, compare Fig. 2.1 and Fig. 3.1). Within the interdisciplinary research project IMPETUS, the Upper Augima catchment was chosen as the study site for all detailed studies carried out in natural vegetation with low human impact. Results of these studies should serve as a reference for studies in areas with high human impact. Other important criteria for the site selection were its representative character for the Upper Ouémé Valley in Benin and comparable climatic zones in West Africa. Population density in the Upper Ouémé Valley was rather low until the 1970ies (see Doevenspeck 2004). Reasons were the low soil fertility coupled with the infestation with tsetse flies, the insect vector of sleeping sickness (trypanosomiasis), and simuliid flies, which transmit river blindness (onchocerciasis). This led to a low human impact on vegetation (Sayer & Green 1992). Campaigns to eliminate river blindness and the availability of drugs to treat trypanosomiasis in cattle have lowered the risk of these illnesses and made the region much more attractive for settlers from other regions. These modifications together with the improvement of infrastructure as well as droughts further in the north led to an enormous migration pressure on the Upper Ouémé Valley (Doevenspeck 2004). The construction of a bridge on the track from Bétérou to Bassila in 1997 doubled population along the track until 2003 as it enables access during the whole year (Doevenspeck 2004). However, the better accessibility led not only to an increase in population, but also to an enormous increase in the conversion of natural vegetation into arable land, in logging activities, and in the need for settlement area (IMPETUS 2003, Doevenspeck 2004).

In the satellite image taken in 2000 (Fig. 2.1 B), the protected state forests, in which settlements and logging activities are not allowed, can be clearly distinguished from their surrounding by means of their dense vegetation cover. Nevertheless, also in other regions of the Upper Ouémé Valley a comparable density of vegetation cover was found within a certain distance to the main roads. This is also true for the selected study site of the Aguima catchment. In contrast, vegetation density is strongly reduced around the regional centres Parakou, Djougou, and Bassila as well as along the main roads. In the whole Upper Ouémé Valley, agricultural land has doubled from 1986 to 2001 (IMPETUS 2003).

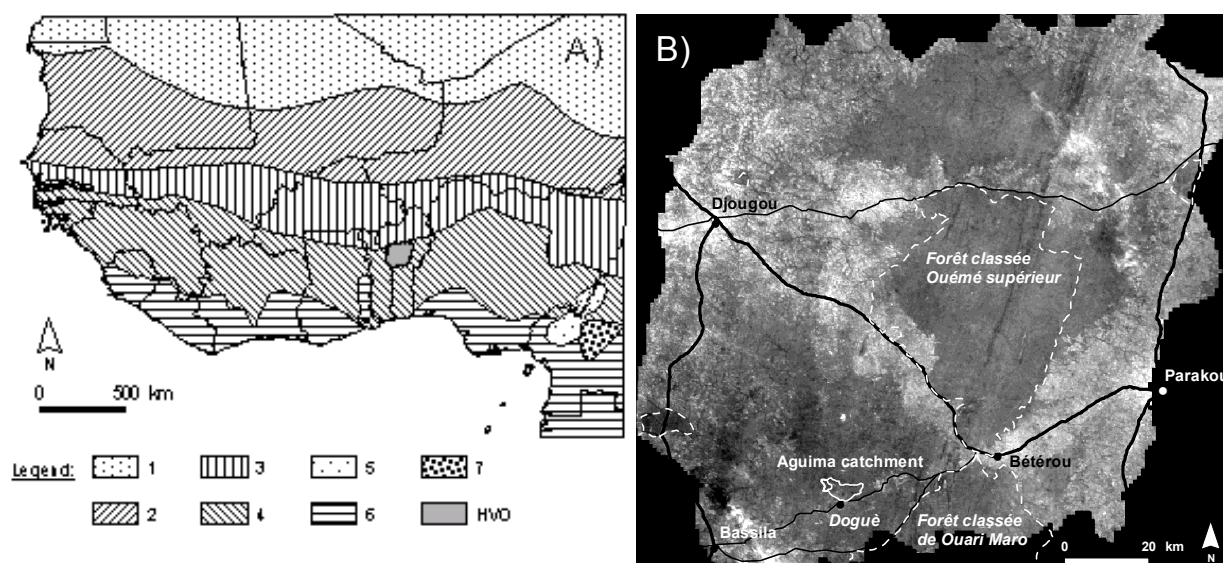


Fig. 2.1. A) Vegetation zones of West Africa based on the classification of Le Houérou (1989) and location of the Upper Ouémé Catchment (HVO). 1: Desert; 2: Sahel Savanna; 3: Northern Sudanian Savanna; 4: Southern Sudanian Savanna; 5: Montane formations; 6: Guinean and Congolian Rain Forest; 7: Mixed Forest-Woodland-Savanna. B) Landsat TM Satellite Image (October 2000) of the Upper Ouémé Catchment (HVO). Dark shades represent strong vegetation signals and can be interpreted as vegetation types with low human impact. White solid line: study site Aguima catchment; white dashed lines: limits of state forests (Forêt classée); broad black lines: main roads; thin black lines: unsurfaced tracks.

2.1 Climate

The study area in central Benin is located in the humid warm tropics (Lauer & Rafiqpoor 2002). A mean annual rainfall of 1,150 mm and a mean annual temperature of 26.8°C were measured at the climate station in Parakou from 1961 until 1990 (WMO 1996). For the studied years of this thesis from 2001 to 2004, annual rainfall was 870, 1,072, 1,180, and 1,247 mm, respectively (climate station Parakou). The onset of the rainy and dry season is triggered by the interannual motion of the inter-tropical convergence zone (ITCZ) which itself is directed by the north-south motion of the sun in the course of the year (Ojo 1977). The rainy season is driven by the south-west monsoon, blowing from the Gulf of Guinea, and carrying humid air masses (McGregor & Nieuwolt 1998). In the study region, most of the annual rainfall occurs during the rainy season from March to October (compare Fig. 2.2). Fluctuations in daily temperature and air humidity are low during the rainy season. At the beginning of the dry season, the south motion of the ITCZ leads to dry winds ('Harmattan') blowing from northeast (central Sahara). The dry season is characterized by high daytime temperatures (>40 °C), rather cool nights (<15 °C), and occasionally very low relative humidity (<10%). Inter-annual fluctuation in solar radiation, however, is low due to the proximity of the study region to the equator. Solar radiation is reduced only by increased cloud cover during the rainy season and high dust loads during the times of the Harmattan (Ojo 1977). Climatic values measured near Doguè at the four climate stations of IMPETUS

(since 2000) and the French project CATCH (since 1997) were of similar orders of magnitude as values measured in Parakou 60 km east of Doguè (Giertz 2004). As data sets of Doguè had several missing values they are not presented here.

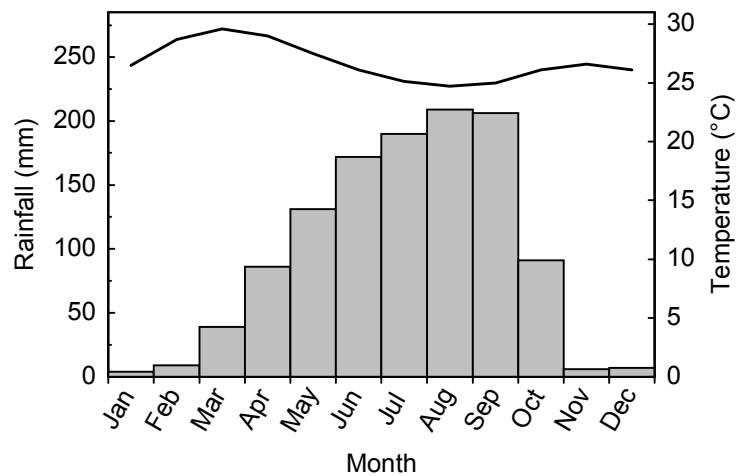


Fig. 2.2. Long-term average (1961-1990) of rainfall (bars) and air temperature (line) measured at the climate station of Parakou (WMO 1996).

2.2 Geology, hydrology, and pedology

Detailed studies on the hydrogeology, hydrology and pedology of the Aguima catchment were carried out by Faß (2004), Giertz (2004), and Junge (2004), respectively. The study area is located on the ‘Plaine du Bénin’ which is part of the Dahomeyiden, an orogen developed on the Westafrican craton (Caby 1989, Petters 1991). The geological composition of the ‘Plaine du Bénin’ is rather heterogeneous due to the different origin of the parent material (Trompette 1979). The basement of the Aguima catchment is dominated by ‘Migmatite de groupe de Pira’ and ‘Migmatite de la zone axiale’ (Affaton *et al.* 1978, OBEMINES 1978).

The landscape of the study area, the pediplain, is characterized by a gently undulating relief of usually less than 4% inclination (Fölster 1983). It was formed during several pedimentation processes in the quaternary period when irregular rainfall distribution led to a sparse vegetation cover resulting in high amounts of runoff (Rohdenburg 1969, Fölster 1983). The material of the weathering bedrock was displaced at retreating scarps and transported across the surface of the new pediments. The complete erosion of watersheds resulted in the unification of neighbouring pediments. Therefore, the pediments are characterized by several substratum layers. Completely weathered bedrock or saprolite of migmatites is found in the deeper part of the solum. Allochthonous pedisediments cover the surface of the landscape. The latter include ferruginous gravel deposit and fine-grained substrate or hillwash (Smyth & Montgomery 1962, Junge 2004). A consolidated layer of saprolitic clay mixed with ferruginous gravel deposit regularly occurs underneath the pedisediments. This layer is rather water-impermeable and has great influence on the soil moisture regime. Most water-runoff

takes place as interflow in the fine-grained substrate above the consolidated layer and also above the ferricretes (see below). Only along preferential pathways water can pass into deeper layers (Faß 2004).

Soil moisture regime is highly variable during the course of the year. The recharge of soil water deposits begins with the onset of the rainy season in March. Field capacity is reached in mid-July, and further raining events thus result in a surplus of soil water. Consumption of soil water begins with the end of the rainy season in October/November, when evapotranspiration exceeds precipitation. Soil water deficit is reached by the end of November, leading to moisture contents around the permanent wilting point (compare Soil Survey Staff 1975, Igué & Youssouf 1995, and the local studies of Faß 2004 and Giertz 2004). Nevertheless, soil water content does not drop much below the wilting point even in the progressed dry season so that water resources remain partly available for plants. This has also been observed in other West African regions (compare Menaut & César 1982). Tree individuals, however, can be assumed to be able to pass with some roots through the consolidated layers and enter the humid zones below (see Le Roux & Bariac 1998).

The soils in the pediplain of the study area are described and classified by Junge (2004) following the nomenclature of the 'World Reference Base for Soil Resources' (FAO-ISRIC-ISSS 1998) and the 'Classification des Sol' (CPCS 1967). Albi-Petric Plinthosols (Sols ferrugineux tropicaux lessivés indurés) are developed on watersheds and lower slopes. They are characterized by a petroplinthic horizon or ferricrete which is cemented by sesquioxides (van Wambeke 1991). The ferricretes on the watersheds were originally formed in inland valleys during the tertiary (Maignien 1966). They attained this position in the landscape due to relief inversion (Goudie 1973, Schwarz 1994, Bremer 1999). Characteristic soils of the upper and middle slopes are Endosceleti-Albic Acrisols (Sols ferrugineux tropicaux lessivés à concrétions). These soils are characterized by clay migration which results in the formation of horizons impoverished or enriched with clay. Gleyosols (Sols hydromorphes) are developed in inland valleys (*Bas fonds*). Annual waterlogging during the rainy season is responsible for their hydromorphic features.

In general, the fertility of the soils in the Aguima catchment is limited. The water holding capacity of the topsoil is low due to the high percentage of sand (60-80%). The rooting space of the soils is limited as ferricrete and the clayey saprolite in the lower soil parts are difficult to penetrate for plant roots. The upper layer is characterized by a soil reaction (*pH*) of 5.5 to 7.0, moderate base saturation (20-60%), moderate cation exchange capacity (15-25 cmol_c kg⁻¹ soil) and low organic carbon contents (about 1.3%) (Junge 2004).

2.3 Vegetation

The vegetation of West Africa shows a clear gradual change from evergreen rain forests in the south where annual rainfalls is above 2,000 mm, to desert vegetation in the north where annual rainfall is below 300 mm. This overall distribution of vegetation was already described at the beginning of the 20th century (e.g. Chevalier 1900 cited in Salzmann 1999, Hubert 1908 cited in Adjanohoun 1989). With regards to the borders of vegetation zones, a great diversity of criteria is used to set up vegetation maps. The resulting nomenclature is thus highly diverse (compare Schnell 1971, 1976, Menaut & César 1982, Lawson 1986, Lawesson 1994, Salzmann 1999), as already stressed by Keay (1959c). Vegetation maps were elaborated mainly based on chorological units (Aubréville 1950, Keay 1959a, Aubréville 1961, Léonard 1965, Adjanohoun 1989), physiognomic classes (Keay 1959c), a combination of the latter two approaches (Aubréville 1937, White 1983b), and climatic and floristic criteria (Le Houérou 1989).

According to the most prominent approaches classifying West African vegetation zones, the study site is situated at the northern limit of the ‘Southern Sudanian Savanna’ (Le Houérou 1989, compare Fig. 2.1 A), in the ‘Sudanian regional centre of endemism, characterized by sudanian woodlands with abundant *Isoberlinia*’ (White 1983b), or in the ‘Zone de transition guinéo-soudanienne’ (Adjanohoun 1989).

In the Upper Ouémé Catchment (compare Fig. 2.1 B), natural vegetation with low human impact is dominated by a woodland-savanna mosaic. Along the undulating pediplain relief, woodland and different savanna types can be found (nomenclature following Yangambi categories, CSA 1956, compare Table 3.1). Tree density decreases from upper to lower hillslope, and vegetation types change from woodland to savanna woodland and tree savanna. In the temporarily inundated depression (*Bas fonds*), grass savanna occurs with scattered tree individuals, which can be interpreted as an azonal vegetation type. More dense formations of woodlands and dry deciduous forest are often found on hilltops. This toposequence is generally described for savanna regions (compare Walter & Breckle 1991, Fig. 2.3). In addition, gallery forest at the riversides as well as typical vegetation on inselbergs can be found as azonal vegetation types (Porembski & Barthlott 2000, Natta 2003).

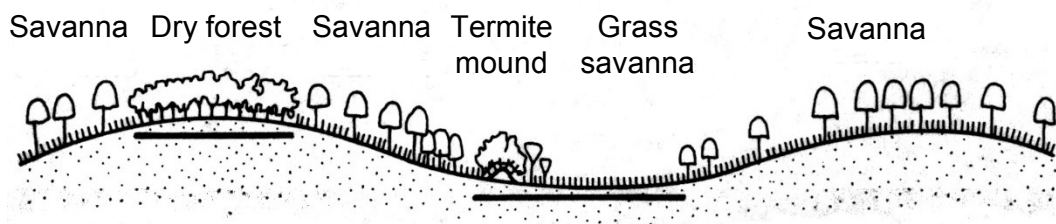


Fig. 2.3. Idealized distribution of vegetation types along a toposequence following Tinley (1982). Bars reflect ferricretes.

2.4 Human impact on the woodland-savanna mosaic

Local population takes advantage of many resources in the woodland-savanna mosaic (Schreckenberg 2000). Most important factors of human impact are grazing activities by cattle herds, fire, and selective logging. Other activities such as the collection of firewood and of vegetables and fruits for nutritive and medicinal purposes are of minor importance for the studied ecosystem (e.g. Sodeik 1999, Schreckenberg 2000, Doevenspeck 2004). Today's hunting activities and their impact on the system are negligible because of the already strongly reduced densities of wildlife. (PAMF 1996).

2.4.1 Pastoralism and grazing regime

Since density of large wild herbivores have declined dramatically in recent years (compare Sodeik 1999, Mistry 2000b, 2001), most important grazing activities in the study area take place by domestic animals, mainly by cattle herds. Cattle husbandry is the domain of the Fulani (French: Peulh) in West Africa. Different groups of Fulani exist in Benin, which are either settled and partly transhumant or live completely nomadic (Sturm 1993, Bierschenk 1997). Traditionally, the Upper Ouémé Valley was only used as grazing area during the dry season (long-distance transhumance) by Fulani from northern Nigeria as well as from northern Benin (Houinato 2001). Due to large scale migration processes caused by periodic droughts in the Sahel regions, expansion of cotton cultivation, and stricter management of national parks in northern Benin, grazing regime has changed considerably in the last 10 years in the Upper Ouémé Valley (Sinsin & Heymans 1988, Wotto 2003, Doevenspeck 2004).

Wotto (2003) carried out a detailed study on grazing regime and impact of grazing on the territory of the village Doguè. With regard to the grazing regime in the course of the year he found that cattle herds of the Fulani settling in Doguè are subjected to long-distance transhumance during the dry season either to Togo or into the adjacent state forests (Forêt classé) in the Upper Ouémé Valley. Meanwhile, the pasture on the territory of the village Doguè is exploited by herds coming from northern Benin or Nigeria. During this time of the year, the open savannas are the preferred pasture due to already resprouting grasses. In addition, the sprouted leaves of *Azelia africana*, *Khaya senegalensis* and *Pterocarpus erinaceus* are cut as fodder. At the beginning of the rainy season when the local herds have returned, fallows and natural pasture near the camps are exploited for resprouting grass. During the rainy season, it becomes more and more difficult to pass through the field-fallow belt surrounding the villages without damaging the growing crops and, therefore, a short-distance transhumance is performed. The herds are driven to sites outside the field-fallow belt and stay there also during the night. Woodlands are the preferred pasture at the beginning of the rainy season. In the progressed rainy season also dense savannas are used, until the beginning of the dry season, when the water table in the depression has fallen far enough to

allow exploitation also of the depression. This general pattern of the grazing regime of the Fulani herdsmen is applied over wide regions in West Africa and has been described by several authors (e.g. for Benin: Sturm 1993, Bierschenk 1997)

Regarding the history of Fulani settlement in the study region, Wotto (2003) found that the first Fulani settlers arrived in 1996. Until 2003, 55 Fulani households were counted which owned about 6,000 cattle. Calculations of Wotto (2003) revealed already a three times overcharge of the pastures of the considered area. It can be assumed that the migration of farmers into the study region will continue and will lead to a conversion of large areas into farmland. Thus, the availability of woodland-savanna sites as pasture will decline continuously (IMPETUS 2003, Doevenspeck 2004). In addition, further restriction for Fulani to use areas in the National parks in northern Benin as well as areas of the Forêt classée surrounding Doguè will lead to an increasing pressure on the pasture of this region (Wotto 2003).

2.4.2 Fire

A high portion of the land cover in the Upper Ouémé Valley is burned annually (Oertel *et al.* 2004). Natural fires, e.g. due to lightning are nowadays rare (Goldammer 1993a). In savanna systems, fire is known to be used by humans for various reasons (compare Gillon 1983, Menaut *et al.* 1991, Roberts 2000, Bassett *et al.* 2003), which are similar to those given by the population in the Upper Ouémé Valley: fires are frequently used around settlements to clear ground for agriculture and to establish fire breaks to protect fields and settlements against uncontrolled fires (own observations). Interviews revealed that a central reason for the population of Doguè to light fires around settlements, but also in savannas and woodlands, was the achievement of higher visibility. Visibility reduces a general fear and in fact the risk of attacks by or accidents with wild animals. Hunters are interested in a higher visibility in order to find their prey, and they also use fires as a hunting method. Herdsmen set fires to initiate an off-season re-growth of perennial herbs as well as to get rid of the unpalatable stubbles (compare Menaut *et al.* 1991, Sturm 1993). However, fires get out of control quite often or are set accidentally and burn down vast areas. Fire activities start at the end of October with fires near the villages in order to establish fire breaks and continue until or even after the first raining events in March.

The occurrence of fires is a highly stochastic process, on the one hand due to lightning activities of humans and on the other hand due to different parameters such as fuel moisture content, available fuel load, natural fire breaks, and wind direction and velocity (DeBano *et al.* 1998, Stott 2000). With the exception of gallery forest and dense forest islands where due to fuel conditions, fires occur with a very low probability (compare Biddulph & Kellman 1998), nearly every site is usually burned annually. However, also savanna and woodland sites of varying size and location may remain unburned each year by chance.

2.4.3 Short history of logging activities in the Upper Ouémé Valley

Logging activities in the Upper Ouémé Valley started about 1950 with the construction of some sawmills along the western border of Benin, especially around Bassila (Fig. 2.1 B, Sodeik 1999). Sawmills were constructed by French entrepreneurs (PAMF 1996). In this time, single trees of different valuable timber species of enormous diameter were exploited. Logging took place especially in dry deciduous forest islands and in gallery forests (mainly *Ceiba pentandra*, *Khaya grandifolia*, *Antiaris africana*, and *Chlorophora excelsa*) as well as in woodlands and savannas (mainly *Azelia africana* and *Khaya senegalensis*). Trees were felled and transported as trunks to the sawmills (PAMF 1996). Until about 1985, all sawmills (private and state-owned) had closed, mostly due to financial problems (Doevenspeck 2004) caused by the decline of valuable timber species (Sodeik 1999). Since then, felled trees are sawn directly in the field and timber boards are exploited. Because felled species became sparse, logging activities are now concentrated on individuals of smaller diameter of remaining individuals. In addition, logging activity have been extended to *Pterocarpus erinaceus* and *Isoberlinia doka* (PAMF 1996). In general, permits to cut timber were, and still are, allocated on an individual tree basis by the Forest Department (Sayer & Green 1992). Nevertheless, most logging activities in the study region take place without concessions. They are therefore completely illegal and enter the vast field of corruption (Siebert & Elwert 2002, Siebert 2003).

3 Methods

3.1 Sampling design

Most data of the present thesis were collected in two types of permanent plots, relevé and gap plots. Both plot types were located in the Upper Aguima catchment. Relevé plots were situated in stratified vegetation types, whereas gap plots were exclusively situated in *Isobertia* dominated woodland. Gap plots comprised gaps created by one selectively logged tree individual. However, in both plot types the same data collection was carried out. Due to an agreement between the landowner and the IMEPTUS project, logging activities were forbidden in the Upper Augima catchment since 2001. In order to study the typical logging regime for the studied region with respect to intensity and quality, one additional representative *Isobertia* dominated woodland stand was chosen outside the Upper Aguima catchment (Fig. 3.1).

3.1.1 Site selection of relevé plots

Within the Upper Aguima catchment– chosen as the test site for all studies carried out in sites with low human impact within the IMPETUS project (see Fig. 2.1 and 3.1) – a woodland-savanna mosaic was found. As overall stratification, the classification approach of the Yangambi conference (CSA 1956, Table 3.1) was used. In contrast to many criteria applied in order to subdivide forest formations according to the Yangambi categories, for the subdivision of woodland and savannas no further criteria were designated by the Yangambi approach. This strict structural classification for these vegetation types was extended by some subdivisions in the present thesis, as described below.

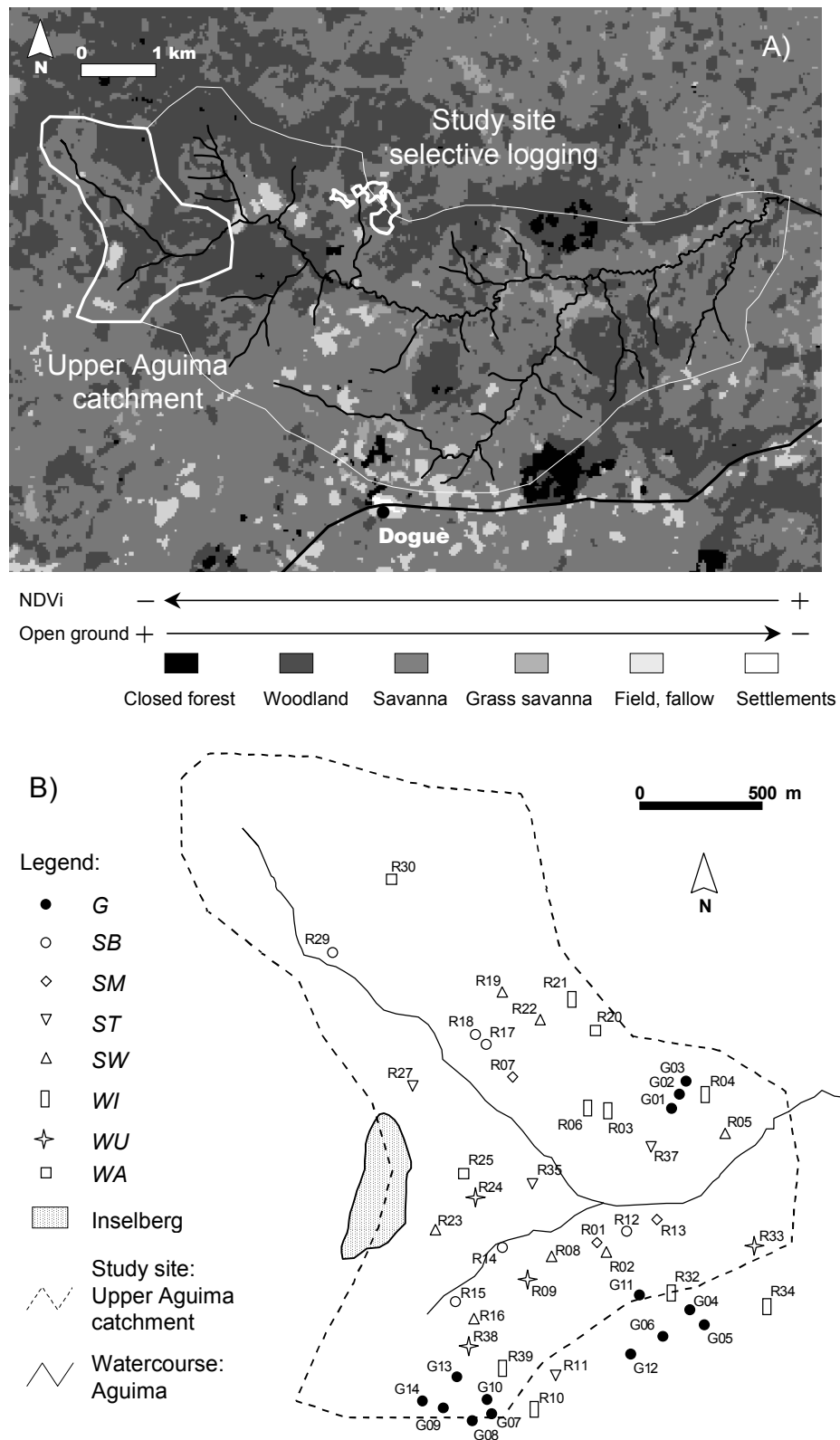


Fig. 3.1. A) Location of the two study areas (Upper Augima catchment and study site: selective logging) (broad white lines) in the Aguima catchment (thin white lines). The presented land-use and land-cover classification is a detail of the classification map of the Upper Ouémé catchment, central Benin (unpublished data Judex & Thamm 2003). B) Location of relevé and gap plots in the Upper Aguima catchment. Abbreviations of vegetation types are given in Table 3.2.

Table 3.1. Definition of vegetation types according to the classification approach of the Yangambi conference (CSA 1956) found in the Upper Aguima catchment.

French	English	Description
Forêt claire	Woodland	Open forest; tree stratum deciduous of small or medium-sized trees with the crowns more or less touching, the canopy remaining light; grass stratum sometimes sparse, or mixed with other herbaceous and suffrutescent vegetation.
Savane	Savanna	Formations of grasses at least 80 cm high, forming a continuous layer dominating a lower stratum. Usually burnt annually. Leaves of grasses flat, basal and cauline. Woody plants usually present.
Savane boisée	savanna woodland	Trees and shrubs forming a canopy which is generally light.
Savane arborée	tree savanna	Trees and shrubs scattered
Savane herbeuse	grass savanna	Trees and shrubs generally absent

At the study site, inland valleys (*Bas fonds*) characterised by stagnant soil moisture during the rainy season are frequently found. As sites influenced by stagnant moisture represent azonal vegetation formations, *Bas fonds* sites were treated separately in this study. Within the *Bas fonds* of the study area, 9 relevé plots were installed. Classified by means of the Yangambi categories, the *Bas fonds* sites are either grass or tree savanna. However, soil analyses by Junge (2004) revealed that the centre of the *Bas fonds* and their margin differed to such a great extent with regards to their degree of stagnation as well as to soil texture that their differentiation was reasonable. Thus, these two *Bas fonds* types were treated separately in this study, 6 plots in the centre of the *Bas fonds* (*SB*) and 3 plots at the *Bas fonds* margin (*SM*) (Table 3.2).

Most of the study site is covered by zonal vegetation formations. Outside of the *Bas fonds*, only three physiognomic vegetation types can be found following the Yangambi categories (CSA 1956). These are tree savanna, savanna woodland and woodland. In vegetation descriptions, woodlands of West Africa are frequently subdivided in terms of one dominating tree species (e.g. White 1983a). Therefore, a further subdivision of woodlands was introduced into the stratification scheme with woodlands dominated by *Isoberlinia doka*, *Uapaca togoensis* and *Anogeissus leiocarpus*, respectively. For each of these five categories, a minimum of 5 plots was chosen, but if further plots were available replicate number was increased up to 8.

In total, seven categories were stratified in the study area, denoted as vegetation types (*Vegtyp*) (Table 3.2). These are based in a first step on the physiognomic categories of Yangambi (CSA 1956) and a separation of zonal and azonal sites, and in a second step on subdivision of woodlands according to the dominance of tree species. During the course of the study, two *Anogeissus* dominated woodland plots (*WA*), one *Uapaca* dominated woodland plot (*WU*), and two tree savanna plots (*ST*) had to be abandoned due to strong human impact, namely by logging activities and installation of cattle pens in the plots. Thus, data of 35 relevé

plots were considered in the present thesis (see Table 3.2). Their spatial distribution is given in Fig. 3.1.

Table 3.2. Abbreviation and number of relevé plots for each vegetation type.

Vegetation type	Abbreviation	Number of relevés
Savanna (<i>Bas fond</i>)	<i>SB</i>	6
Savanna (Margin <i>Bas fond</i>)	<i>SM</i>	3
Tree savanna	<i>ST</i>	4
Savanna woodland	<i>SW</i>	7
Woodland dominated by <i>Isoberlinia doka</i>	<i>WI</i>	8
Woodland dominated by <i>Uapaca togoensis</i>	<i>WU</i>	4
Woodland dominated by <i>Anogeissus leiocarpus</i>	<i>WA</i>	3

3.1.2 Site selection of gap plots

Logging of trees in the study region took place mostly in woodlands dominated by *Isoberlinia doka* (*WI*) (Chapter 2.4.3). Logging events were rarely observed within the *WI* sites of the Upper Aguima catchment. To study effects of the selective logging of single tree individuals, gaps created by exploitation of a single tree with a dbh larger than 45 cm were chosen. Minimum distance to the next gap had to be larger than 60 m. In total, 14 gaps matching these criteria were found in the Upper Aguima catchment within *Isoberlinia* woodland (Fig. 3.1). These gaps were created either in 1998 or in 2000, and their sizes varied from 50 to 100 m². The gap plots were placed in the centre of each gap.

3.1.3 Plot design of relevé and gap plots

Each relevé and gap plot was directed to the north and had an outer size of 30 m x 30 m. A 5 m x 15 m plot was installed north of the centre of the 30 m x 30 m plot (Fig. 3.2). All data of the tree layer with individuals >1 cm diameter at breast height (dbh) were sampled in the 30 m x 30 m plot. Within the 5 m x 15 m plot, data referring to the herb layer was collected with an additional focus on seedling and saplings of woody species. Herb biomass was harvested in a 1 m x 1 m biomass plot within each of the 30 m x 30 m plot but outside the 5 m x 15 m plot (Fig. 3.2). Size of the outer plot was chosen in accordance with many studies in West Africa. With regard to the herb-layer plot, a plot size of 5 x 15 m was chosen as a compromise between requirements for this study and the frequently used plot sizes of 10 x 10 m and 5 x 5 m (e.g. Hahn 1996, Sinsin 1993, Schmidt 1973, César 1992). Microclimate, insolation and fire temperature were measured in the centre of the 30 x 30 m

plot, requiring a frequent control. It was aimed to locate the herb-layer plot in the centre of the larger one and in proximity to the central measurement point, but without the need of passage through this plot. The rectangular shape (5 x 15 m) of the herb-layer plot optimises these requirements. Another advantage is the minimized distance from the measurement point to the corners of the herb layer plot (compare Fig. 3.2).

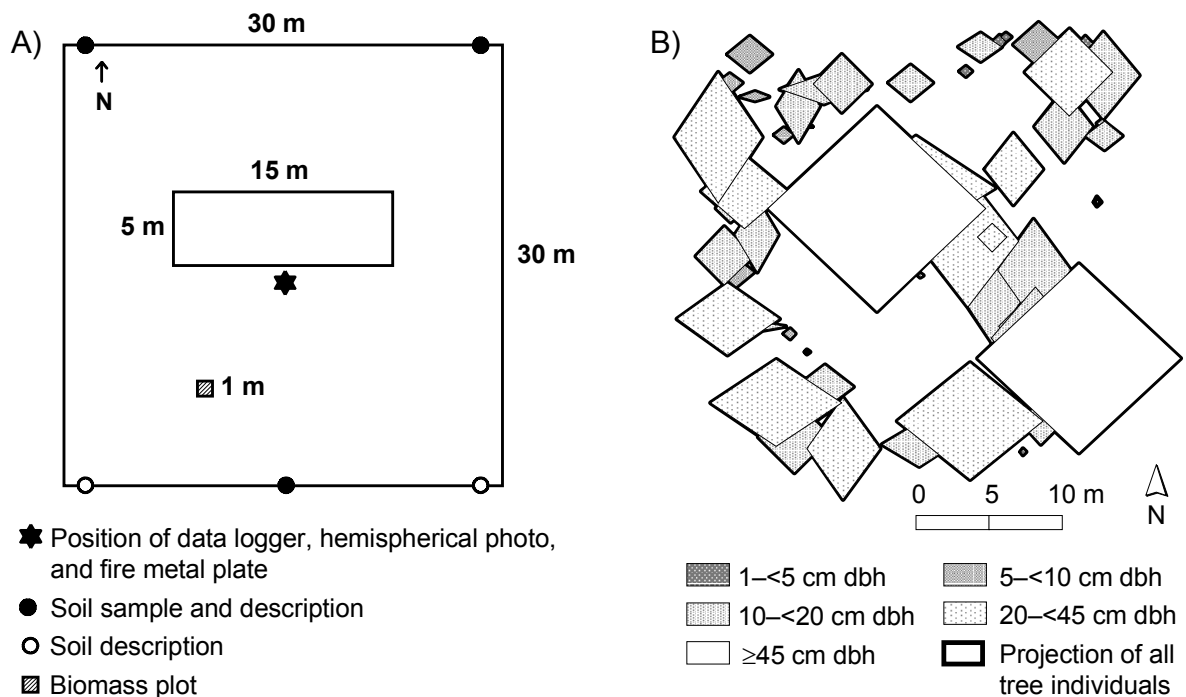


Fig. 3.2. A) Design of relevé and gap plots. In the 30 m x 30 m plot, all tree individuals larger than 1 cm dbh were mapped. In the 5 m x 15 m plot, tree saplings, tree seedlings, and the herb layer were sampled. B) Crown projection of single trees and the projection area of all tree individuals (example from R09).

3.2 Sampling of vegetation data in relevé and gap plots

3.2.1 Identification of species

Samples of species were collected and tentative identifications were conducted in the field. Unidentified or critical species were dried and compared to available identified specimens in the National Herbarium at Cotonou or identified in cooperation with members of the ‘Flore du Benin’ project.

Publications used for identification purposes were Aubréville (1950), Hutchinson *et al.* (1954–1972), Irvine (1961), Berhaut (1967), Letouzey (1970, 1972), Berhaut (1971–1988), Geerling (1982), Merlier & Montégut (1982), Scholz & Scholz (1983), Brunel *et al.* (1984), Thies (1995), Maydell (1990), Poilecot (1995, 1999), and Arbonnier (2002). The nomenclature of all species follows Lebrun & Storck (1991–1997).

Species of the genera *Gardenia* and *Strychnos* were sampled as *Gardenia spec.* and *Strychnos spec.*, respectively, due to difficulties of determination. Within the genera *Vigna*, only the species *V. filicaulis*, *V. frutescens*, *V. luteola*, *V. racemosa* and *V. reticulata* were differentiated, all other species were summarized as *Vigna spec.*.

3.2.2 Sampling of tree layer data

Height and diameter of trees

Within each 30 x 30 m plot, all tree individuals >1 cm dbh were permanently and individually marked. Position within the plot and maximum tree height were measured with a combined range finder and hypsometer (VERTEX III, Haglöf, Inc., Finland) and field compass (KB 14/400g, SUUNTO, Inc., Finland). Dbh was measured with a measuring tape. In order to characterize tree structure of the relevé plots, tree data were grouped in four height classes (0-<2 m, 2-<5 m, 5-<10 m, ≥10 m) and in five diameter classes (<5 cm dbh, 5-<10 cm dbh, 10-<20 cm dbh, 20-<45 cm dbh, ≥45 cm dbh). These classes are thought to be ecologically meaningful. Individuals of smaller size classes are still affected in their crown by surface fires, those of medium size classes dominate the lower tree layer, and tree individuals of larger size class build the upper tree layer. Most individuals with a dbh ≥45 cm have reached their fertile phase.

Calculation of tree cover

For each tree individual in the 30 x 30 m plot, crown range in north-south and east-west direction was estimated by perpendicular crown projection. Cover of each tree individual was calculated as a rhombus:

$$Cover = \frac{(crown\ length\ in\ north-south\ direction) * (crown\ length\ in\ east-west\ direction)}{2}$$

Even though this is still an approximation, it overestimates the cover of tree individuals much less than the calculation as an ellipse. In order to calculate the cover of all tree individuals in a plot as perpendicular projection on the ground, the four corner points of each crown were imported to ArcView Gis (3.2). The corners of the crown of each tree individual were converted with the extension Edit Tools (3.6) to a polygon. In order to receive the projection area of all individuals, in contrast to the sum of the cover of all individuals, the extension Geoprocessing was used. Additionally the projection was calculated for different strata (e.g. all individuals with a dbh >10 cm, all individuals <10 m height, compare Fig. 3.2).

Estimation of tree cover

Total cover of trees as well as the cover of each single tree species was estimated as perpendicular projection of all leaves reaching into the 30 x 30 m plot. Cover of tree species was estimated according to the decimal scale of Londo (Dierschke 1994).

Woody biomass

Woody biomass was calculated after Schöngart (2003) as:

$$\text{Woody biomass} = \frac{\text{height [m]}}{2} * \left(\frac{\text{dbh [m]}}{2} \right)^2 * \pi * \text{wood density [t/m}^3\text{]}$$

Data on wood density were not available for the 51 sampled tree species. Own pilot studies on wood density of six dominating tree species by means of core extraction and gravimetric measurements (Kramer & Akça 1995) revealed a mean value for these species of 0.69 [t m⁻³] (*Azelia africana*: 0.70, *Anogeissus leiocarpus*: 0.78, *Daniellia oliveri*: 0.53, *Isobertinia doka*: 0.63, *Khaya senegalensis*: 0.68, *Pterocarpus erinaceus*: 0.76). Brown (1997) gives wood densities for many African tree species within the range of 0.5 - 0.79 [t m⁻³]. Taking into account only those occurring in the southern Sudanian savanna, a mean value of 0.61 [t m⁻³] was calculated. However, only some of the 51 sampled tree species were mentioned by Brown (1997). For the calculation of woody biomass finally 0.65 [t m⁻³] was chosen as a reasonable compromise as dense woods were sampled in this thesis in contrast to Brown (1997), where light wooded species of humid sites were dominating.

3.2.3 Sampling of herb layer data*Species composition*

Vegetation surveys were conducted in the 5 m x 15 m plot (Fig. 3.2) in October 2002 at the peak of flowering of grass species according to Braun-Blanquet (Dierschke 1994). With respect to the herb layer, cover of each species was estimated according to the decimal scale of Londo (Dierschke 1994), considering all leaves being in the projection of the plot.

Structural parameters

The structural parameters: cover of herbs (HE_C), cover of grasses (G_C), cover of non-grass litter (LNG_C), cover of grass litter (LG_C) and the sum of the two litter fractions (L_C), cover of open ground (OG_C), cover of dead woody biomass (DWB_C diameter >1 cm) and cover of termite mound (TM) were estimated in October 2001 and 2002 at biomass maximum of the herb layer and peak of flowering of grass species. Concerning herbs and grasses, also their maximum height (HE_H , G_H) was measured and volume (HE_{Vol} , G_{Vol}) calculated as height * cover. Grazing impact (GI) in the plots was estimated as percentage of grazed plants

and trampling damage (*TD*) in classes of 1 to 5 (1: no *TD*, 2: low *TD*, 3: medium *TD*, 4: strong *TD* and 5: very strong *TD*). These data were sampled in the 5 m x 15 m plot as well as in an adjacent 1 m x 1 m biomass plot (Fig. 3.2).

Biomass

After sampling of structural parameters, herb biomass was harvested at the end of October in the 1 m x 1 m biomass plots (Fig. 3.2). Biomass was separated into the fractions grasses, herbs and litter which were dried to weight constancy.

3.2.4 Sampling of data on seedlings and saplings of woody species

From 2001 to 2004, number of seedlings and saplings of woody species were sampled at the end of the rainy season in September within all 5 m x 15 m plots. Species of each tree individual was determined and its age was estimated. Seedlings from the respective year could clearly be distinguished from older individuals by growth form. In the category saplings, individuals with an estimated age between one and five years were grouped.

3.3 Sampling of data on environmental parameters in relevé and gap plots

3.3.1 Soil

Soil samples were taken in cooperation with Birte Junge (see Junge 2004) in September 2001. A soil description was made at five locations at the borders of the plots by extracting cores with a Pürckhauer driller (Fig. 3.2). The depth of the different soil layers was recorded. From three of the five locations, soil samples of the upper two layers were taken with an Edelmann driller and merged as a mixed sample for each plot. Analyses of grain size distribution after Köhn (1928) and pH (CaCl₂) were conducted by the Laboratory of the Hydrology Research Group, University of Bonn. All chemical analyses were done on air-dried soil samples (<2 mm grain size) in duplicate by the Laboratory of the Institute for Soil Science, University of Bonn. The exchangeable cation concentration was determined for Na⁺, K⁺, Ca²⁺ and Mg²⁺ according to Trüby & Aldinger (1989). Test for carbonate content with HCl in the field revealed that the soil samples contained no carbonate at all. In consequence no carbonate determination was performed in the laboratory. Organic content (*C_{org}*) and total nitrogen concentration (*N*) were determined by a C/N-Analyser. Analysis of available phosphate (*P*, P₂O₅) was carried out after Bray & Kurtz (1945) using NH₄F.

3.3.2 Microclimate

Air temperature, air humidity, and vapour pressure deficit

A data logger (Tinytag Plus TGP-1500 Gemini Data Loggers, Ltd., UK) was placed in the centre of each relevé and gap plot in 1.3 m height, above maximum volume of the herb layer, and protected by a radiation shield. Air temperature and relative air humidity were logged every 10 minutes. The first measurement campaign started in September 2001. The logged data were exported with the GLM Windows Software (Gemini Data Loggers, Ltd., UK) in intervals of three month. The measurements continued until December 2002 with an interruption from December 2001 to February to March 2002 due to fire events in the study area. Several data loggers suffered from technical problems during the course of the measurement period, especially those recording air humidity. Therefore and due to loss of data loggers the number of data loggers, and recorded time series declined continuously, mainly in the last period from August to December 2002.

The vapour pressure deficit (*VPD*) was calculated according to Arya (2001) from air temperature (*T*) and relative air humidity (*H*).

$$VPD = (6.107 \cdot 10^{((7.5 \cdot T)/(237+T))}) - ((6.107 \cdot 10^{((7.5 \cdot T)/(237+T))}) \cdot H/100)$$

For each of the parameter, temperature, humidity, and vapour pressure deficit, values were controlled for plausibility and diurnal mean, maximum, minimum and amplitude were calculated. For graphical presentation 10-day-moving averages were calculated.

Hemispherical photographs

At the beginning of October 2002, during the rainy season, hemispherical photos were taken with the HemiView System (Delta-T Devices, Ltd., UK). This system includes a self-levelling unit with a digital camera and a fisheye lens. Direction towards the north and south are marked by flashlights on the photographs. Own measurements revealed that values did not differ considerably if the mean of five photographs distributed over the plot were taken into account or if only one photograph at the centre was considered. Therefore, at each plot one photograph above the herbaceous layer was taken in the centre of the plot. To benefit from uniform sky conditions, photographs were taken shortly before sunrise or after sunset. Photographs were post-processed with the HemiView Software, HMV1 (Delta-T Devices, Ltd., UK).

The most reasonable parameters had to be chosen for analysis out of the many parameters calculated by the HemiView Software. Visible sky (*VS*) gives the overall proportion of the sky hemisphere that is visible. The global site factor (*GSF*) is calculated as the ratio of total radiation below the canopy to total radiation above the canopy. Likewise, indirect site factor (*ISF*) and direct site factor (*DSF*) are calculated using indirect and direct radiation below and

above the canopy, respectively. HemiView algorithms estimate leaf area index (*LAI*) as half of the total leaf area per unit ground area, what is a rough approximation.

3.3.3 Fire

Five different fire chinks were used which change their colour if exposed to the specific temperatures (120, 195, 215, 245, 295, 320, 335, 365, 460, 505, 600°C) for an estimation of fire temperature (compare Bloesch 2002). For each plot, one metal plate with markers of the chinks was set up in the centre of the plot 30 cm above ground. The height was chosen as compromise between data found in the literature. Gillon (1983) summarized 50 cm as maximum fire temperature in savannas, whereas Bloesch (2002) found highest fire temperature at 10 cm above ground and Hopkins (1965a) directly above the soil. Metal plates were placed in the field at the beginning of December 2001 and 2002 and controlled every week. When fires passed, date and maximum temperature were recorded.

3.3.4 Topographical position

From the centre of each plot inclination (*Inc*) was measured by an inclinometer (PM-5/400 PC, SUUNTO, Inc., Finland) and exposition (*Exp*) was measured by a field compass (KB 14/400g, SUUNTO, Inc., Finland). Relative topographic position (*TopH*) of each plot was measured as absolute height above sea level minus absolute height of run-off line based on a digital elevation model derived from Aster Satellite data (unpublished data Drey & Thamm 2004).

3.4 Survey of logging history and intensity

The survey on logging history at the village Doguè is based on informal interviews with the council of elders of the village of Doguè as well as on the information of inhabitants who guide the tree fellers to logging sites and on own observations.

As logging activity was relatively sparse in the Upper Aguima catchment, one representative *Isobertinia doka* dominated woodland (*WT*) near Doguè characterized by a high intensity of selective logging was chosen as study site in order to study logging intensity and quality (Fig. 3.1). At this site with an extension of 18.8 ha, logging took place in 1999, 2001, and 2002. In April 2002, all logged tree individuals were mapped with a handheld GPS (Garmin III+) and data were introduced in a GIS (ArcView 3.2). The remaining stump of each logged tree individual as well as woody debris were used to determine the species and to estimate dbh and number and size of explored timber boards. Height was calculated via a dbh-height regression based on the data from permanent plots. Woody biomass was calculated for extracted timber boards and felled trees following Chapter 3.2.2.

3.5 Data analysis

3.5.1 Tabular comparison of vegetation data

Data on tree and herb layer were treated separately since e.g. Hahn (1996) and Devineau *et al.* (1997) showed that floristically distinct herb layer groups can be associated to different tree layer groups and vice versa. Data on vegetation composition were converted into vegetation tables. Two approaches were chosen for tabular comparison. In the first approach, data were sorted by phytosociological criteria, based on the method of Braun-Blanquet as described in Dierschke (1994) and Mueller-Dombois & Ellenberg (1974). The resulting groups of relevé plots of this phytosociological sorting were denoted as floristic blocks. In the second approach, the position of vegetation types (*Vegtyp*, columns) were fixed by in the order *SB*, *SM*, *ST*, *SW*, *WI*, *WU*, and *WA* (Table 3.2), but relevé plots within each vegetation type were sorted. Position of species (rows) in the tables was ordered primarily by their occurrence and additionally by their dominance.

The tabular procedure for these two approaches was exclusively carried out in order to compare both classification approaches with each other with regard to floristic composition of tree and herb layer. It was not aimed to integrate neither resulting floristic blocks nor vegetation types into phytosociological syntaxonomic systems.

3.5.2 Statistical analysis

Univariate and multivariate data analyses were carried out. Univariate analyses and pairwise comparison of multivariate data were computed in R 1.8.0 (2003). All other multivariate analyses were performed with the Software package CANOCO for Windows Version 4.51. Boxplots are computed in Xact (Version 7.22b, Scilab GmbH).

For all parameters it was tested whether they were normal distributed before introduction into any statistical analysis. Some parameters showed normal distribution, others were only fairly normal distributed due to both rather low sampling number and heterogeneity of samples. However, transformation did not improve distribution of data towards a normal distribution. Therefore non-parametric analyses were carried out for most univariate data analyses. Though multivariate statistics are also based on the assumption of normal distribution, they are known to be much more robust against violation of this assumption (ter Braak & Smilauer 2002).

When many parameters are measured in the same plots – as it is the case in the present thesis – and when several test of significance are carried out simultaneously, the probability of type I error becomes larger than the nominal value α (Sokal & Rohlf 1995, Legendre & Legendre 1998). In these cases the significance level should be reduced by applying Bonferroni correction or comparable methods (review in Wright 1992). Nevertheless, this is a controversial issue (Cabin & Mitchell 2000). Moran (2003) states that from mathematical to

logical to practical reasons, many arguments can be given in order to reject the Bonferroni correction for ecological studies. One important point is, that the Bonferroni correction is based on the assumption of completely independent parameters, which is not given in ecological data for all parameters (Crawley 2002). As in the present thesis a high number of parameters are highly correlated with each other, no Bonferroni correction or other method for this purpose have been applied a priori, but ecological relevance of the results has been regarded carefully as recommended by Cabin & Mitchell (2000).

3.5.2.1 Univariate data analysis

Rank sum test of Kruskal-Wallis and pairwise comparison

Each univariate data set was analysed for significant differences between all groups by a global H-test of Kruskal-Wallis (1952 in Bortz *et al.* 2000). If significant differences between groups occurred, a pairwise comparison following Conover (1971, 1980 in Bortz *et al.* 2000) was calculated. Significance level was set to 0.05.

Correlation and regression analysis

In general, Spearman's rank correlation coefficient (r_s) was used for univariate correlation analysis as several data sets missed the assumptions of parametric statistics. In order to determine slope and point of intersection for selected data sets, linear regression analysis was carried out, and, in order to stay comparable to non-parametric analyses, the Pearson's correlation coefficient (r) was given for these cases (Sokal & Rohlf 1995).

Boxplots

Boxplots were computed in Xact (Version 7.22b, Scilab GmbH) as extended boxplots after Velleman & Hoaglin (1981). Values and markers are the same throughout all boxplots in the present thesis (compare Fig. 3.3).

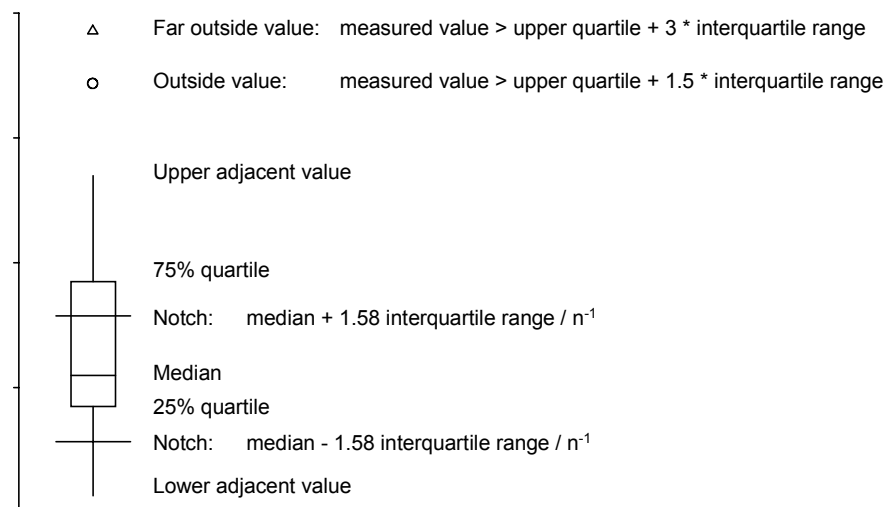


Fig. 3.3. Explanation of values used in boxplots.

3.5.2.2 Multivariate data analysis

For species data sets, Detrended Correspondence Analysis (*DCA*) was chosen for two reasons. Firstly, the calculated length of gradient for the analysed data sets recommended unimodal models (ter Braak & Smilauer 2002). Secondly, an arch effect occurred calculating Correspondence Analysis (*CA*) for the data sets (compare Hill & Gauch 1980, Gauch 1982, Jongman *et al.* 1987, Økland 1990, Palmer 1993). Canonical Correspondence Analysis (*CCA*) was chosen as constrained unimodal method for the joint analysis of species and environmental parameter data sets. Rare species may have an overproportional large influence on the analyses (ter Braak 1995, Lawesson 1997, ter Braak & Smilauer 2002). Accordingly, only species with more than two occurrences were used in the analyses of the herb species. This was the case for 296 of the 327 species. As the data set of the tree layer contained overall only 51 species, all species were considered. Nevertheless the effect of the species with very low number of occurrences was always checked after the analyses, and they were found to have low influence on the results.

Detrended Correspondence Analysis

A *DCA* was carried out with ‘detrended by segments’ in order to determine the length of gradient. As comparable amounts of floristic variability were explained by the first four axes, the option ‘detrending by fourth order polynomial’ was chosen for the calculation of the presented *DCA* (ter Braak & Smilauer 2002). ‘Inter sample distance’ and ‘Hill scaling’ were chosen since the analysis was aimed to be focussed on sample position. Species were log-transformed ($\log(x+1)$) to increase the influence of subordinate species compared to dominate ones (compare Lepš & Smilauer 2003).

Canonical Correspondence Analysis

Canonical Correspondence Analyses (*CCA*) were calculated to gain knowledge on the explanation of floristic variability by environmental parameters. Species were log-transformed ($\log(x+1)$) in the run of each *CCA* and ‘inter sample distance’ and ‘Hill scaling’ were chosen. Many of the environmental parameters were strongly and significantly correlated with each other. The inclusion of these correlated parameters into the respective *CCA* would lead to an overestimation of explained environmental variability (Økland & Eilertsen 1994). Therefore a model-selection procedure as described below was used to include only parameters which significantly improve the model and to exclude automatically parameters which are collinear or strongly correlated with already selected parameters (see Lepš & Smilauer 2003). Another advantage of the application of the model-selection procedure is that inclusion of noisy or irrelevant environmental variables which can seriously distort the representation of gradients can be avoided (compare McCune 1997). A manual step by step selection with subsequent Monte Carlo permutation test implemented in CANOCO

allows to choose parameters based on their statistical significance and ecological plausibility (Økland 1996). In the first step of the model-selection procedure, explained floristic variability and P-value were calculated for each single parameter being included separately into the model. The parameter with the highest explanation of floristic variability which showed a significant P-value (<0.05) was chosen and included into the model as a covariable. This procedure was repeated until no significant parameters were left. In those few cases where the significance level was near 0.05 ecological plausibility was also considered to decide whether to include or exclude a parameter (see comments on Bonferroni correction above).

Variance partitioning procedure

Other studies in West Africa suggested that position in the relief is a parameter explaining distribution of species and vegetation types (see Chapter 2.3). Additionally vegetation types (*Vegtyp*) themselves and visible sky (*VS*) as a proxy for tree cover are assumed to explain high amounts of floristic variability. Thus, it is of great interest to test whether the groups of parameters selected in the model-selection procedure explain the same floristic variability as the above named parameters or whether the explanation of both groups is independent. This was done by means of variance partitioning procedure (Borcard *et al.* 1992, Økland & Eilertsen 1994, Legendre & Legendre 1998, Lepš & Smilauer 2003). *CCA* are calculated for each of the subsets of environmental variables (X_1 and X_2 in [Fig. 3.4]) and for all parameters of both subsets together. The explained floristic variability of each subset is the portion $A+B$, $A+C$, and $A+B+C$ in (Fig. 3.4), respectively. In order to extract the shared portion of explained floristic variability (A) $A+B$ or $A+C$ were subtracted from the explained floristic variability of $A+B+C$.

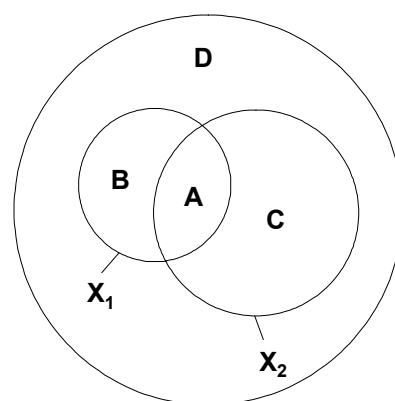


Fig. 3.4. Partitioning of the floristic variability in the species data into the contributions of two subsets of environmental variables (X_1 , X_2). A: explained floristic variability shared by X_1 and X_2 ; B: floristic variability explained by X_1 but not by X_2 ; C: floristic variability explained by X_2 but not by X_1 ; D: floristic variability not explained by X_1 and X_2 (residual floristic variability).

Principal response curve analysis

By means of Principal Response Curve analysis (*PRC*), time series of different experimental treatments can be compared to one time series of ‘control treatments’ (van den Brink & ter Braak 1998, 1999). In this study, treatment levels are gap plots and vegetation types. The *PRC* is based on a Redundancy Analysis (*RDA*) with the interaction of measurement time and vegetation type used as explanatory variables and measurement time coded as a 1/0-matrix introduced as covariables. Interaction effects including the ‘control treatment’ are omitted from the explanatory variables in order to represent a reference point for each measurement time. In CanoDraw, the canonical regression coefficients and species scores are transformed for graphical presentation (ter Braak & Smilauer 2002, Lepš & Smilauer 2003). Two approaches were calculated in the present thesis. To test for significant differences between time series of gaps and each vegetation type, *PRC* was computed for each of the seven couples considering the respective vegetation type as ‘control treatment’ followed by a Monte Carlo permutation test with split-plot design restricted to the measurement times. For a compromised illustration of the results of these seven *PRC*, an overall analysis for all vegetation types and the gap plots as ‘control treatment’ was calculated. The resulting graph was presented as the implied message did not differ from the results of each single analysis

Pairwise comparison of multivariate data

In order to test for significant differences in multivariate vegetation data, a Monte Carlo permutation test is recommended (Legendre & Legendre 1998, Tabachnick & Fidell 2001, ter Braak & Smilauer 2002). Comparable to the global H-test for univariate data (see Chapter 3.5.2.1), each multivariate data set was tested for significant differences between vegetation types applying Canonical Correspondence Analysis (*CCA*) followed by a Monte Carlo permutation test (5,000 replicates). Species data were treated as constrained variables and vegetation types as unconstrained variables (0-1 matrix = dummy variables) (Lepš & Smilauer 2003). As for all presented data sets significant differences occurred between vegetation types based on multivariate data, it was of interest to detect by means of pairwise comparison, which vegetation types differed significantly from each other.

For multivariate data, no implemented pairwise comparison based on a permutation test exist. Therefore, a multiple comparison procedure based on *CCA* was constructed where each pair of vegetation types was tested for significant differences. The significance level of each pair of vegetation types was computed applying *CCA* including dummy variables of the two vegetation types as explanatory variables and species data as response variables, followed by a Monte Carlo permutation test (5,000 replicates). The result of each single comparison enters into a matrix containing the significance levels of all single comparisons. This matrix was transformed to a 0-1 matrix where significance levels smaller than 0.05 (internal P-value)

were set to 1 and the others to 0. From this matrix, the number of significant groups and the 'membership' of each vegetation type to these groups was extracted by logical combination.

In order to test for the necessity for a Bonferroni correction of the internal P-value of 0.05 within the described pairwise comparison based on *CCA*, this type of pairwise comparison was computed for univariate data of the present thesis that are also analysed by means of non-parametric pairwise comparison (see Chapter 3.5.2.1). The non-parametric pairwise comparison, however, included an internal correction of the P-value. Except for vegetation types with a low number of replicates, both univariate approaches revealed almost the same significance groups for the vegetation types, though no Bonferroni correction of the internal P-value was applied within the univariate pairwise comparison based on *CCA*. Therefore, also within the multivariate pairwise comparison procedure, no Bonferroni correction was applied for the internal P-value of 0.05 (see also comments on Bonferroni correction above).

The described procedure was programmed in R 1.8.0 (2003) using the *CCA* function (Legendre & Legendre 1998, R-package *vegan*). Results of *CCA* of selected data sets computed in R and Software package *CANOCO* for Windows Version 4.51 showed that only minor differences between these two programs occurred. The advantage of R is its flexibility especially for programming. Thus, all pairwise comparisons were computed in R. The advantage of *CANOCO* is its graphical tool *CanoDraw* that was used for graphical presentations in the present thesis (see above).

4 Results

4.1 Floristic characteristics of the relevé plots

This chapter focuses on the description of the floristic composition of relevé plots by means of two classification approaches. The first classification approach is based on the physiognomic classification approach of the Yangambi conference in 1956 (CSA 1956), extended by a separation of zonal and azonal sites as well as a subdivision of woodlands according to dominant tree species (see Chapter 3.1.1). Stratified categories were denoted as vegetation types (*Vegtyp*) (Table 3.2). In the second approach floristic blocks are derived by a strict phytosociological classification. Beside the comparison between these two approaches, significance of vegetation types (*Vegtyp*) and floristic blocks is tested based on floristic composition. Tree and herb layer are treated separately (Chapter 3.2.2 and 3.2.3), and tree layer is defined as the cover of all individuals larger 10 cm dbh (Chapter 3.2.2).

4.1.1 Tabular comparison

4.1.1.1 Tree layer

Vegetation types

Relevé plots of the tree layer are shown in the Appendix (A-Table 2). The relevé plots were ordered according to the stratified vegetation types (Table 3.2). Within vegetation types, species were ordered by their occurrence and their dominance. In total, 49 tree species out of 22 families were found in the relevé plots. The three tree species *Isoberlinia doka*, *Uapaca togoensis* and *Anogeissus leiocarpus*, which were chosen to subdivide different woodland types, showed indeed clear dominance in the different woodland types but they also occurred in relevé plots of other vegetation types. *Terminalia macroptera* and *Terminalia schimperiana* as well as *Syzygium guineense* were restricted to *SB* and *SM* plots. Some species were observed in all vegetation types, e.g. *Daniellia oliveri* and *Vitellaria paradoxa*, whereas many species were completely absent from the *Bas fonds*. Representative species of the latter species group were *Burkea africana*, *Lannea acida*, *Monotes kerstingii* and *Parinari curatellifolia*. Even though species groups could be distinguished in A-Table 2, the overall impression is a diffuse gradient of tree species distribution from open savannas to woodlands.

Floristic blocks

The ordination of the tree species data according to phytosociological criteria is shown in Table 4.1, where the relevé plots of the *Bas fonds* were grouped together as well as plots of the woodlands. This ordination of relevé plots and species revealed more distinct species groups as compared to table A-Table 2.

In total, four floristic blocks of relevé plots were distinguished in Table 4.1. The first floristic block representing *Bas fonds* conditions was again characterized by *Terminalia macroptera* and *Terminalia schimperiana* (compare A-Table 2). The third floristic block is defined by *Isoberlinia doka*, *Uapaca togoensis* and *Monotes kerstingii*. Between the first and the third floristic block, a transition block (block 2) characterized by *Daniellia oliveri* occurred where typical species of both the first and the third block were mostly absent. The fourth floristic block of relevé plots was characterized by the absence of the characteristic species of the first three blocks.

Within the third floristic block of relevé plots, *Anogeissus leiocarpus*, *Ficus sur*, *Crossopteryx febrifuga*, and *Khaya senegalensis* differentiated a sub-block. *Vitellaria paradoxa*, *Pterocarpus erinaceus* and *Burkea africana* occurred in all relevé plots except of those in the *Bas fonds*. One plot, R19, was characterized by the absence of characteristic species and could not be associated to any of the four floristic blocks. In R15 tree species (dbh >10 cm) were completely absent.

Table 4.1. Cover of tree species larger 10 cm dbh in the relevé plots. Presented are species used for classification (compare complete species list A-Table 2). Relevé plots and species were sorted according to phytosociological criteria. Abbreviations of vegetation types are given in Table 3.2.

Cover of trees	2	2	1	2	15	2	10	10	15	20	48	65	35	35	18	20	45	55	75	55	65	60	70	55	55	60	65	75	65	45	50	70	45	45	0				
Floristic block	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	5	-				
Vegetation type	SB	SB	SB	SB	SM	SM	SM	SB	ST	ST	SW	WU	SW	SW	ST	ST	SW	WI	WU	WI	WI	WI	WI	WI	WI	WI	WI	WU	WU	WA	SW	WA	WA	WA	SW	SW	SB		
Plot	R14	R17	R12	R29	R07	R13	R01	R18	R35	R27	R08	R09	R02	R16	R11	R37	R05	R39	R38	R21	R10	R03	R04	R06	R32	R34	R33	R24	R25	R22	R30	R20	R23	R19	R15				
Species																																							
<i>Terminalia schimperiana</i>	2	1	.	.	28	1	3	
<i>Terminalia macroptera</i>	.	1	3	
<i>Syzygium guineense</i>	.	.	1	1	.	.	.	1	
<i>Daniellia oliveri</i>	12	26	8	5	15	9	13	1	9	3	.	.	6		
<i>Isoberlinia doka</i>	7	4	11	9	7	.	56	8	28	34	12	24	19	34	32		
<i>Uapaca togoensis</i>	8	1	2	3	42	.	35	.	.	2	12	.	2	18	39	87	4	4		
<i>Monotes kerstingii</i>	2	.	.	2	3	1	4	15	.	1	1	.	.	.	2	1	4	1	.		
<i>Anogeissus leiocarpus</i>	1	11	3	9	4	10	15	11	8	.	33	25			
<i>Ficus sur</i>	2	1	2	.	1	1	1	.	.		
<i>Crossopteryx febrifuga</i>	3	
<i>Khaya senegalensis</i>	1	
<i>Vitellaria paradoxa</i>	.	2	1	.	.	.	3	7	6	14	23	9	1	7	3	9	7	2	4	4	4	4	1	2	4	12	4	3	5	10	4	11	6	.	.	.			
<i>Pterocarpus erinaceus</i>	.	.	4	1	10	1	4	1	7	5	7	3	7	1	3	10	1	12	2	1	6	1			
<i>Burkea africana</i>	3	7	4	6	2	9	.	.	.	8	1	6	2	11	4	7	11	1	13	.	7	6	7	15	.			

4.1.1.2 Herb layer

Vegetation types

The table of the herb layer of all relevé plots ordered according to the vegetation types is shown in the Appendix (A-Table 3). In total, 327 species out of 69 families were found. Sixteen species groups were distinguished in table A-Table 3. The number of species within each species group and association of each species group with the vegetation types are summarized in table Table 4.2. For the herb layer, the distinction of the different stratified vegetation types was much clearer than for the tree layer (compare Chapter 4.1.1.1). However, species distribution showed again a clear gradual turnover from *SB* to *WA*.

Table 4.2. Summary of species groups (1-16) that were found for species in the herb layer of the relevé plots (compare [A-Table 3]). Abbreviations of vegetation types are given in Table 3.2.

Species group	<i>SB</i>	<i>SM</i>	<i>ST</i>	<i>SW</i>	<i>WI</i>	<i>WU</i>	<i>WA</i>	Number of species
1	X							13
2	X	X						12
3	X	X	X	X				13
4	X	X	X	X	X	X	X	18
5		X	X	X	X	X	X	14
6		X	X	X	X	X		8
7		X	X	X	X			5
8			X	X	X	X	X	34
9			X	X	X	X		7
10			X	X	X			22
11			X	X				6
12				X	X	X	X	14
13				X	X	X		7
14				X	X			5
15				X				4
16					X	X	X	14

First of all, relevé plots in the *Bas fonds* were clearly distinct from the relevé plots of all other vegetation types. Species that exclusively occurred in *SB* were *Hyparrhenia rufa*, *Cyperus rotundus*, and *Scleria aterrima*. Second, 34 species of the species group 8 such as *Aspilia helianthoides* and *Pandiaka involucrata* were found in all vegetation types except the two temporarily inundated ones, *SB* and *SM*. The group 4 was a third remarkable species group containing 18 species that were found in all vegetation types from the inundated ones to those with a dense tree canopy. Species with a high constancy were e.g. *Cassia mimosoides* and *Monechma ciliatum*. Especially the herb layer of *SW* and *WI* showed a large species pool, whereas denser formations, *WU* and *WA*, were characterized by the absence of species, e.g. species of the 7th, 10th, 11th, 14th, and 15th species group. The most characteristic species in the three woodland types, *WI*, *WU*, and *WA*, was *Andropogon tectorum* with a constancy of 100% and high cover values (compare A-Table 3). The results in table A-Table 3, however, strongly support the decision not to follow strictly the structural criteria of Yangambi (CSA 1956).

Floristic blocks

In the phytosociological ordination of the relevé table of the herb layer (Table 4.3), five floristic blocks of relevé plots were distinguished (plots and species sorted). The first floristic block contained relevé plots of the *Bas fonds*. Typical species were e.g. *Cyperus rotundus*, *Diplacrum africanum*, and *Hyparrhenia rufa*. The second floristic block of relevé plots was composed of *SM* and *SW* plots. This block was mainly characterized by the absence of species of the 1th and the 3th to 5th block of relevé plots. The third floristic block with a high abundance of *Andropogon schirensis* and *Hyparrhenia diplandra* was distinguished from the second block by the absence of species and the occurrence of species being frequent in the woodland types. The fourth block of plots was characterized by *Hyparrhenia involucrata* and *Ischaemum amethystinum*, species which indicate disturbance. These plots had indeed a strong impact of grazing. The fifth block was characterized by a high abundance of *Andropogon tectorum* and some other species. This floristic block included exclusively woodlands. For the other four floristic blocks, the phytosociological ordination does not follow the ordination of the stratified vegetation types. After the first block, assembling all *SB* plots, *SM* and *SW* were grouped together in block 2 and are characterized by species which also occur in the *Bas fonds* plots and by a smaller group of species which were mainly found in the *ST* plots of block 3. The fourth block of plots was characterized by *Hyparrhenia involucrata* and *Ischaemum amethystinum*, species which indicate disturbance. These plots had indeed a strong impact of grazing. Only woodland plots were found in the fifth block which is characterized by a high abundance of *Andropogon tectorum* and some other species.

4.1.2 Multivariate ordination

Using multivariate statistical methods, this chapter focuses on the comparison between the two classification approaches, vegetation types and floristic blocks, as well as on the test for significant groups within both classifications. In this context, the results of the detrended correspondence analysis (*DCA*) of four data sets are presented (see Table 4.4), i.e. tree and herb layer for both the whole data set and for a reduced data set without *Bas fonds* plots. This data reduction was introduced because *SB* and *SM* plots strongly dominated the ordination in the *DCA* as shown below, and therefore, limits the interpretation of the relation of the other five vegetation types.

Table 4.4. Summaries of detrended correspondence analyses (*DCA*) based on species cover of the tree and the herb layer of the relevé plots. X1-X4 = *DCA*-axis 1 to 4; LG = length of gradient in standard deviation units (*SD*); *SB*, *SM* = relevé plots of the *Bas fonds*.

	X1	X2	X3	X4	Total inertia	LG (<i>SD</i>)
DCA of the tree layer						
Data: relevé plots, <i>SB</i> and <i>SM</i> included (see Fig. 4.1, Fig. 4.2)						
Eigenvalue	0.697	0.391	0.281	0.191	5.161	8.013
Cumulative floristic variability (%)	13.5	21.1	26.5	30.2		
Floristic variability (%)	13.5	7.6	5.4	3.7		
Data: relevé plots, <i>SB</i> and <i>SM</i> excluded (see Fig. 4.5)						
Eigenvalue	0.414	0.28	0.222	0.15	3.401	3.010
Cumulative floristic variability (%)	12.2	20.4	26.9	31.3		
Floristic variability (%)	12.2	8.2	6.5	4.4		
DCA of the herb layer						
Data: relevé plots, <i>SB</i> and <i>SM</i> included (see Fig. 4.3, Fig. 4.4)						
Eigenvalue	0.662	0.139	0.107	0.093	2.904	3.814
Cumulative floristic variability (%)	22.8	27.6	31.3	34.5		
Floristic variability (%)	22.8	4.8	3.7	3.2		
Data: relevé plots, <i>SB</i> and <i>SM</i> excluded (see Fig. 4.6)						
Eigenvalue	0.258	0.131	0.105	0.079	1.796	2.166
Cumulative floristic variability (%)	14.4	21.7	27.5	31.9		
Floristic variability (%)	14.4	7.3	5.8	4.4		

The length of gradient is an indicator for floristic diversity over all relevé plots. A length of gradient of 4 standard deviation units (*SD*) reflects one species turnover along the first *DCA*-axis. The analysed tree layer of all relevé plots revealed a very long gradient of 8 *SD*, which means that a species turnover occurred two times along the first *DCA*-axis. The length of gradient of all other analyses was much shorter (Table 4.4). For a length of gradient >4 *SD*, unimodal methods, either correspondence analysis (*CA*) or *DCA*, are recommended, while gradient length <3 *SD* involves linear methods (ter Braak & Smilauer 2002). Accordingly, the

first three analyses, would suggest unimodal methods (compare Table 4.4), whereas the fourth analysis recommended linear methods. However, in order to have comparable results, a *DCA* was also used in the latter case.

In each of the four presented analyses, the first four axes of the *DCA* explain between 30 to 35% of all floristic variability of the data sets (Table 4.4). For the tree layer data sets, the explanation of the first axis is 13.5% and 12.2%, respectively. The first axis in the *DCA* of the herb layer including all relevé plots explained 22.8%. This value was much higher than explanation of floristic variability in the *DCA* of herb layer without the *Bas fonds* plots (15.5%). However, only for the data set of the herb layer including all relevé plots, a clear dominating gradient on the first *DCA*-axis was observed with an explained floristic variability of 22.8 % versus 4.8, 3.7, and 3.2% on the second, third, and fourth axes. For the other data sets, the first *DCA*-axis was less dominant (compare Table 4.4).

The figures that are presented in the following chapters are based on the *DCA* summarized in Table 4.4. Relevé plots were marked according to both classification approaches, the vegetation types and the floristic blocks of relevé plots (compare Chapter 4.1.1).

4.1.2.1 Tree layer

Vegetation types

The sample scores of the first two *DCA*-axes for the tree layer data of all plots are shown in Fig. 4.1 where the plots are marked according to the different vegetation types. All relevé plots of one vegetation type are wrapped with an envelope. In this analysis, five plots (*SB*: R12, R14, and R17; *SM*: R01, R07) strongly influenced the extension of the first and second *DCA*-axes (Fig. 4.1 A). R12, R14 and R17 contained very low numbers of species (2 to 4), singular combination of species and very low cover. As a consequence of *DCA*-algorithms, these relevé plots expanded the ordination space and the relevé plots were found in extreme positions. R01 and R07 were also characterized by low numbers of species and, in addition, contained one species with a very high cover (R01: *Terminalia schimperiana*, R07 *Daniellia oliveri*, compare A-Table 2) which caused also their extreme positions in Fig. 4.1 A. The other *Bas fonds* relevé plots (R13, R18 and R29) had low species numbers as well, but these species combinations were more similar to those in other relevé plots.

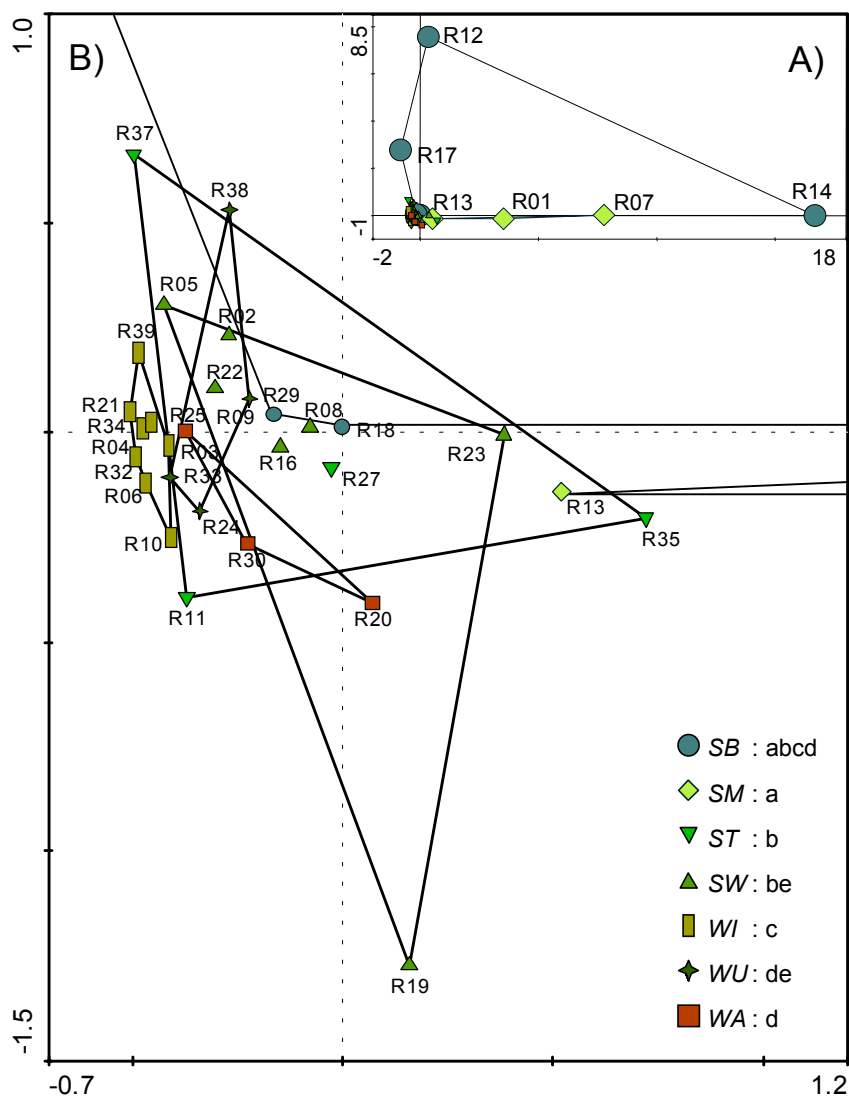


Fig. 4.1. Sample scores of the first and second *DCA*-axes based on the cover of tree species larger 10 cm dbh in the relevé plots. Relevé plots are marked according to vegetation types; abbreviations are given in Table 3.2. A) All sample scores included. B) Detail of panel A). The first and second *DCA*-axes explained 13.5% and 7.6% of floristic variability, respectively (compare summary of *DCA* in Table 4.4). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Fig. 4.1 B gives a detail of Fig. 4.1 A. In this figure, all vegetation types showed a wide overlap with each other, except *WI* which was located in the most extreme negative position along the first axis. Nevertheless, the pairwise comparison between the vegetation types with respect to cover of tree species revealed four main significant groups represented by *SM*, *ST*, *WI*, and *WA*. In addition, *SB* showed similarity to all other vegetation types and *SW* had similarities to *ST* and *WU* (Fig. 4.1).

Floristic blocks

Fig. 4.2 B shows the same detail of the *DCA* plot as Fig. 4.1 B, but in this case relevé plots are marked according to the floristic blocks outlined in Chapter 4.1.1.1. In this figure, the groups appear well separated. This is in accordance with the results of the pairwise comparison between the floristic blocks which revealed that all blocks differ significantly from each other. R19 was not grouped to any floristic block of plots as characteristic species were missing in this plot (compare Chapter 4.1.1.1). In the ordination by means of *DCA* this aspect was also obvious.

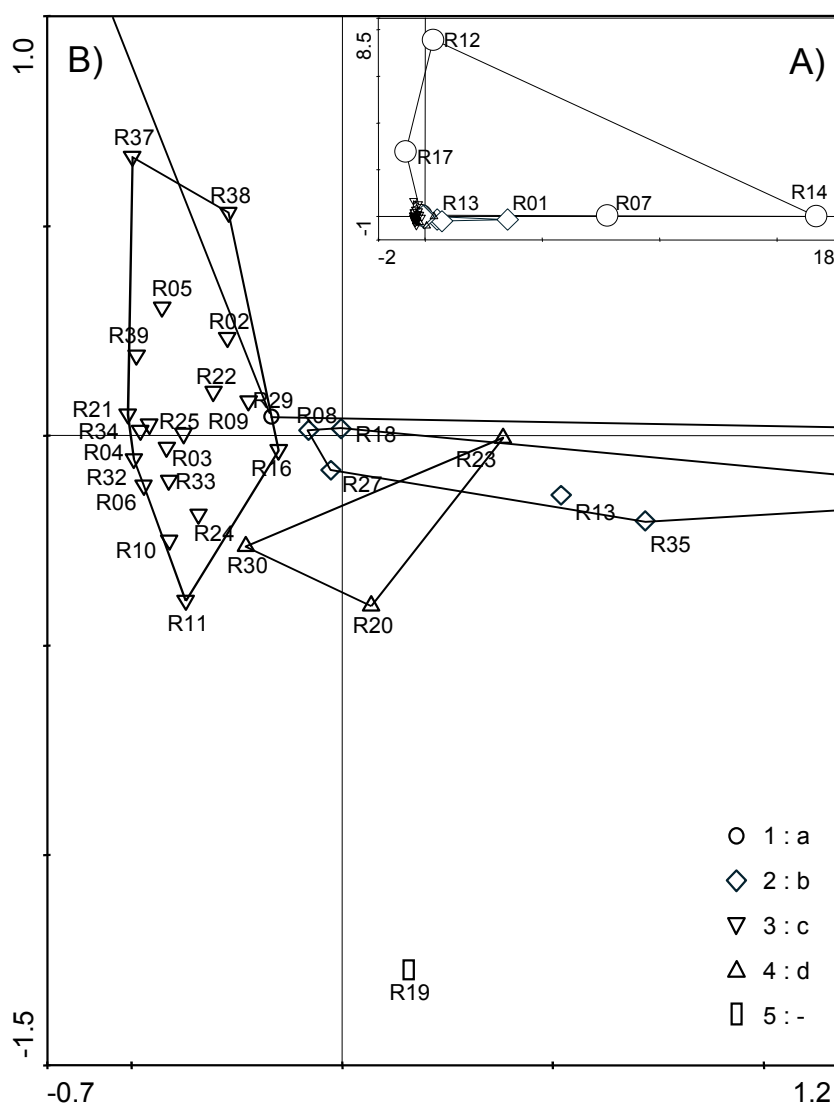


Fig. 4.2. Sample scores of the first and second *DCA*-axes based on the cover of tree species larger 10 cm dbh in the relevé plots. Relevé plots are marked according to floristic blocks of relevé plots (compare Table 4.1). A) All sample scores included. B) Detail of panel A). The first and second *DCA*-axes explained 13.5% and 7.6% of floristic variability, respectively (compare summary of *DCA* in Table 4.4). Statistically significant groups computed by pairwise comparison between floristic blocks of relevé plots are indicated by letters.

4.1.2.2 Herb layer

Vegetation types

Sample scores of the first two *DCA*-axes for the herb layer were marked according to the vegetation types shown in Fig. 4.3. The relevé plots of *SB* and *SM* were located on the positive side of the first *DCA*-axis and are well separated from the other vegetation types which appear rather aggregated on the negative side of the first *DCA*-axis. The floristic composition of *SB* and *SM* was responsible for the distinct gradient along the first *DCA*-axis with the high explanation of 22.8 % (compare Table 4.4). Pairwise comparison between the vegetation types also showed that both *SB* and *SM* belong to a common single significant group. This underlines again the floristic difference of *SB* and *SM* from all other vegetation types. The other five vegetation types showed a continuous transition in the following order: *SW* - *ST* - *WI* - *WU* - *WA*. Hereby, each vegetation type was similar to its neighbour (Fig. 4.3). This result is in agreement with the results shown in A-Table 2.

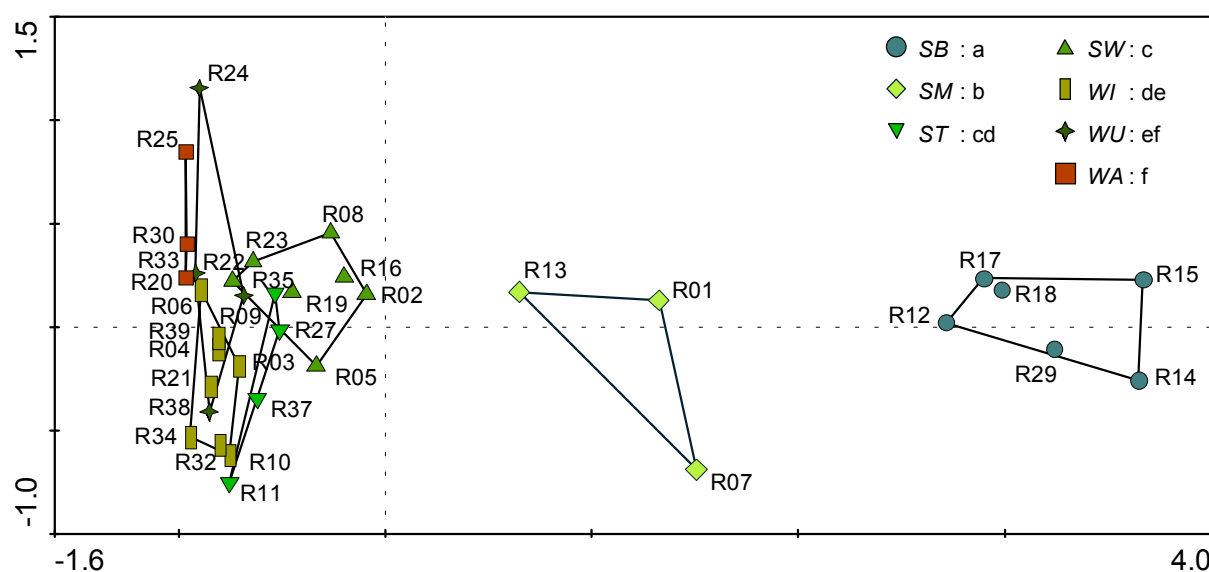


Fig. 4.3. Sample scores of the first and second *DCA*-axes based on the species cover in the herb layer of the relevé plots. Relevé plots are marked according to vegetation types; abbreviations are given in Table 3.2. The first and second *DCA*-axes explained 22.8% and 4.8% of floristic variability, respectively (compare summary of *DCA* in Table 4.4). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Floristic blocks

Fig. 4.4 is based on the same *DCA* as Fig. 4.3, but relevé plots were marked according to the floristic blocks of relevé plots from Chapter 4.1.1.2. The floristic groups appeared well ordered along the first *DCA*-axis, except for the fourth group (Fig. 4.4). The latter floristic group was also rather diffuse from a floristic point of view (compare Table 4.3). Especially the fifth floristic group is expanded along the second *DCA*-axis. Pairwise comparison between the floristic groups showed that all groups differed significantly from each other.

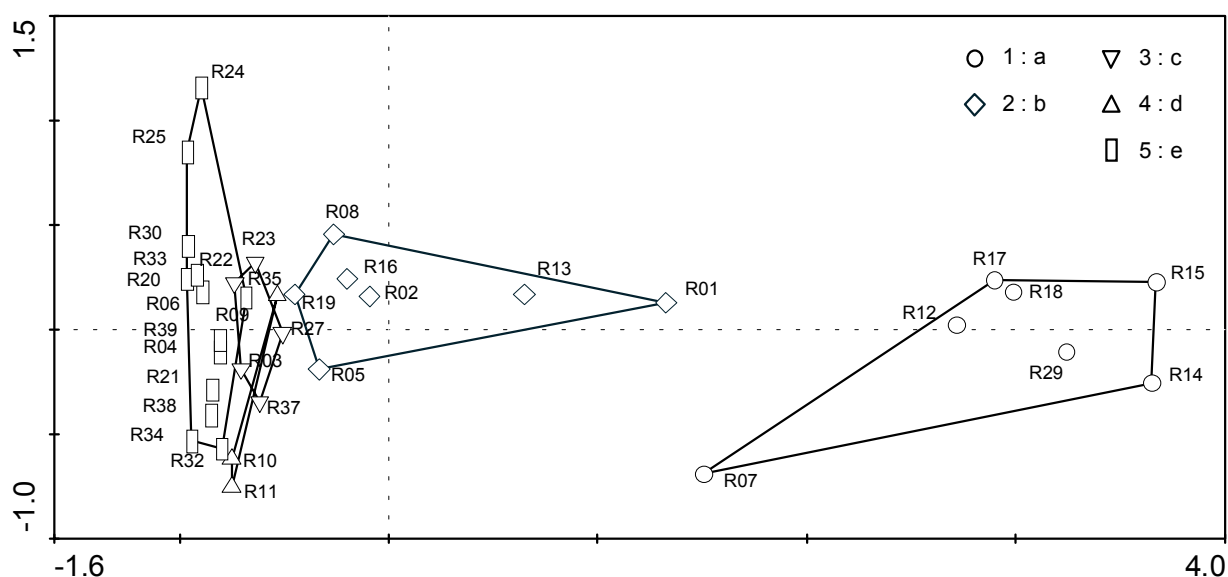


Fig. 4.4. Sample scores of the first and second *DCA*-axes based on the species cover in the herb layer of the relevé plots. Relevé plots are marked according to floristic blocks of relevé plots (compare Table 4.3). The first and second *DCA*-axes explained 22.8% and 4.8% of floristic variability, respectively (compare summary of *DCA* in Table 4.4). Statistically significant groups computed by pairwise comparison between floristic blocks of relevé plots are indicated by letters.

4.1.2.3 Tree and herb layer – *Bas fonds* relevé plots excluded

In this chapter, *DCA* analysis based on data sets where *SB* and *SM* relevé plots were excluded are presented. The significant groups of the pairwise comparison were not influenced by this reduction of data.

Tree layer (vegetation types)

As a consequence of the reduction of the data set by *SB* and *SM*, the length of gradient was reduced (see Table 4.4). In addition, the amount of floristic variability being explained by each of the first four axes became more similar compared to the *DCA* of the whole data set (Table 4.4). This means that for *ST*, *SW*, and the woodlands no strong single, but several

rather equal gradients could be detected. Nevertheless, a separation of the relevé plots of the vegetation types is still visible in Fig. 4.5. *ST* and *SW* relevé plots were ordered along the first *DCA*-axis. These two groups showed a wide overlap, especially if ignoring the exceptional relevé plot R19. The location of woodland relevé plots in Fig. 4.5 was mainly influenced by the second *DCA*-axis where especially *WI* and *WU* relevé plots appeared well distinguished.

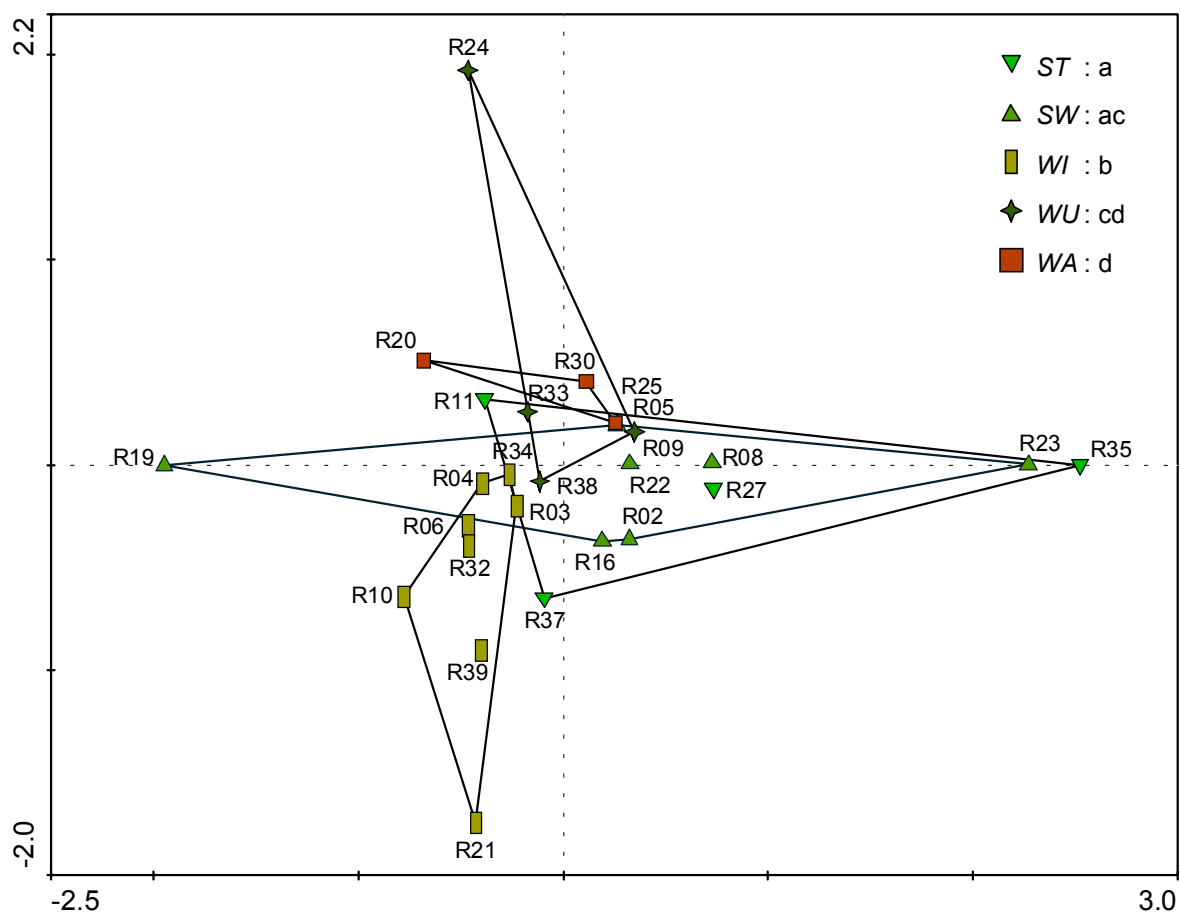


Fig. 4.5. Sample scores of the first and second *DCA*-axes based on the cover of tree species larger 10 cm dbh in the relevé plots. For this analysis, relevé plots of the *Bas fonds* (*SB* and *SM*) were excluded. Relevé plots are marked according to vegetation types; abbreviations are given in Table 3.2. The first and second *DCA*-axes explained 12.2% and 8.2% of floristic variability, respectively (compare summary of *DCA* in Table 4.4). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Herb layer (vegetation types)

For the reduced species data set of the herb layer (without *SB* and *SM*), a reduction of the length of gradient in *DCA* was low compared to the reduction for the tree data set (see Table 4.4). This reflects a weaker influence of *SB* and *SM* relevé plots on the floristic variability in the herb layer than on the tree layer. In the biplot of the *DCA*-analysis shown in Fig. 4.6, the relevé plots of the vegetation types were mainly spread along the first *DCA*-axis in the order *SW*, *ST*, *WI*, *WU*, and *WA*. The same tendency was also visible for the complete data set (*SB* and *SM* included, Fig. 4.3).

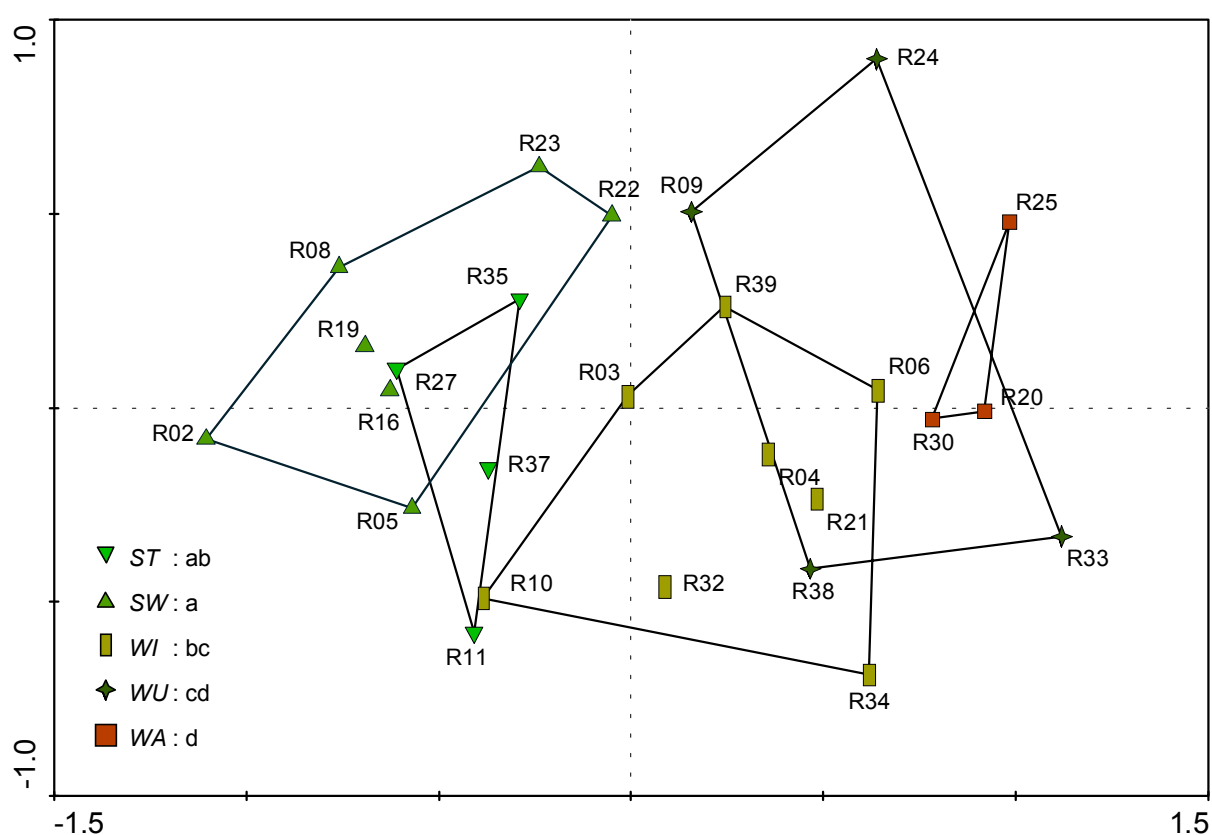


Fig. 4.6. Sample scores of the first and second *DCA*-axes based on the species cover in the herb layer of the relevé plots. For this analysis, relevé plots of the *Bas fonds* (*SB* and *SM*) were excluded. Relevé plots are marked according to vegetation types; abbreviations are given in Table 3.2. The first and second *DCA*-axes explained 14.4% and 7.3% of floristic variability, respectively (compare summary of *DCA* in Table 4.4). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

4.2 Structural characteristics of vegetation types

This chapter focuses on structural characteristics of the studied vegetation types. For the tree layer (Chapter 4.2.1), the distribution of height and diameter classes as well as tree cover and tree biomass are presented. For the herb layer (Chapter 4.2.2), cover, height, volume and mass of grass, herb and litter fraction are shown. In addition, the parameters cover of open ground, cover of dead woody biomass and cover of termite mounds are given in A-Table 6.

4.2.1 Tree layer

Diameter classes

Diameter class distribution of tree individuals in all relevé plots showed a general tendency of an age pyramid with smaller diameter classes occurring with a higher density than larger ones (Fig. 4.7). However, especially in *WU* the trees of medium diameter class had largest densities. The maximal density of the smallest trees (<5 cm dbh) with 500 tree individuals ha⁻¹ was found in *SW*, whereas a maximum density of 200 and 33 tree individuals ha⁻¹ occurred for the diameter class 20-<45 cm dbh in *SW* and the diameter class ≥45 cm dbh in *WI*, respectively. As expected, woodland types (*WI*, *WU*, and *WA*) and *SW* showed higher tree densities than *SB*, *SM*, and *ST*. This was especially the case for the medium diameter classes 10-<20 and 20-<45 cm dbh. The change from open to closed stands, however, is not abrupt but has a gradual character. The multivariate pairwise comparison between the vegetation types based on the diameter class distribution supported this observation. Even though the ‘open savanna’ (*SB*) was clearly distinguished from ‘dense woodlands’ (*WU* and *WA*), a wide overlap of statistical groups was found.

Height classes

With respect to the height class distribution of vegetation types presented in Fig. 4.8, vegetation types can be divided into two groups. The first group (*SB*, *SM*, and *ST*) showed a rather similar density within each height class, whereas the second group (*SW*, *WI*, *WU*, and *WA*) was characterized by high abundance of taller tree individuals, especially of the height class 5-<10 m. The latter vegetation types generally build up higher stands than the first group.

Separation of vegetation types by means of height class distribution was much clearer than by means of diameter classes. Pairwise comparison between vegetation types by means of height classes revealed four significant groups being characterised by *SB*, *ST*, *SW*, and *WU* (Fig. 4.8). *SM* showed similarities to *SB*, *ST*, and *SW*, whereas *WI* and *WA* were similar to *ST*, *SW*, and *WU*.

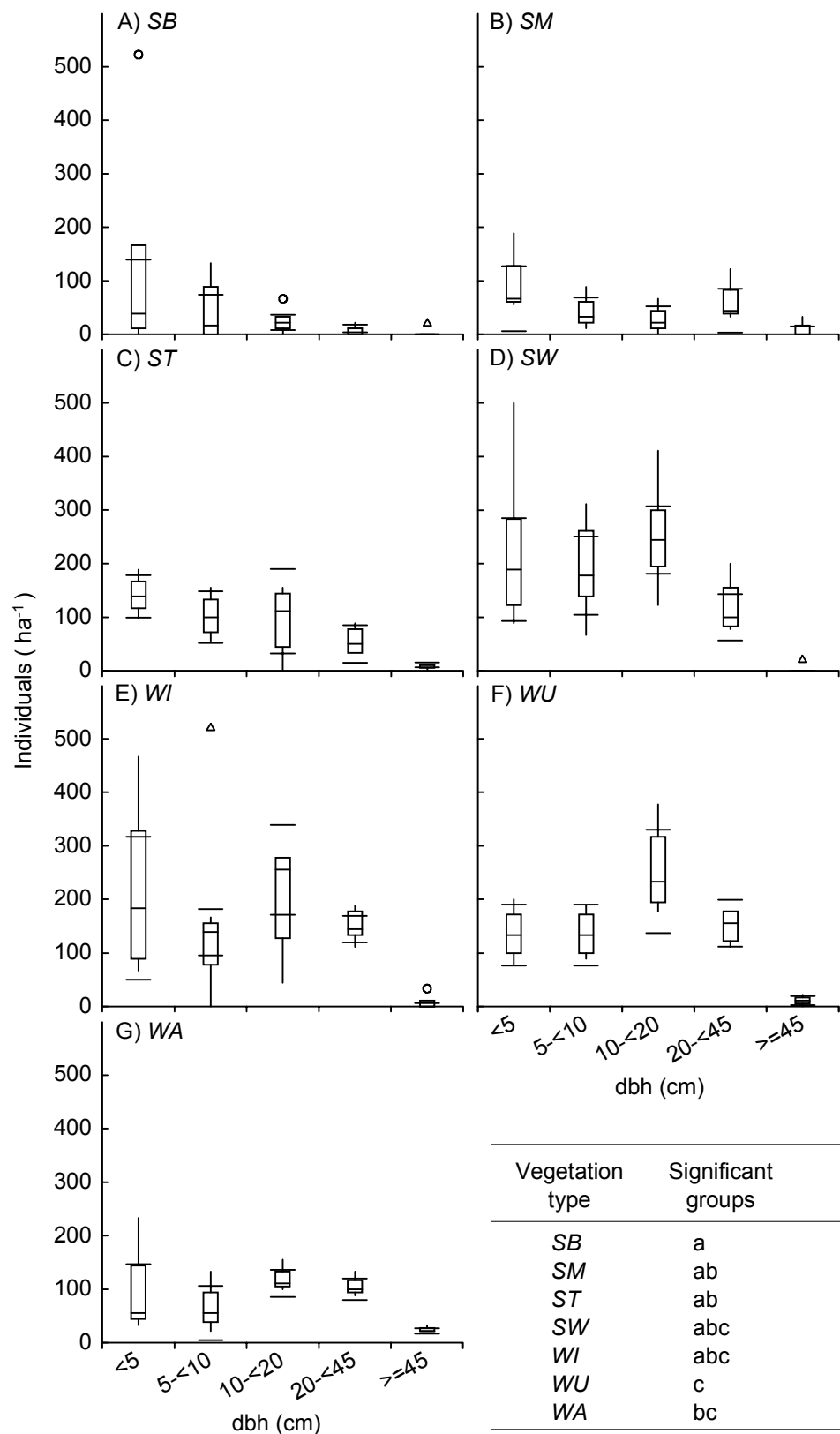


Fig. 4.7. Boxplots of the diameter class distribution in each vegetation type (abbreviations are given in Table 3.2). The overall largest dbh of 73 cm was measured for *Daniellia oliveri* in the relevé plot R01 (SB). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

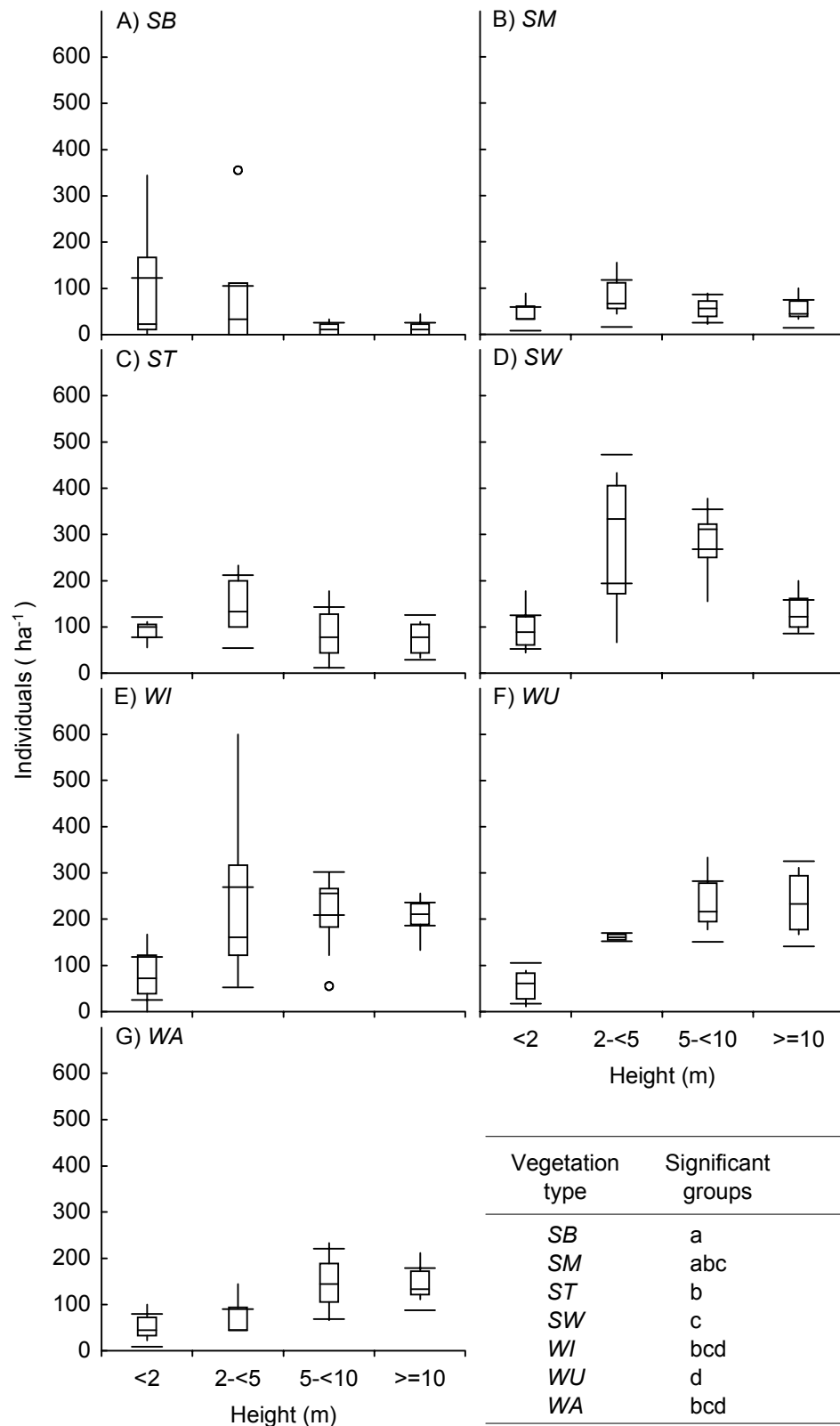


Fig. 4.8. Boxplots of the height class distribution in each vegetation type (abbreviations are given in Table 3.2). The overall highest tree individual with a height of 29 m belonged of the species *Anogeissus leiocarpus* (R25, *WA*). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Tree cover

Values for tree cover in the vegetation types ranged from below 10% in the *SB* and *SM* relevé plots up to 75% in the *WU* relevé plots (Fig. 4.9). The clear gradual change from *SB* to woodlands – as visible in the results of the pairwise comparison – reflects the classification criteria being used for vegetation stratification in the field.

Estimated and calculated tree cover differed from each other (Fig. 4.9). The estimated value was lower than the calculated one in the savanna (*SB*, *SM*, and *ST*). In contrast, the estimated tree cover was similar to or higher than the calculated one in the woodland relevé plots. In addition to the overall cover of trees shown in Fig. 4.9, the calculated cover of each diameter class and height class is given in the Appendix (A-Table 4, A-Table 5).

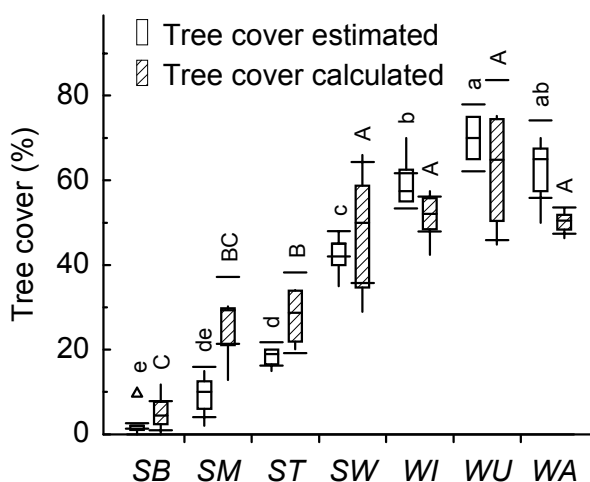


Fig. 4.9. Boxplot of calculated and estimated tree cover for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups within estimated values and within calculated values computed by pairwise comparison between vegetation types are indicated by letters.

Woody biomass

Woody biomass calculated for tree individuals larger 10 cm dbh ranged between 5 t ha⁻¹ for *SB* and 100 t ha⁻¹ for *WA* (Fig. 4.10 A). Also for woody biomass, a gradual change from *SB* to woodlands could be observed that is well represented in the results of pairwise comparison. However, woody biomass of each relevé plot was strongly dominated by trees of large diameter and height classes (A-Table 4, A-Table 5).

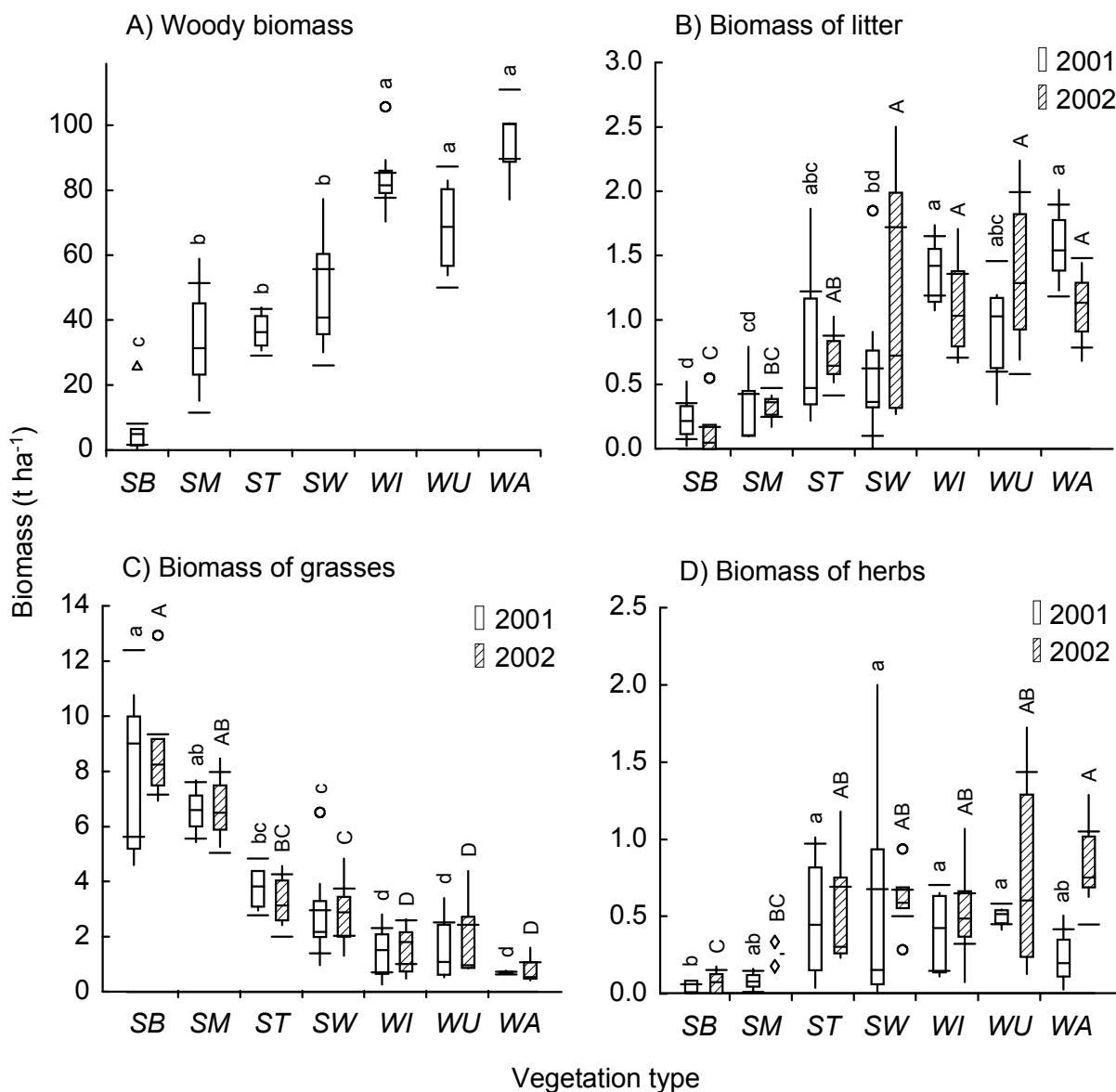


Fig. 4.10. Boxplot of (A) woody biomass, (B) biomass of litter (L_B), (C) biomass of grasses (G_B), and (D) biomass of herbs (HE_B) for vegetation types (abbreviations are given in Table 3.2). For (B)-(D) data are shown for 2001 and 2002. Statistically significant groups within one year that were computed by pairwise comparison between vegetation types are indicated by letters.

4.2.2 Herb layer

Cover, height, and volume of grasses

Cover (G_C), height (G_H), and volume of grasses (G_{Vol}) are shown for 2001 and 2002 in A-Table 6 in the Appendix. Grass cover strongly declined for both years from high values of above 90% in *SB* to low values of about 20 to 40% in the woodlands (*WI*, *WU*, *WA*). The volume of grasses – being calculated from cover and maximal height – showed a similar tendency as grass cover. For the maximal height of grasses no differences between vegetation types occurred in 2001, but a slight gradient was found in 2002.

Cover, height, and volume of herbs

Concerning herbs, all three parameters, cover (HE_C), height (HE_H), and volume (HE_{Vol}), were found to be rather similar for all vegetation types in both 2001 and 2002, *SB* being one exception (A-Table 6). This vegetation type showed lowest values for all three parameters.

Cover of litter

Cover of litter (L_C) was lowest in *SB* and highest in *WI* in both 2001 and 2002 (A-Table 6). A tendency of higher values in the woodlands than in the savanna plots (*SB*, *SM*, *ST*, and *SW*) was observed. The fraction of non-grass litter (LNG_C) showed clearly higher values in the woodlands than in the savannas, whereas for the grass fraction (LG_C) no distinct trend could be detected.

Biomass of the herb layer and litter

The amount of biomass of the herb layer (HE_B) being sampled in 1 x 1 m biomass plots in 2001 and 2002 is shown in Fig. 4.10 B, C, and D. After the woody-biomass compartment, biomass of grasses (G_B) with values up to more than 12 t ha⁻¹ was the second important biomass fraction. Grass biomass was highest in *SB* and *SM* relevé plots and declined to low values of about 1.5 t ha⁻¹ in the woodlands. Especially in *WA*, very low mass of grasses was found in 2001 (Fig. 4.10 C).

The biomass of litter (L_B) was lowest in *SB* (about 0.25 t ha⁻¹). Compared to the grass biomass, this fraction is negligible for *SB*, and also for *SM* (Fig. 4.10 B). The biomass of litter, however, increased to values of about 1.5 t ha⁻¹ for the woodlands and, thus, showed a range comparable to the mass of the grass fraction in these vegetation types. The biomass of herbs showed both a similar amount and a similar pattern compared to the biomass of litter (Fig. 4.10 D). It can be summarized that the herb layer of the two savanna plots *SB* and *SM* was dominated by the mass of grasses, whereas woodlands (*WI*, *WA*, and *WU*) were characterized by a mixture of equal fractions of grasses, herbs, and litter. *ST* and *SW* showed an intermediate biomass composition of the herb layer compared to these two extremes.

Correlation analysis of the structural parameters (volume of herbs and grasses, cover of litter, Table 4.5) between biomass plots (1 x 1 m) and relevé plots (5 x 15 m) in 2001 and 2002 revealed high correlation coefficients. Especially for grasses, the structural parameters between the two plots types were found to be very similar that is reflected in the regression analysis by slopes near 1. Relations with respect to herbs and litter were less clear, especially in 2001 (Table 4.5).

Table 4.5. Correlation and regression analysis of structural parameters sampled in biomass and relevé plots, and correlation and regression analysis of structural parameters and biomass sampled in biomass plots (data from 2001 and 2002). PI = point of intersection (y-axis); r = correlation coefficient (Pearson); *** = $P < 0.001$.

Parameter 1	Parameter 2	2001			2002		
		PI	Slope	r	PI	Slope	r
<i>Biomass plot (B) vs. relevé plot (R)</i>							
(B)	(R)						
Volume of grasses (G_{Vol})	Volume of grasses (G_{Vol})	0.40	0.99	0.90 ***	0.39	0.94	0.91 ***
Volume of herbs (HE_{Vol})	Volume of herbs (HE_{Vol})	0.12	1.23	0.64 ***	0.10	1.34	0.78 ***
Cover of litter (L_C)	Cover of litter (L_C)	3.75	0.23	0.46 ***	2.87	0.87	0.84 ***
<i>Biomass plot (B)</i>							
(B)	(B)						
Mass of grasses (G_{Vol})	Volume of grasses (G_{Vol})	0.06	0.32	0.94 ***	0.21	0.21	0.91 ***
Mass of herbs (HE_{Vol})	Volume of herbs (HE_{Vol})	0.02	0.14	0.72 ***	0.02	0.24	0.82 ***
Mass of litter (L_C)	Cover of litter (L_C)	2.15	16.49	0.77 ***	10.26	9.83	0.72 ***

Within the biomass plots, grass biomass and grass volume showed very strong correlations with r of 0.94 (2001) and 0.91 (2002, Table 4.5). Biomass of herb and biomass of litter also correlated positively with the structural parameters volume of herbs and cover of litter, respectively.

4.3 Environmental parameters of vegetation types

In this chapter, environmental parameters are described in detail for the seven vegetation types. These are microclimatic parameters (Chapter 4.3.1), fire (Chapter 4.3.2), topography and soil (Chapter 4.3.3). Additional parameters such as cover of termite mounds, cover of grass and non-grass litter, cover of open ground, cover of dead woody biomass, trampling damage, and grazing impact are given in A-Table 6.

4.3.1 Microclimate

As microclimatic parameters, insolation, air humidity, air temperature, and vapour pressure deficit are presented. In addition, correlations between these parameters and tree cover are shown.

Insolation

Insolation of the vegetation types measured as visible sky (VS) from hemispherical photographs taken in October 2002 are given in Fig. 4.11. The visible sky (VS) measured in October in this region is a good approximation of insolation during the rainy season with the

slight restriction that some species already started to shed their leaves in October. Median values for visible sky ranged from about 0.65 in the savanna plots *SB* to about 0.20 in the woodlands. In accordance with the parameter cover of trees larger than 10 cm dbh (compare Fig. 4.9), visible sky showed a gradual change from *SB* relevé plots with a high insolation to relevé plots of woodlands with a low insolation (Fig. 4.11). *SM*, *ST*, and *SW* relevé plots were found between the two extremes. This relation was also detected by means of pairwise comparison. Additionally the different radiation parameters direct (*DSF*), indirect (*ISF*), and global site factor (*GSF*), leaf area index (*LAI*) and visible sky (*VS*) are highly correlated with each other (see A-Table 7).

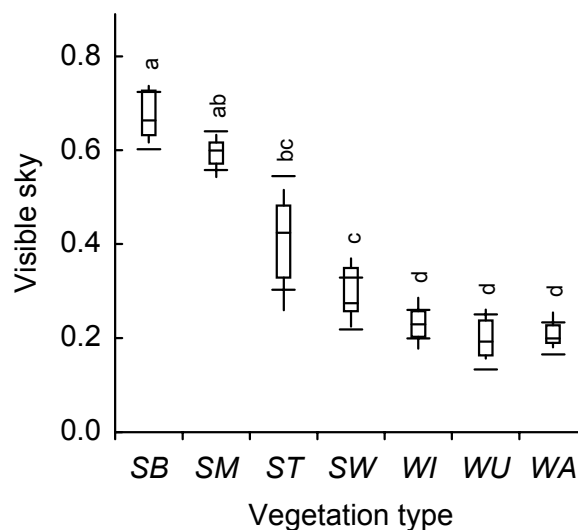


Fig. 4.11. Boxplots of visible sky (*VS*) measured in October 2002 for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Air humidity, temperature, and vapour pressure deficit

Microclimatic parameters measured in the relevé plots from September 2001 to December 2002 followed the general macroclimatic pattern (Chapter 2.1). Precipitation measured at the climate station in Doguè showed that the rainy season in 2001 ended in mid October and the rainy season of 2002 lasted from the beginning of April to the end of October (A-Fig. 1 D). Mean air temperature in the relevé plots was rather constant during the measurement period, but the amplitude of air temperature was much higher during the dry season (minimum value of 7 °C in December and a maximum values of 40 °C in March) than during the rainy season (A-Fig. 1 B). The annual course of air humidity (A-Fig. 1 A) with low values during the dry season and high values during the rainy season was strongly influenced by precipitation. The vapour pressure deficit (*VPD*, A-Fig. 1 C), however, showed the inverse course of air humidity. During the rainy season, both the maximum of air humidity and the minimum of *VPD* frequently reached 100% and 0%, respectively. The amplitude of air temperature (T_{amp}), the minimum of air humidity (H_{min}), and the maximum of vapour pressure deficit (VPD_{max}) were used as representative parameters in order to compare the vegetation types.

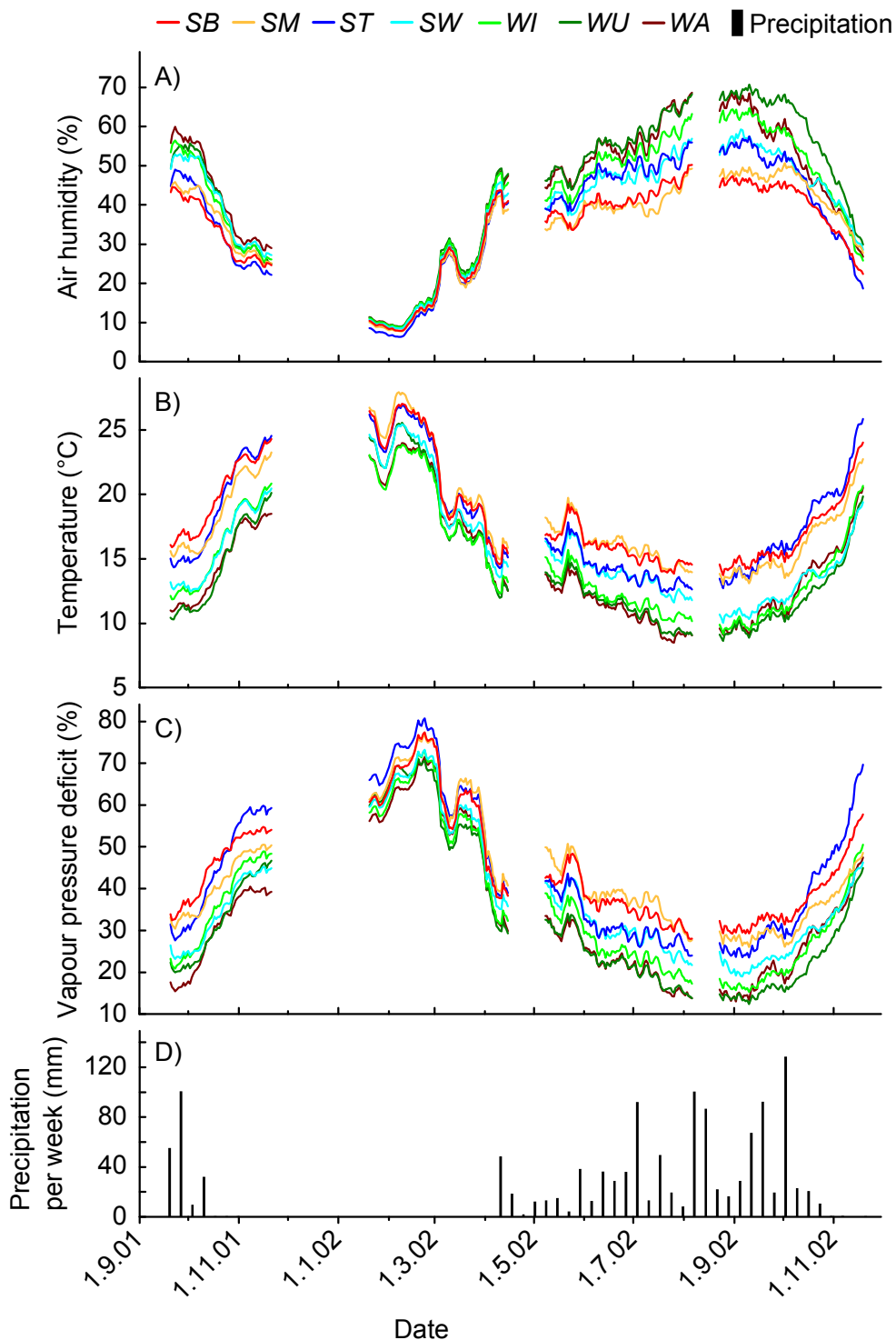


Fig. 4.12. 10-day-moving average on the bases of the mean of diurnal values of the relevé plots of each vegetation type for (A) minimum air humidity (H_{min}), (B) the amplitude of air temperature (T_{amp}), and (C) the maximum of vapour pressure deficit (VDP_{max}). Interruptions of the graphs resulted from periods needed for data download and logger maintenance. At the beginning of the measurement period, data from all relevé plots were considered. As a matter of a continuous loss of data loggers, at the end of the measurement period only 60% of the relevé plots were still considered. (D) Precipitation measured at the meteorological station in Doguè (precipitation data from Giertz 2004).

The annual course of the three microclimatic parameters shown in Fig. 4.12 A-C for each vegetation type also followed the macroclimate, but differences between vegetation types are well visible. In general, in open savannas (*SB*, *SM*) a lower minimal air humidity (H_{min}), a higher amplitude of air temperature (T_{ampl}) and a higher maximal VPD (VPD_{max}) was measured than in woodlands (*WI*, *WU*, *WA*). *ST* and *SW* showed an intermediate position (Fig. 4.12 A-C). This differentiation between vegetation types was more pronounced during the rainy season than during the dry season. This was especially true for the minimum of air humidity (Fig. 4.12 A). Pairwise comparison for the 10-day-mean of the upper three microclimatic parameters from 25.9. to 5.10.2001, a period where for all relevé plots data were available, supports this observation (A-Fig. 2 A-C).

Regression of microclimatic parameters on tree cover

The microclimatic parameters visible sky (VS), minimum of air humidity (H_{min}), amplitude of air temperature (T_{ampl}), and maximum of vapour pressure deficit (VPD_{max}) were significantly correlated with the cover of trees larger 10 cm dbh (A-Table 7). One of the strongest correlation was found for visible sky with a correlation coefficient of 0.916 (Fig. 4.13).

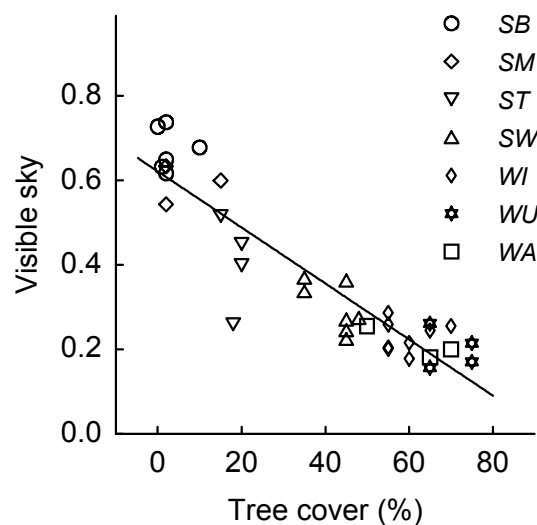


Fig. 4.13. Linear regression of cover of trees larger than 10 cm dbh and visible sky (VS) measured in all relevé plots ($r = 0.916$, $P < 0,001$).

4.3.2 Fire

With regards to the parameter fire, the date of fire occurrence (DF) was observed and fire temperature (FT) was measured in all relevé plots (Fig. 4.14). In both studied years the first relevé plots burnt in December (10.12.01 and 20.12.02) whereas in some woodland relevé plots fire did not occur at all. Woodlands burnt generally later than savanna plots, but this was only significant for *WU* in the dry season 2001-02 (Fig. 4.14).

Fire temperature measured in burnt relevé plots ranged from 215 °C to values larger than 600 °C (Fig. 4.14 B). Relevé plots in more open savannas were affected by a higher fire temperature than relevé plots in the woodlands which is supported by pairwise comparison, but a high variability in fire temperature within and between the two studied years led to a rather diffuse picture.

Both fire temperature and data of fire were measured in two years. For both parameters, no significant correlation between the respective data of the two years was found ($r_s = 0.23$, $P = 0.181$; $r_s = 0.22$, $P = 0.198$).

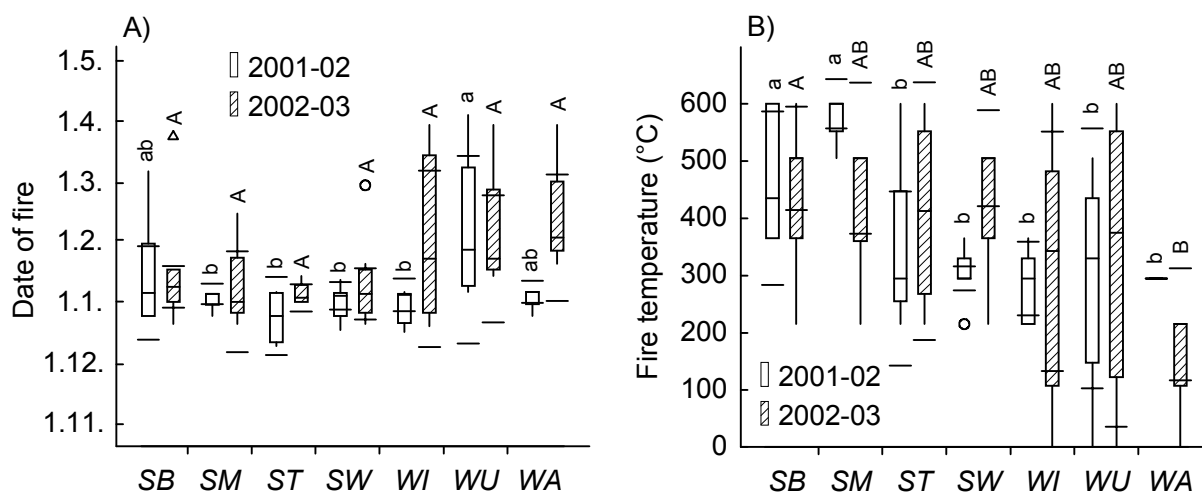


Fig. 4.14. (A) Boxplots of the date of fire occurrence (*DF*) and (B) fire temperature (*FT*) for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

4.3.3 Topography and soil

Topographic position and inclination

Within the gently undulating relief of the study area with slopes of normally less than 4%, the vegetation types were located along a topographical gradient (Fig. 4.15 A). The relative topographic position (*TopH*) measured in relation to the run-off line of *Bas fonds* shown in Fig. 4.15 ranged from 0-3 m for *SB* relevé plots up to a maximum of 22 m (*ST*, *WI*). Along the topographical gradient, *SB* and *SM* relevé plots were located in lower relative topographic positions and the woodlands in upper ones. *SW* took a medium relative topographic position and *ST* appeared undistinct (Fig. 4.15 A). Pairwise comparison revealed three significant groups being characterized by *SB* and *SM* (low *TopH*), *SW* (medium *TopH*), and *WI* (high *TopH*, Fig. 4.15 A).

With regard to inclination (*Inc*), values were below 4% for all vegetation types, except the relevé plots of the margin of the *Bas fonds* (*SM*) with a maximum inclination of 7% (Fig. 4.15 B). *WA* relevé plots showed very low inclinations below 1% indicating their hill-

top location. The inclination of *SB*, *ST*, *SW*, *WI*, and *WU* were rather similar, supported by the pairwise comparison.

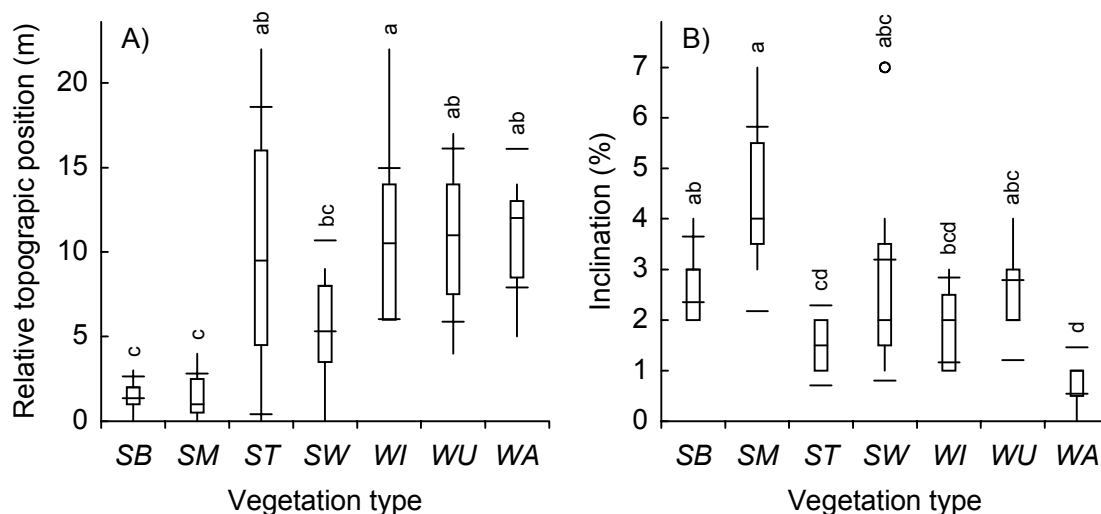


Fig. 4.15. (A) Boxplots the relative topographic position (*TopH*) measured in relation to the run-off line of *Bas fonds*. (B) Inclination (*Inc*) for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Soil depth and soil texture

Total depth of soils (*Sdp*) in the relevé plots ranged between 39 cm (*WU*) and 153 cm (*WA*, Fig. 4.16 A). Pairwise comparison revealed three significant groups, with the first representing deep soils (*SB*, *SM*) and the third representing shallow soils (*WI*). However, additional similarities between several pairs of vegetation types were found, and *SW* was similar to all other vegetation types (Fig. 4.16 A).

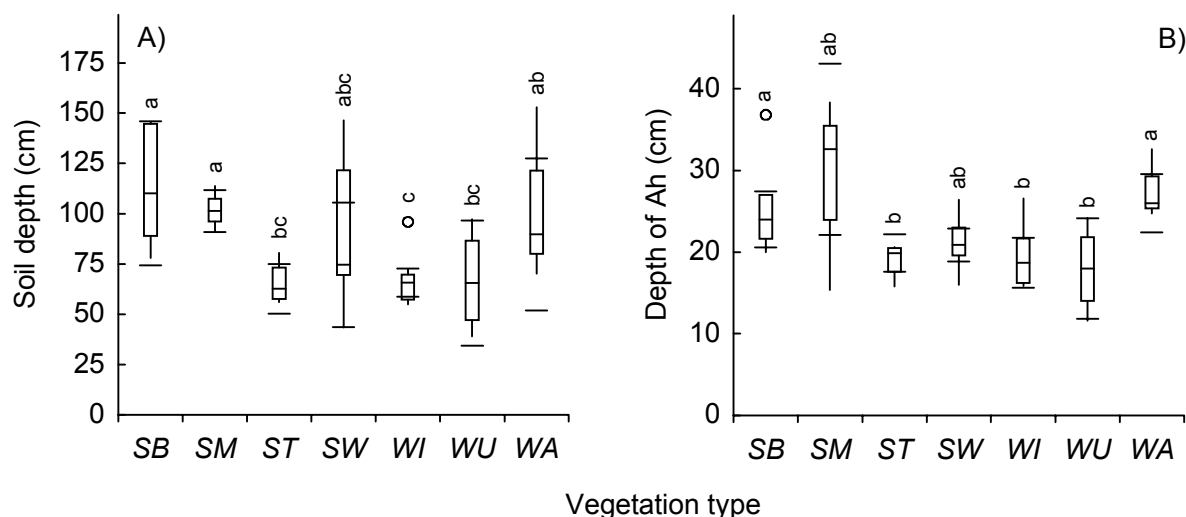


Fig. 4.16. (A) Boxplots of total soil depth (*Sdp*) and (B) the depth of the Ah-horizon (*Sdp_{Ah}*) for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

The depth of the Ah-horizon (Sdp_{Ah}) given in Fig. 4.16 B can be grouped into vegetation types with a profound Ah-horizon (SB , SM , WA) and with a shallow Ah-horizon (ST , SW , WI , WU). This was also supported by pairwise comparison. It has to be stressed that the upper soil layer in WA relevé plots were deeper than those of WI and WU relevé plots, but WA relevé plots were similar to SB , SM ; and SW (Fig. 4.16 B). This was to some extent also the case for total soil depth (Fig. 4.16 A). Thus, deep soils were found either in *Bas fonds* (SB , SM) or on top hill (WA), whereas more shallow soils occurred along slopes.

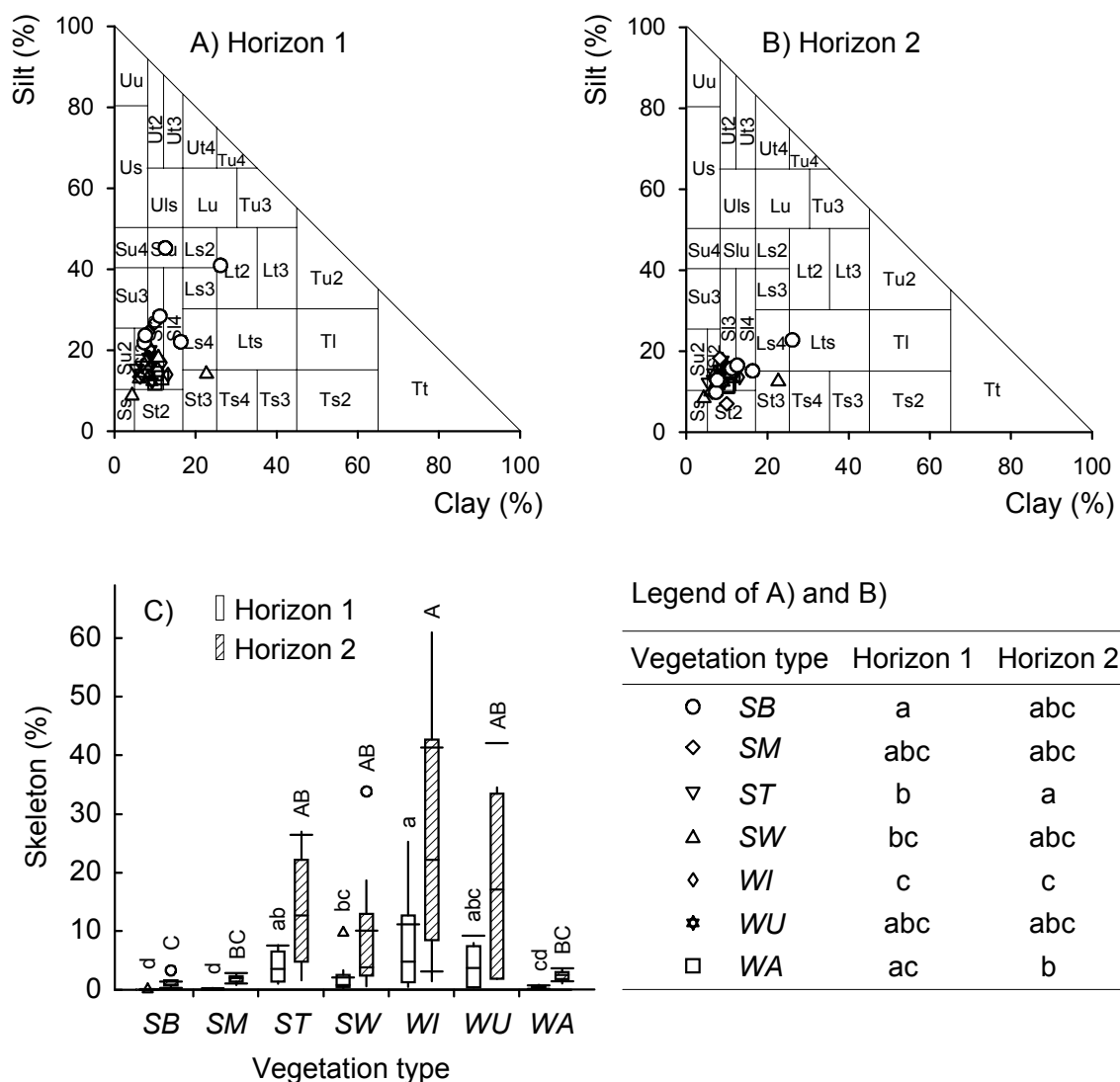


Fig. 4.17. Classification of the relevé plots of all vegetation types based on the portions of sand, silt and clay for the upper two horizons (A, B). Classification of soil types follows AG Boden (1994). T = clay, t = clayey, U = silt, u = silty, S = sand, s = sandy, L = loam, l = loamy, 2 = poor, 3 = medium, 4 = high. Example: S12 = slight loamy sand. (C) Boxplots of skeleton (Sk) in the two upper horizons for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Studies on the soil texture of the two upper horizons revealed that the soil type of the 35 relevé plots was very homogeneous (Fig. 4.17 A and B), and the amount of fractions were strongly correlated between the two sampled horizons with correlation coefficients from 0.65

to 0.90. For both horizons, loamy sands (S12-S14) were frequently found with a sand fraction of about 75%. Exceptions mainly occurred for *SB* relevé plots that contained a higher content of silt and clay and one *SW* relevé plot with a high content of clay (compare Fig. 4.17 A and B). Despite the high similarity for the classification of soil types, multivariate pairwise comparison based on the parameters clay, silt, and sand content resulted in three significant groups (see Fig. 4.17 for details). With regard to the skeleton fraction of the first and second horizon, Fig. 4.17 C shows that the skeleton fraction was generally higher in the second than in the first horizon. For both horizons, *SB* relevé plot contained the lowest fraction of skeleton.

Chemical properties

All considered chemical parameters showed strong and significant correlation between the upper two horizons (r_s from 0.54 to 0.64). Only for the C/N-ratio and plant available phosphorus (*P*), correlations were not significant ($r_s = 0.28$, $P = 0.11$; $r_s = 0.22$, $P = 0.20$). The *pH* measured in the two upper horizons ranged from 4.4 (*SB*) to 6.9 (*WI*, Fig. 4.18 A). For the upper horizon, lowest *pH*-values occurred for *SB* and *SM*, medium *pH*-values for *SW*, *WU*, and *WA*, and highest *pH*-values for *ST* and *WI* (compare significant groups of pairwise comparison). The second horizon showed a similar tendency as the first one, but *pH*-values were slightly lower (Fig. 4.18 A).

The sum of basic cations (*Bas*: Ca^{2+} , K^+ , and Mg^{2+}) presented in Fig. 4.18 B was dominated by calcium with values of up to $6.0 \text{ cmol}_c \text{ kg}^{-1}$, whereas magnesium and potassium showed values below 2.4 and $0.4 \text{ cmol}_c \text{ kg}^{-1}$, respectively (see A-Fig. 3 A-C). In the second horizon about half of the amount of plant available basic cations (*Bas*) was measured compared to the first horizon. The sum of basic cations showed a tendency of lower values within *SB* and *SM* than in the other vegetation types, which is supported by the results of the pairwise comparison (Fig. 4.18 B).

The C/N-ratio shown in Fig. 4.18 C ranged from 12 to 20 and from 8 to 32 for the first and the second horizon, respectively. For the first horizon, *SB* was significantly lower than *SW* and the woodlands. *SM* and *ST* were similar to rather all vegetation types. A similar trend was found for the second horizon (Fig. 4.18 C).

Plant available phosphorus (*P*) in the first horizon was below 3 ppm for all vegetation types and both horizons, except *ST* in the first horizon where values up to 5 ppm occurred (Fig. 4.18 D). However, no significant differences between vegetation types were found. In the second horizon, plant available phosphorus was mostly lower than 1 ppm and pairwise comparison only revealed significant differences between *SM* and two woodlands (*WU* and *WA*, Fig. 4.18 D).

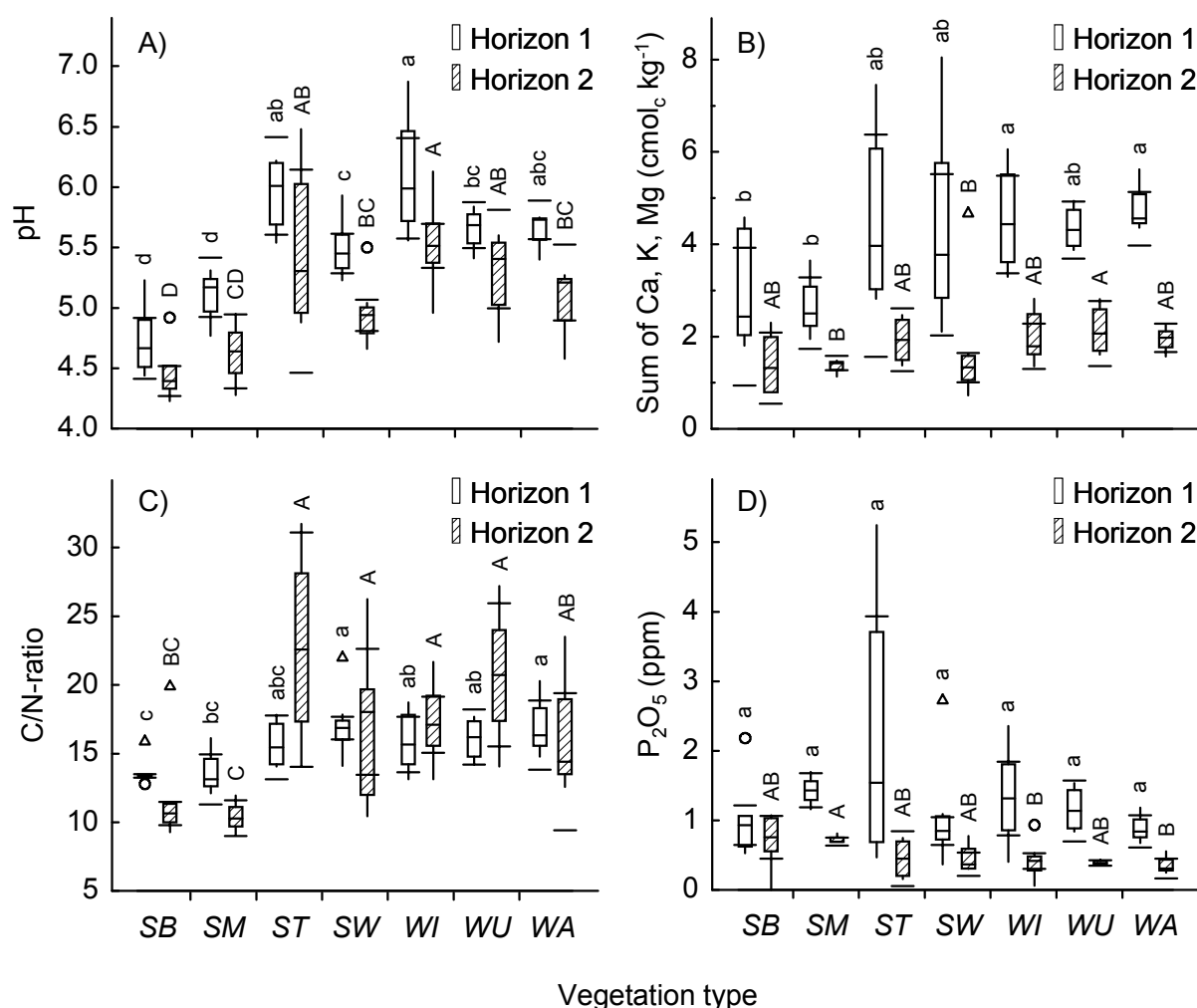


Fig. 4.18. Boxplots of selected parameters of soil chemistry [A) *pH*; B) Sum of calcium, potassium, and magnesium (*Bas*); C) C/N-ratio (*C/N*); D) phosphate (*P*)] for the two upper horizons for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

4.3.4 Correlation between environmental parameters

Since many of the above presented environmental parameters showed a comparable significance pattern between the vegetation types, several parameters might be inter-correlated. To clarify this point, environmental parameters, 46 in total, were analysed by means of correlation analysis (Spearman rank correlation). Because often *SB* and *SM* show values far outside the range of the other vegetation types this was done for the relevé plots with and without *SB* and *SM* relevé plot (see A-Table 8 and A-Table 9). Comparing these two approaches, a higher amount of significant correlations occurred for the data set where *SB* and *SM* relevé plots were included.

For the case where *SB* and *SM* relevé plots were included (A-Table 8), several environmental parameters were significantly correlated with many others, e.g. visible sky (*VS*) and *pH* with 36, cover of grasses (*G_C*) with 34, and available magnesium (*Mg*) of the upper horizon with

32 other environmental parameters. On the other hand, several parameters appeared to be more independent from the others. Examples are cover of termite mounds (*TM*), exposition (*Exp*), date of fire (*DF*), and plant available phosphorus (*P*), for which 0, 2, 2, and 4 significant correlations were computed, respectively (A-Table 8).

With respect to the correlation analysis without *SB* and *SM* relevé plots (A-Table 9), significant correlations mostly occurred between parameters that belong to a different block of parameters such as microclimate or soil, even though high numbers of correlations occurred. For example, visible sky (*VS*) was correlated with 16 environmental parameters, 7 of which belong to microclimate and 4 to the amount of grasses (A-Table 9).

The presented cross tables clearly demonstrate the strong inter-correlation between the environmental parameters measured for the relevé plots. Thus, much of the information carried by environmental parameters is redundant. Therefore, for the correlation of environmental parameters with species data, only a reduced number of environmental parameters was entered into the respective *CCA*, and within the *CCA* for this reduced set of environmental parameters a model-selection procedure was applied to avoid redundancy in correlation (see Chapter 4.4).

4.4 Relation of species data and environmental parameters

In Chapter 4.1 and 4.3, floristic pattern and environmental conditions of the studied plots were presented in detail. In this chapter, floristic variability is related to local environmental conditions. Four data sets were considered: the tree and the herb layer, both with and without *SB* and *SM* plots. Because environmental data showed strong inter-correlations, a model-selection procedure was applied as described in Chapter 3.5.2.2. Based on the results of the correlation analysis, only 26 of the environmental parameters presented before have been included into this analysis (A-Table 10 gives the list of all parameters in the first column). From the soil parameters, only the first horizon was included as it dominates the whole nutrient stock and is presumably most relevant for herbs and grasses. In terms of biomass of grasses (G_B), biomass of herbs (HE_B) and litter (L_B), trampling damage (*TM*), grazing impact (*GI*), date of fire (*DF*) and fire temperature (*FT*), the means of 2001 and 2002 have been chosen. Details of the explained floristic variability of single environmental parameters to the respective species data sets and their significance levels are given in the Appendix (A-Table 10 to A-Table 13).

4.4.1 Significance of environmental parameters – model selection procedure

For each of the four considered species data sets, environmental parameters selected within the model-selection procedure explained in total between 21.21 to 26.12% of the floristic variability (see Table 4.6 and Table 4.7). The overall highest explained floristic variability by one single parameter was 19% by visible sky (*VS*) in the herb layer data set, including *SB* and *SM* (A-Table 10). For illustration, the selected environmental parameters for the four data sets are plotted as supplementary variables in the figure of the *DCA*-analysis already presented in Chapter 4.1.2 (see Fig. 4.19).

Table 4.6. Explained floristic variability (eFV) expressed as percent of the total inertia for two species data sets of the herb layer (with and without *Bas fonds*). For details concerning the model-selection procedure see A-Table 10 and A-Table 11. For abbreviation of environmental parameters see A-Table 1.

Herb layer, <i>Bas fonds</i> included		Herb layer, <i>Bas fonds</i> excluded	
Total inertia: 2.904		Total inertia: 1.796	
Parameter	eFV (%)	Parameter	eFV (%)
Summary of the model-selection procedure			
<i>VS</i>	19.15	<i>VS</i>	8.25
<i>VS, S</i>	23.80	<i>VS, GI-M</i>	13.87
		<i>VS, GI-M, Mg</i>	19.24
		<i>VS, GI-M, Mg, S</i>	24.44
Vegetation types as nominal data			
<i>Vegtyp</i>	38.91	<i>Vegtyp</i>	24.02
Variance partitioning: Vegetation types (<i>Vegtyp</i>) vs. selected model			
<i>VS, S, Vegtyp</i>	43.86	<i>VS, GI-M, Mg, S, Vegtyp</i>	41.55
shared FV (<i>VS, S, Vegtyp</i>)	18.85	shared FV (<i>VS, GI-M, Mg, S, Vegtyp</i>)	6.91
<i>VS, S</i> - shared eFV	4.95	<i>VS, GI-M, Mg, S</i> - shared eFV	17.54
<i>Vegtyp</i> - shared eFV	20.06	<i>Vegtyp</i> - shared eFV	17.11
Variance partitioning: Vegetation types (<i>Vegtyp</i>) vs. visible sky (<i>VS</i>)			
<i>VS</i>	19.15	<i>VS</i>	8.25
<i>VS, Vegtyp</i>	41.34	<i>VS, Vegtyp</i>	28.24
shared eFV (<i>VS, Vegtyp</i>)	16.72	shared eFV (<i>VS, Vegtyp</i>)	4.03
<i>VS</i> - shared eFV	2.43	<i>VS</i> - shared eFV	4.23
<i>Vegtyp</i> - shared eFV	22.18	<i>Vegtyp</i> - shared eFV	19.99
Variance partitioning: Vegetation types (<i>Vegtyp</i>) vs. relative topographical height (<i>TopH</i>)			
<i>TopH</i>	8.75	<i>TopH</i>	4.88
<i>TopH, Vegtyp</i>	41.27	<i>TopH, Vegtyp</i>	28.04
shared eFV (<i>TopH, Vegtyp</i>)	6.39	shared eFV (<i>TopH, Vegtyp</i>)	0.86
<i>TopH</i> - shared eFV	2.36	<i>TopH</i> - shared eFV	4.03
<i>Vegtyp</i> - shared eFV	32.51	<i>Vegtyp</i> - shared eFV	23.16

In the herb layer data set including *SB* and *SM* plots, the parameter visible sky (*VS*) was strongly positively correlated with the first *DCA*-axis (Fig. 4.19 B). *CCA*-calculation using visible sky (*VS*) as co-variable revealed that only four parameters were still significantly correlated with the species data, whereof sand fraction (*S*) was highest in explained floristic variability (A-Table 10). This parameter was negatively correlated with the first *DCA*-axis (compare Fig. 4.19 B). In the next step of the model-selection procedure including visible sky (*VS*) and sand fraction (*S*) as co-variables, none of the remaining environmental parameters were significant (A-Table 10). The two selected environmental parameters, visible sky (*VS*) and sand fraction (*S*), explained 23.80% of the floristic variability (Table 4.6).

Table 4.7. Explained floristic variability (eFV) expressed as percent of the total inertia for two species data sets of the tree layer (with and without *Bas fonds*). For details concerning the model-selection procedure see A-Table 12 and A-Table 13. For abbreviation of environmental parameters see A-Table 1.

Tree layer, <i>Bas fonds</i> included		Tree layer, <i>Bas fonds</i> excluded	
Total inertia: 4.958		Total inertia: 3.248	
Parameter	eFV (%)	Parameter	eFV (%)
Summary of the model-selection procedure			
<i>S</i>	7.47	<i>S</i>	7.86
<i>S, U</i>	12.57	<i>S, U</i>	14.20
<i>S, U, G_B-M</i>	16.92	<i>S, U, G_B-M</i>	20.13
<i>S, U, G_B-M, Mg</i>	21.21	<i>S, U, G_B-M, Mg</i>	26.12
Vegetation types as nominal data			
<i>Vegtyp</i>	25.30	<i>Vegtyp</i>	21.61
Variance partitioning: Vegetation types (<i>Vegtyp</i>) vs. selected model			
<i>S, U, G_B-M, Mg, Vegtyp</i>	42.16	<i>S, U, G_B-M, Mg, Vegtyp</i>	44.12
shared FV (<i>S, U, G_B-M, Mg, Vegtyp</i>)	4.34	shared FV (<i>S, U, G_B-M, Mg, Vegtyp</i>)	3.61
<i>S, U, G_B-M, Mg</i> - shared eFV	16.87	<i>S, U, G_B-M, Mg</i> - shared eFV	22.50
<i>Vegtyp</i> - shared eFV	20.96	<i>Vegtyp</i> - shared eFV	18.00
Variance partitioning: Vegetation types (<i>Vegtyp</i>) vs. visible sky (<i>VS</i>)			
<i>VS</i>	7.16	<i>VS</i>	6.13
<i>VS, Vegtyp</i>	28.31	<i>VS, Vegtyp</i>	26.78
shared eFV (<i>VS, Vegtyp</i>)	4.15	shared eFV (<i>VS, Vegtyp</i>)	0.96
<i>VS</i> - shared eFV	3.01	<i>VS</i> - shared eFV	5.17
<i>Vegtyp</i> - shared eFV	21.15	<i>Vegtyp</i> - shared eFV	20.66
Variance partitioning: Vegetation types (<i>Vegtyp</i>) vs. relative topographical height (<i>TopH</i>)			
<i>TopH</i>	4.63	<i>TopH</i>	6.02
<i>TopH, Vegtyp</i>	28.51	<i>TopH, Vegtyp</i>	26.78
shared FV (<i>TopH, Vegtyp</i>)	1.42	shared FV (<i>TopH, Vegtyp</i>)	0.85
<i>TopH</i> - shared eFV	3.21	<i>TopH</i> - shared eFV	5.17
<i>Vegtyp</i> - shared eFV	23.88	<i>Vegtyp</i> - shared eFV	20.76

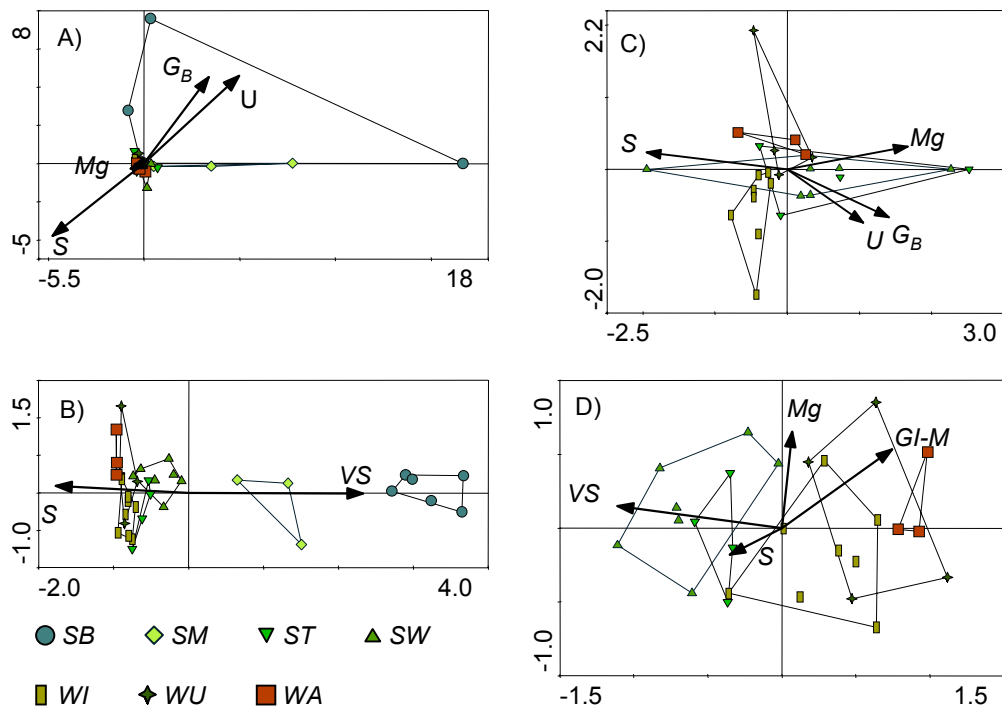


Fig. 4.19. Graphic representation of environmental parameters plotted as supplementary variables in the respective DCA-biplots (compare Chapter 4.1.2). A) DCA of species data of the tree layer, *SB* and *SM* plots included; B) DCA of species data of the herb layer, *SB* and *SM* plots included; C) DCA of species data of the tree layer, *SB* and *SM* plots excluded; D) DCA of species data of the herb layer, *SB* and *SM* plots excluded. Abbreviation of are given in A-Table 1.

In the herb layer data set excluding *SB* and *SM* plots, the environmental parameters tree cover (*TC*) and visible sky (*VS*) explained with 8.26 and 8.25% the highest floristic variability (A-Table 11). In order to be able to compare the analysis of the herb layer data including *SB* and *SM*, only visible sky (*VS*) was included as a co-variable in the first step of the model selection. The amount of floristic variability explained by *VS* for the reduced herb-data set is, however, only less than half of the amount of the complete herb-data set (19.15%, see Table 4.6). The next environmental parameters that were included during the model-selection procedure were grazing impact (*GI-M*), exchangeable Mg (*Mg*), and sand fraction (*S*) (A-Table 11). *VS*, *GI-M*, *Mg* and *S* explained 24.44% of the floristic variability (Table 4.6). All four selected environmental parameters point in different directions in the biplot of the DCA where they were plotted as supplementary variables, indicating that they influence different gradients of the plant species data (Fig. 4.19 D).

During the model selection procedure concerning the two tree layer data sets, environmental parameters that represent the structure of the tree layer (e.g. visible sky (*VS*) and tree cover (*TC*), A-Table 12 and A-Table 13) were not considered even though they showed high and significant values of explanation. Regardless of whether *SB* and *SM* plots were included or excluded from the analysis, for the tree data set the same environmental parameters were included during the model selection. Slight differences occurred only for the amount of explained floristic variability (see Table 4.7). The soil fraction parameters sand (*S*) and silt

(*U*), were selected to be included in the first two steps of the model-selection procedure (A-Table 12 and A-Table 13). Next, the parameters grass biomass (G_B-M), and finally exchangeable Mg (Mg) were selected. Thus, three of the four selected environmental parameters belong to the soil characteristics. The graphical illustration of the environmental parameters is given in Fig. 4.19 A and C.

4.4.2 Variance partitioning: vegetation types versus environmental parameters

As shown in Chapter 4.3, many of the considered environmental parameters were related to the vegetation types being used for stratification. The information of the nominal key parameter vegetation type (*Vegtyp*) was correlated with the vegetation data using a 0-1 matrix. The parameter vegetation type (*Vegtyp*), explained between 24.02 and 38.91% of the floristic variability in the four considered species data sets (Table 4.6 and Table 4.7). For the herb and tree layer data sets including *SB* and *SM*, the explanation by vegetation types (*Vegtyp*) was always higher than using the selected environmental parameters (herbs: 38.91 vs. 24.02%; trees: 25.30 vs. 21.61%). For the two cases excluding *SB* and *SM*, the explanation by *Vegtyp* was lower than or equal to the approach using environmental parameters.

The variance partitioning procedure was used to compare the amount of explained floristic variability of the parameter vegetation type (*Vegtyp*) compared to the environmental parameters. In order to do so, variance partitioning was carried out for the parameter vegetation type (*Vegtyp*) versus all environmental parameter data sets that were included in the models presented above. In addition, the same analysis was computed for only two single environmental parameters, visible sky (*VS*) and relative topographical height (*TopH*) (see Table 4.6, Table 4.7, and Fig. 4.20). Visible sky was selected because this parameter is strongly related with tree cover. Tree cover and density are the most important parameter used to define vegetation types in West Africa (compare Table 3.1) and therefore visible sky (*VS*) can be supposed to represent an ordinal variable of the nominal variable vegetation type (*Vegtyp*). As outlined in Chapter 1.1.1, West African vegetation types are often described to be very well related to topography. Therefore, the parameter relative topographical height (*TopH*) was tested separately as well.

The variance partitioning procedure considering vegetation types (*Vegtyp*) and all selected environmental parameters included in the models revealed for three of the considered species data sets, herb layer without *Bas fonds*, tree layer with and without *Bas fonds*, that the amount of explained floristic variability that was shared by the two groups was generally low with values between 3.61% and 6.91% (Table 4.6, Table 4.7, and Fig. 4.20). This means that the parameter vegetation type and each group of environmental parameters explained mainly different parts of the floristic variability. The herb layer species data set including *SB* and *SM* represents the exception. Here, the shared floristic variability of 18.85% was very high

(Table 4.6). In the latter case, the floristic variability only explained by the group of environmental parameters was small with 4.95% (Table 4.6). For the other species data sets this value was above 17%.

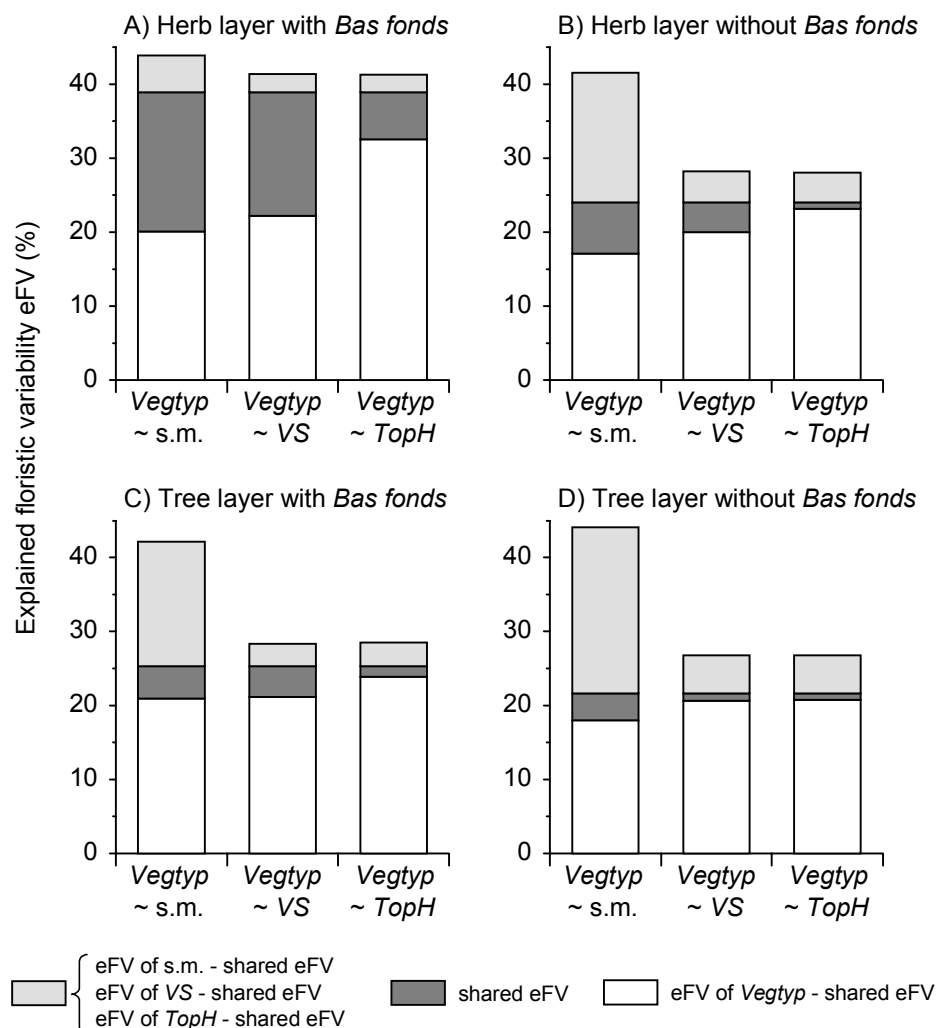


Fig. 4.20. Illustration of the results of variance partitioning for the four species-data sets (A-D) shown in Table 4.6 and 4.7. eFV = explained floristic variability, s.m. = selected model, VS = visible sky, TopH = relative topographic height, Vegtyp = vegetation type.

The variance partitioning procedure carried out for vegetation type (*Vegtyp*) versus visible sky (*VS*) revealed a comparable picture to the above mentioned analysis. The shared floristic variability between vegetation types (*Vegtyp*) and visible sky (*VS*) was only slightly lower than between vegetation types (*Vegtyp*) and the respective group of environmental parameters (Table 4.6, Table 4.7, and Fig. 4.20). This was especially the case for the herb layer including *SB* and *SM* with a shared floristic variability of 18.85% and 16.72%, respectively (Table 4.6). This emphasises the strong relation of vegetation types with light conditions that was also shown in Chapter 4.3.1. The only exception within the analysed data sets is the tree layer data set excluding *SB* and *SM* with a shared floristic variability of 0.96% between vegetation types (*Vegtyp*) and visible sky (*VS*).

With regard to the key parameter relative topographical height (*TopH*), the amount of shared floristic variability between this parameter and the parameter vegetation type (*Vegtyp*) was low for three data sets (Table 4.6, Table 4.7, and Fig. 4.20). But again, the herb layer including *SB* and *SM* is exceptional. Here, 8.75% of the floristic variability was explained by relative topographical height (*TopH*), and 6.39% was shared by relative topographical height (*TopH*) and vegetation types (*Vegtyp*). For all data sets, several environmental parameters such as visible sky (*VS*), tree cover (*TC*), trampling damage (*TD*), and several soil related ones were still significant when relative topographical height was considered as a co-variable (A-Table 10 - A-Table 13).

4.5 Logging history and intensity

On the territory of the village Doguè, the first timber logging took place in the 1960ies. Two entrepreneurs from the village Bassila started to cut single individuals of *Khaya senegalensis* and *Azelia africana* with power saws and exported the trunks to the sawmills in the surroundings. Until about 1985 almost all individuals of *Khaya senegalensis* and *Azelia africana* with considerable diameters were explored. After this time *Ceiba pentandra*, *Antiaris africana*, *Chlorophora excelsa*, etc. were explored in the forest islands around the village. In the woodlands and savannas focus species became *Pterocarpus erinaceus*, *Isobertinia doka*, *Pseudocedrela kotschy* and *Diospyros mespiliformis*. In 2000 many new tracks were installed from the main road deep into the woodlands and savannas in order to enable the transport of timber boards by lorries. It can be assumed that tree fellers, once arrived at a site, exploit all tree individuals that are profitable for felling at the respective point of time.

Table 4.8. Density of logged tree individuals in 1999, 2001, and 2002 in a woodland dominated by *Isobertinia doka* (*WI*) with a size of 18.8 ha. Density of tree individuals that were used or not used for timber board extraction are listed separately.

Year	Density of tree individuals (ha ⁻¹)															
	Timber boards exploited						Timber boards not exploited									Sum
	1999		2001		2002		1999			2001			2002			
<45	≥45	<45	≥45	<45	≥45	1-<20	20-<45	≥45	1-<20	20-<45	≥45	1-<20	20-<45	≥45		
<i>Azelia africana</i>								0.05							0.05	0.11
<i>Isobertinia doka</i>			0.05	5.16	0.05	1.54		0.05			0.74	0.37		0.21	0.27	8.46
<i>Khaya senegalensis</i>		0.74		0.11				0.05								0.90
<i>Pterocarpus erinaceus</i>				0.21	0.05	0.53		0.05		0.11	0.11		0.05	0.05	0.11	1.28
<i>Other species</i>							0.05	0.21		1.06	3.03	0.05	1.65	0.85	0.11	7.02
Sum		0.74	0.05	5.48	0.11	2.07	0.05	0.37	0.05	1.17	3.88	0.43	1.70	1.12	0.53	17.77

The documentation of logging activity at the additionally studied area near Doguè showed that tree individuals of usually more than 45 cm dbh were felled (Table 4.8). Sawing of timber boards took place directly in the field. About 90% of the wood of the logged trees was left in

the field and only 10% was taken out of the system as timber boards (derived from data in Table 4.8, compare Chapter 3.2.2). A remarkable high number of trees with a dbh below 45 cm growing around the focus individual were felled to use parts of their trunks to facilitate sawing activities (Table 4.8). Also valuable timber species were used for this purpose. Until 2000, 0.74 individuals ha^{-1} of *Khaya senegalensis* were still found for logging in the studied area, whereas for *Azelia africana* no individuals with a diameter of interest were left (Table 4.8). In 2001 and 2002, mainly *Isobertinia doka* and some *Pterocarpus erinaceus* individuals were explored. Logged individuals were evenly distributed over the studied *Isobertinia* woodland. In total, 9.3 tree individuals larger than 45 cm dbh were logged per hectare. For the size classes 20-<45 cm dbh and 1-<20 cm dbh, 5.5 and 2.9 individuals ha^{-1} were felled, respectively. Calculation of the extension of crowns, based on measurements in the relevé plots, averages 75, 35, and 10 m^2 for these three diameter classes. Assuming no overlap of crowns, the respective gaps occupied 7%, 2%, and 0.3% of the studied area.

4.6 Comparison between gaps and vegetation types

4.6.1 Environmental parameters

Environmental parameters measured for the gap plots as well as pairwise comparison between gap plots and relevé plots of the different vegetation types are given in A-Table 14. All insolation parameters that depend on tree cover (*VS*, *ISF*, *DSF*, *GSF*, and *LAI*) differed significantly from the relevé plots in the *Bas fonds* (*SB*, *SM*) and from the woodlands (*WI*, *WU*, *WA*), but they were similar to the wooded savanna (*SW*) and tree savanna (*ST*) (A-Table 14, *VS* in Fig. 4.21 A). For the microclimatic parameters amplitude of air temperature (T_{ampl}), minimum of air humidity (H_{min}), and maximum of vapour pressure deficit (VPD_{max}), the gap plots differed significantly from the woodlands (*WI*, *WU*, *WA*) and the wooded savanna (*SW*), whereas no significant differences occurred for relevé plots in the *Bas fonds* (*SB*, *SM*) and for tree savanna (*ST*), except for T_{ampl} , where the gap plots differed also significantly from *SB* (A-Table 14, H_{min} in Fig. 4.21 B).

For the other environmental parameters, the gap plots generally differed significantly from *SB* (A-Table 14). In Fig. 4.21 C and D, the parameter grass biomass (G_{B-02}) and sand fraction (*S*) are shown. With respect to grass biomass, relevé plots in the *Bas fonds* (*SB*, *SM*) showed significantly higher grass-biomass values than the gap plots and values in the *WA*- and *WI*-plots were significantly lower (Fig. 4.21 C). For the sand fraction, only the *SB*-plots differed significantly from the gap plots having lower values (Fig. 4.21 D).

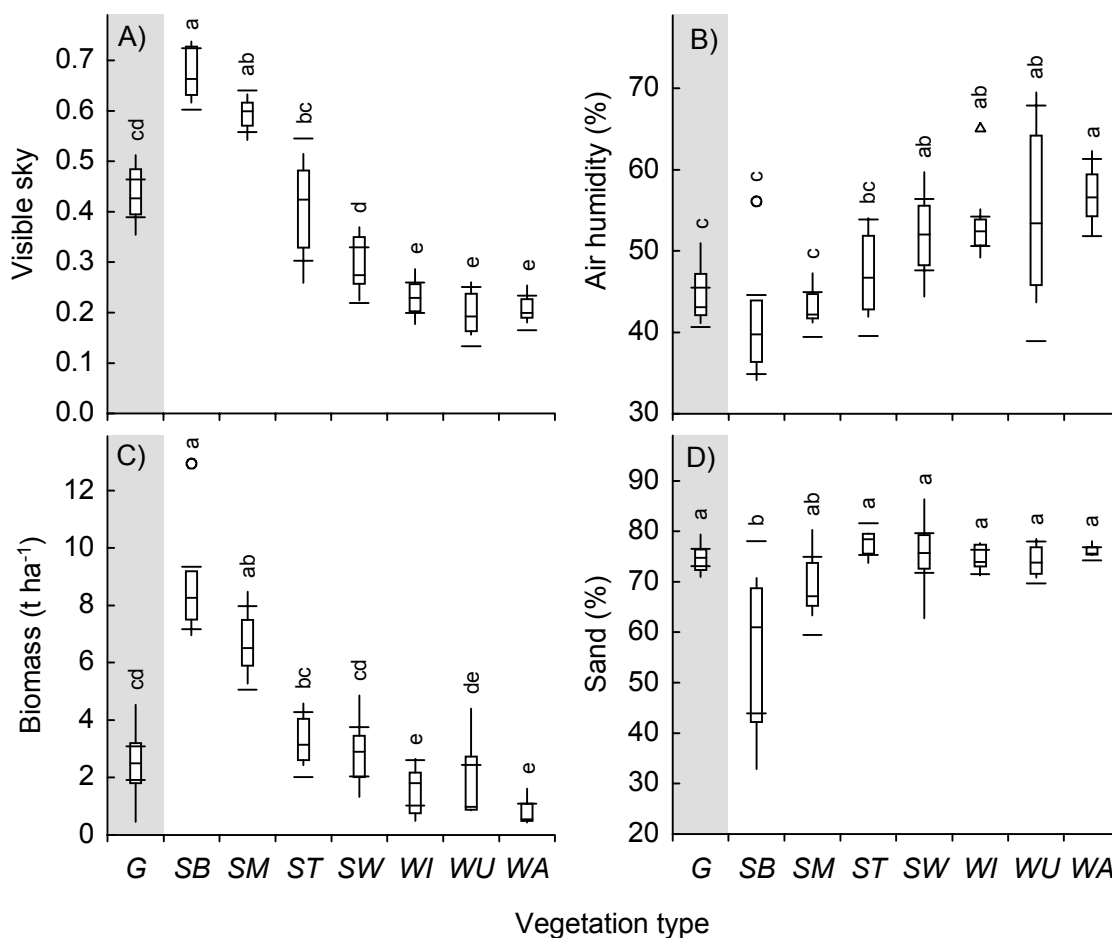


Fig. 4.21. Boxplots of four environmental parameters [A] visible sky (VS); B) minimum of air humidity (H_{min}); C) grass biomass sampled in 2002 (G_B-02); D) sand fraction of the upper horizon (S] for the gap plots (G) and the relevé plots of the different vegetation types. Abbreviations of vegetation types are given in Table 3.2. Statistically significant groups computed by pairwise comparison between gap plots and the relevé plots of different vegetation types are indicated by letters.

Table 4.9. Number of species found in gap plots compared to number of species found in relevé plots of different vegetation types with regards to species groups extracted for the herb layer in Chapter 4.1.1.2 (compare Table 4.2 and A-Table 3). Abbreviations of vegetation types are given in Table 3.2.

Species group	SB	SM	ST	SW	WI	WU	WA	Number of species in relevé plots	Number of species in gap plots
1	X							13	1
2	X	X						12	2
3	X	X	X	X				13	7
4	X	X	X	X	X	X	X	18	15
5		X	X	X	X	X	X	14	12
6		X	X	X	X	X		8	6
7		X	X	X	X			5	4
8			X	X	X	X	X	34	28
9			X	X	X	X		7	4
10			X	X	X			22	17
11			X	X				6	3
12				X	X	X	X	14	9
13				X	X	X		7	3
14				X	X			5	5
15				X				4	2
16					X	X	X	14	9

4.6.2 Species data of the herb layer

Concerning species data of the herb layer, in Chapter 4.1.1.2 16 species groups were identified for the different vegetation types (Table 4.2). Gap plots had only three species in common with the first two species groups representing species of the *Bas fonds* (*SB*, *SM*, Table 4.9). For all other species groups, a high overlap of species occurred. This indicates for presence-absence data, that the gap plots are similar to all vegetation types except those of the *Bas fonds*. However, regarding also the cover data for single species, differences were more evident. For example, *Cassia mimosoides* (species group 4 in Table 4.9) occurred in all vegetation types but showed much higher cover-values in gap plots than in relevé plots. *Aframomum alboviolaceum* (Species group 8 in Table 4.9) showed high cover-values especially in *SW* and *WI*. This species was present in gap plots but only with low cover-values. *Andropogon tectorum* (Species group 12 in Table 4.9) that was found with high abundances especially in woodlands plots also occurred frequently in gap plots but with low cover-values. Overall 21 species were found exclusively in the gap plots, 14 species with one occurrence, four species with two occurrences and three species occurring in three gap plots.

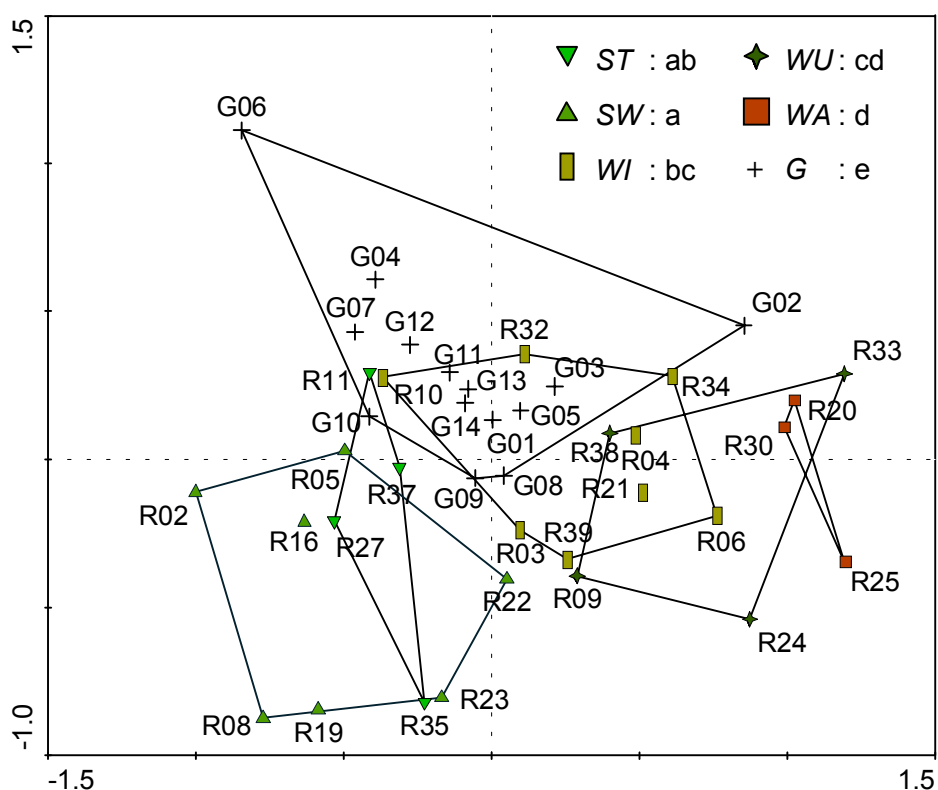


Fig. 4.22. Sample scores of the first and second *DCA*-axes based on species cover in the herb layer of the gap plots (G) and relevé plots without *Bas fonds* plots. Relevé plots are marked according to vegetation types; abbreviations are given in Table 3.2. The first and second *DCA*-axes explained 10.3% and 6.5% of floristic variability, respectively. Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

Also by means of pairwise comparison, no difference was found between the two groups of gap plots of different age. Thus, as gap plots of different ages could not be separated, they were treated as one group. Pairwise comparison for the herb layer of gap and relevé plots revealed that the gap plots differed significantly from all other relevé plots (Fig. 4.22). Despite their significant difference, gap plots showed the largest overlap with *WI* in the *DCA*-diagrams, presented here for the vegetation types without the *Bas fonds* plots (*SB* and *SM*, Fig. 4.22).

4.6.3 Seedlings and saplings of woody species

The number of species and the density for both seedlings and saplings of woody species recorded for the relevé and gap plots from 2001 to 2004 are given in Fig. 4.23 A-D. Clear differences between years as well as between vegetation types were observed for these two parameters. In general, species numbers of seedlings and saplings increased from *Bas fonds* plots to woodland plots. Gap plots showed a medium position (Fig. 4.23 A-D). Comparing the four studied years, the number of species counted for seedlings was high in 2001, medium in 2002 and low in 2003 and 2004 (Fig. 4.23 A). This pattern occurred in all vegetation types and in the gap plots. Also the density of seedlings mostly followed this pattern (Fig. 4.23 C). For saplings, however, maximal values for the number of species and the density of individuals was found in 2002 (Fig. 4.23 B and D).

The density of seedlings and saplings of the three dominant tree species of the woodlands, *Isobertinia doka*, *Uapaca togoensis*, and *Anogeissus leiocarpus*, are shown in Fig. 4.23 E-J. *U. togoensis*, and *A. leiocarpus* were characterized by a high density of seedlings with a maximum in the respective woodland type (*WU*, *WA*) and a low density of saplings (Fig. 4.23 G-J). This indicates a high seedling-mortality rate for these two species. Contrary, for *I. doka* both seedlings and saplings were found with a similar density indicating a low seedling-mortality rate. For this species, the highest density of saplings occurred in the gap plots in 2002 with a high density of seedlings in the previous year. In addition, saplings of *I. doka* and *U. togoensis* were neither found in *SB* nor in *WA* plots.

Pterocarpus erinaceus (Fig. 4.24 A and B) and *Daniellia oliveri* (Fig. 4.24 C and D) represent tree species regenerated in the gap plots and in all vegetation types, except *SB*. With respect to the density of saplings, they showed clear differences, with high densities in *ST* and *SW* for *P. erinaceus* and high densities in *SM* and *WA* for *D. oliveri* (Fig. 4.24 A-D). *Terminalia macroptera* (Fig. 4.24 E and F) is a typical species of the *Bas fonds* (*SB*, *SM*) that also showed there its highest density. For *Pteleopsis suberosa* (Fig. 4.24 G and H), high densities of saplings were found in savanna plots (*SM*, *ST*, *SW*), and seedlings and saplings of *Uvaria chamae* (Fig. 4.24 I and J) mainly occurred in *WU* and *WA*.

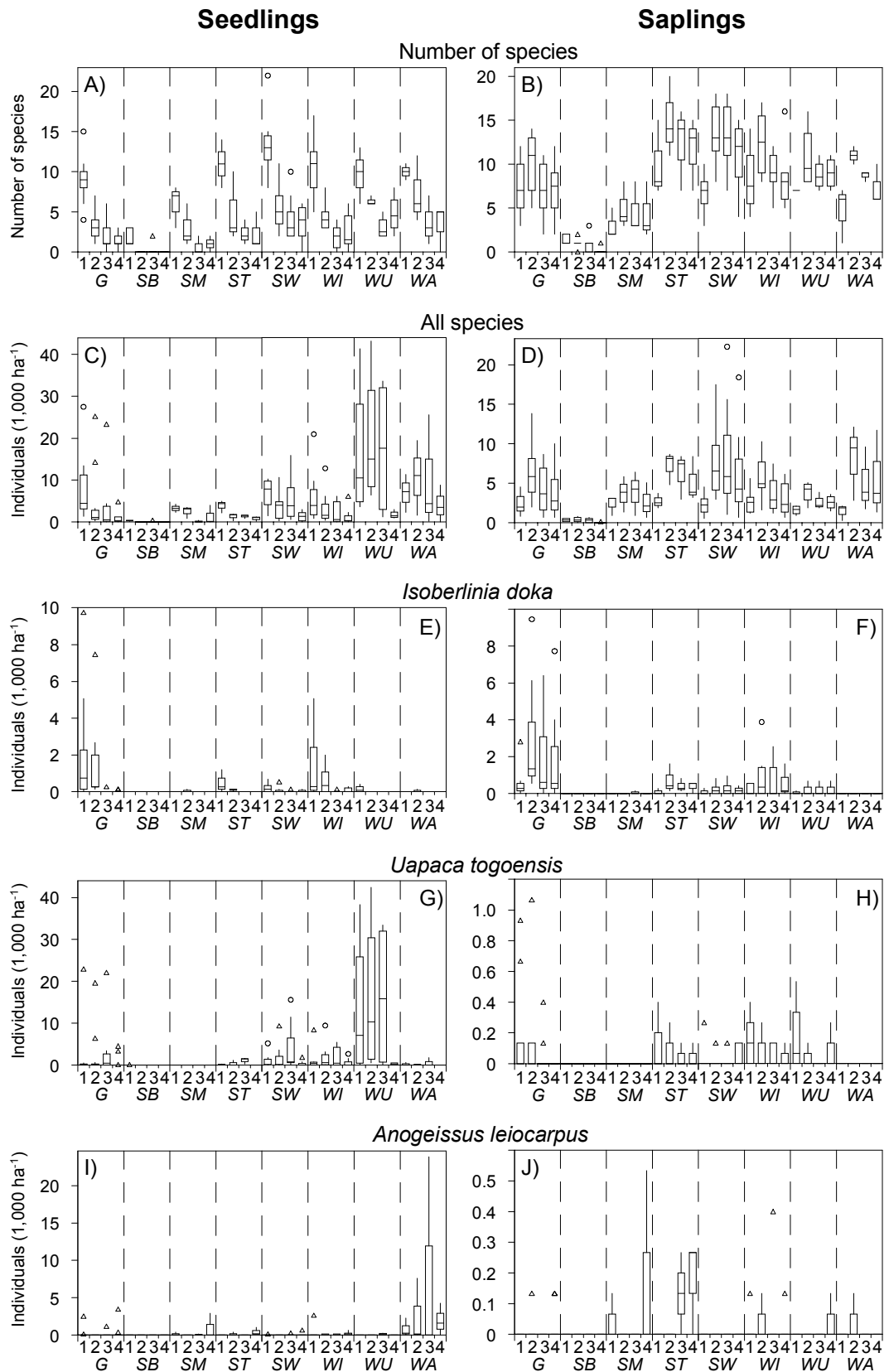


Fig. 4.23. Species number of seedlings and saplings of woody species (A, B), density of seedlings and saplings for all woody species (C, D), and density of seedlings and saplings for the three dominant tree species of the woodlands (E-J) sampled during four years (1 = 2001; 2 = 2002; 3 = 2003; 4 = 2004) in gap plots (G) and plots of the different vegetation types. Abbreviation of vegetation types are given in Table 3.2.

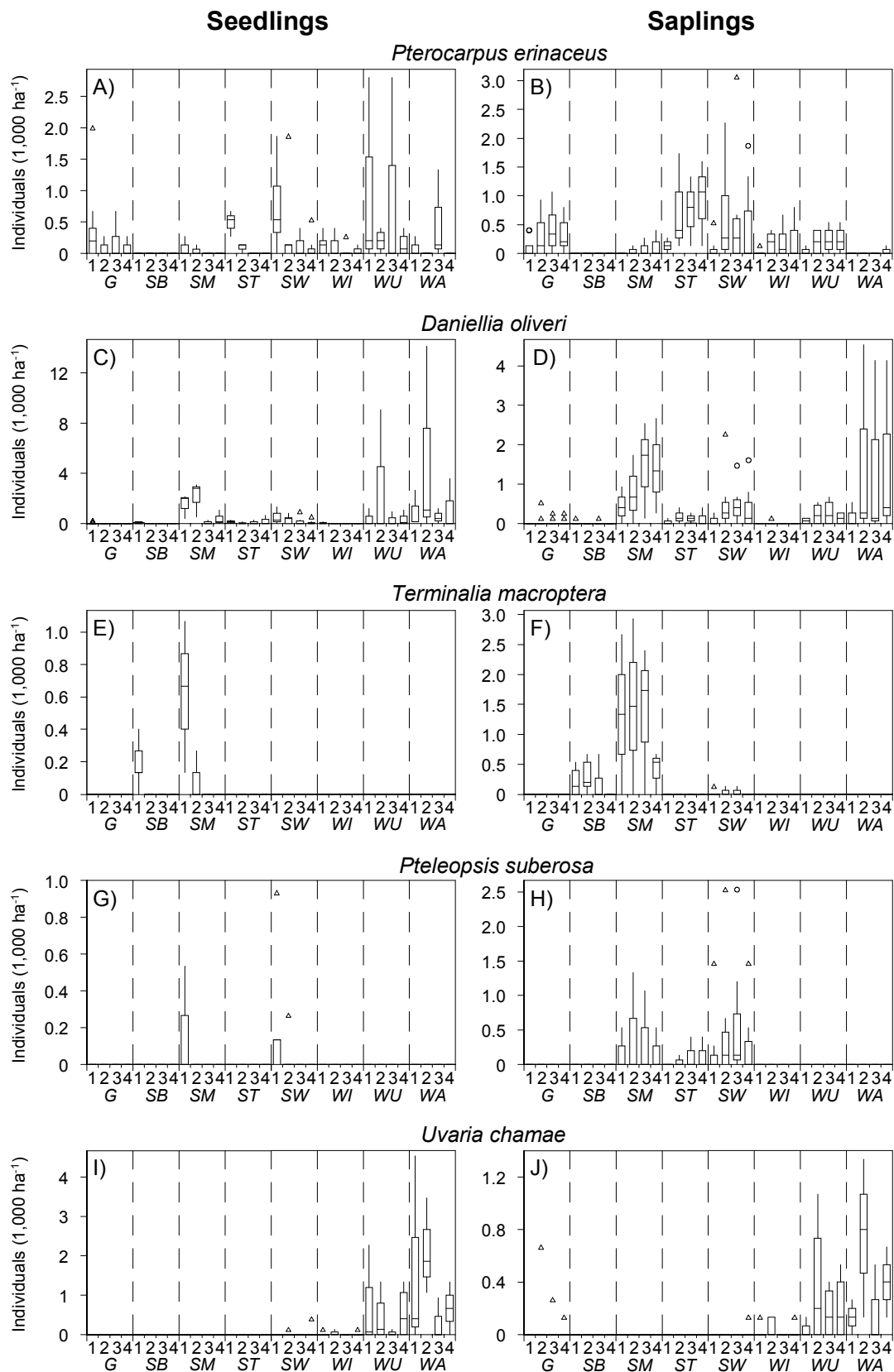


Fig. 4.24. Density of seedlings and saplings for selected woody species sampled during four years (1 = 2001; 2 = 2002; 3 = 2003; 4 = 2004) in gap plots (G) and plots of the different vegetation types. Abbreviation of vegetation types are given in Table 3.2.

Comparison between the species composition of gap plots with those of the different vegetation types was carried out with Principal Response Curves analysis (*PRC*) in order to consider the time-series aspect of the data (Fig. 4.25). For illustration, data of the gap plots were defined as base line and data of the different vegetation types are given in relation to this base line (Fig. 4.25 A and C). With regard to the species composition of seedlings, all vegetation types differed significantly from the gap plots, except *ST* and *WI*, computed by pairwise comparison between each vegetation type and the gap plots by means of *PRC*. This is illustrated in the plots as these two vegetation types were plotted near the base line in Fig. 4.25 A. Species scores of the first axis (Fig. 4.25 B) reveal that this axis was strongly influenced by the species already presented in detail in Fig. 4.23 and Fig. 4.24. Especially *Uapaca togoensis* was of importance due to absolute species scores. For the species composition of saplings, all vegetation types differed significantly from the gap plots without exception, but again *ST* and *WI* were most similar to the gap plots (Fig. 4.25 C). Concerning the species scores of the first axis (Fig. 4.25 D), species such as *I. doka*, *T. macroptera* and *D. oliveri* expanded the first *PRC*-axis most strongly. In contrast to the *PRC* of the seedlings (Fig. 4.25 B), *U. togoensis* and *A. leiocarpus* showed an intermediate position on the first *PRC*-axis, whereas species such as *Vitellaria paradoxa*, *Trichilia emetica*, *Pseudocedrela kotschyi*, *Pterocarpus erinaceus*, and *Parinari curatellifolia* were of importance (Fig. 4.25 D).

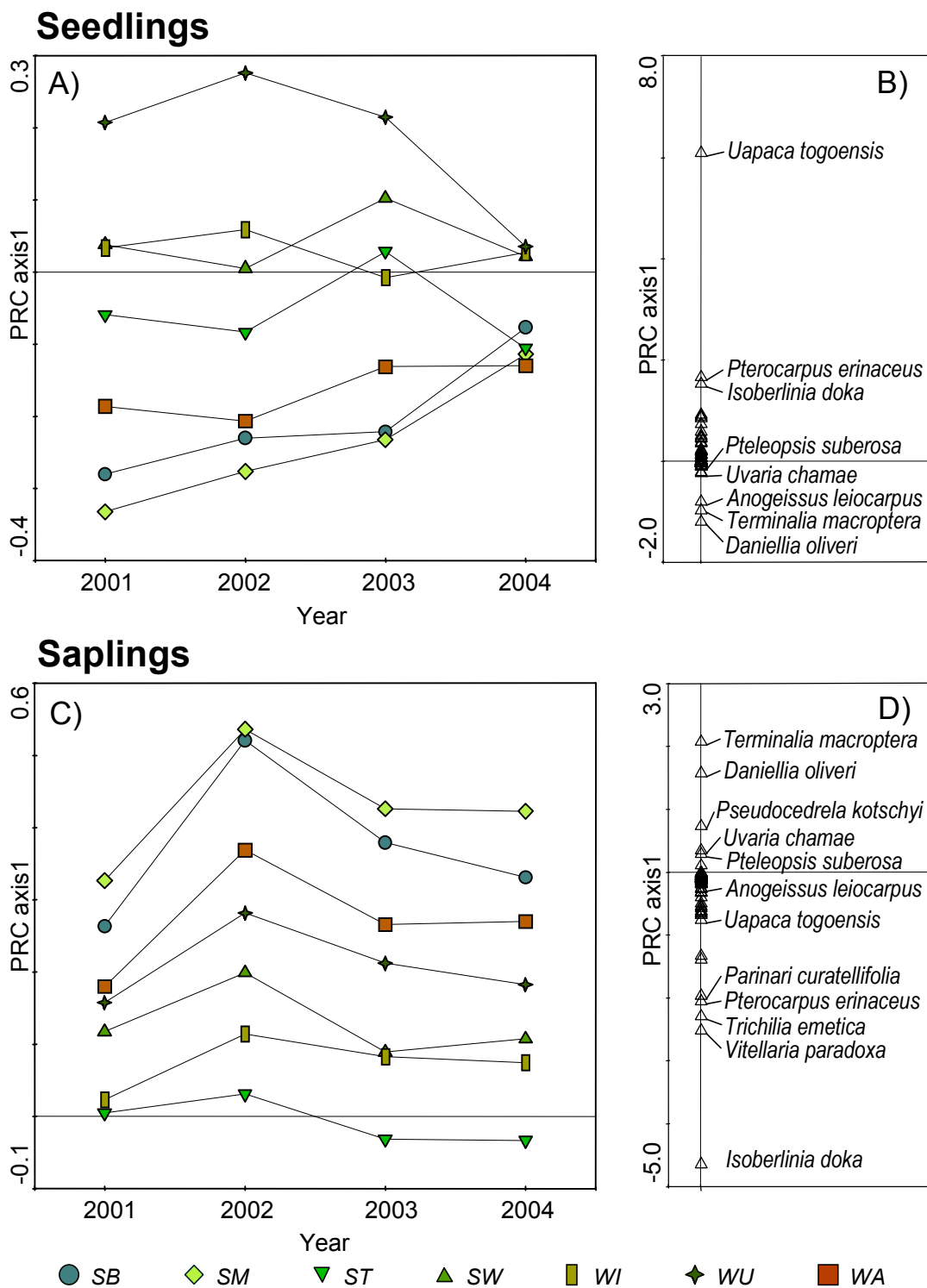


Fig. 4.25. Comparison between species composition of seedlings (A, B) and saplings (C, D) of woody species by means of principal response curves analysis (PRC) for four years (2001-2004) sampled in gap plots and different vegetation types. Sample scores of the first PRC-axis are given in panel A) and C). Panel B) and D) show the respective species scores of the first PRC-axis. The base lines in panel A) and C) represented by gap plots. Abbreviation of vegetation types are given in Table 3.2. In addition, each PRC was carried out for gap plots and plots of each single vegetation type to test for significant differences. For seedlings, all vegetation types differed significantly ($P < 0.05$) from the gap plots except *ST* and *WI*. For saplings, all vegetation types differed significantly ($P < 0.05$) from the gap plots without exception.

5 Discussion

5.1 Classification of vegetation types and floristic characteristics

Classification of species data of the tree and herb layer sampled at the study area revealed a clear gradual species turnover from open savannas in the *Bas fonds* to woodlands. Two ordination approaches of the tree and herb layer data were carried out. The first approach was based on the physiognomic categories of Yangambi (CSA 1956) extended by a separation of zonal and azonal sites and a subdivision of woodlands by dominant tree species. In the second approach, vegetation data were classified according to phytosociological criteria. Significant differences between groups occurred for both ordination approaches. However, for both the tree and especially the herb layer the classification based on phytosociological criteria revealed more distinct groups of relevé plots. This was additionally confirmed by multivariate data analysis. Though phytosociological groups were more distinct, it was also possible to relate physiognomic characteristics to species composition.

Menaut (1983) suggested that for an overall comparability and comprehensibility it would be very useful to apply the Yangambi categories for an overall stratification, and then to apply detailed phytosociological classification within each of the Yangambi categories. This was first done by Langdale-Brown (1959-60 cited in Menaut 1983), and also successfully applied e.g. in central Ivory Coast by César (1992), in north-eastern Ivory Coast by Poilecot *et al.* (1991), and in the northern Benin by Reiff (1998). This led to relations of physiognomic vegetation types with floristic characteristics for specific regions. Vice versa, Adjanohoun (1964), Schmidt (1973) and Spichiger (1975) were able to relate phytosociological units to characteristic physiognomic features for savannas in the Guinea zone (Ivory Coast). These examples together with this study indicate that on a local to regional scale, a relation between floristic and physiognomic features can be established.

In this context, some important aspects have to be considered. For example, grass savannas (according to Yangambi) can be found on shallow soils with limited water supply as well as in depressions with temporarily stagnant water (e.g. Schmidt 1973). The establishment of trees is limited in both cases leading to a similar physiognomic structure, but profoundly different species composition. The necessity to differentiate these two azonal sites appears evident. In this study, the extension of the physiognomic Yangambi criteria by differentiating azonal sites in the *Bas fonds* and zonal sites outside of the *Bas fonds* proved to be floristically meaningful. Therefore, the differentiation of zonal and azonal sites within the Yangambi classification should improve its applicability. The subdivision of the woodland formation

according to the three dominant tree species (*Isoberlinia doka*, *Uapaca togoensis* and *Anogeissus leiocarpus*) proved to be reasonable and revealed significant different species composition. A differentiation of *Isoberlinia* and *Uapaca* dominated woodlands is also described by Houinato (2001) and *Anogeissus* dominated woodland and forests are known over wide regions (Sobey 1978, Hahn 1996, Neumann & Müller-Haude 1999, Hennenberg 2005 *unpublished dissertation*). Nevertheless, the three studied woodland types are more similar to each other than to the other structural vegetation types. Thus, the subdivision according to dominating species distinguishes on a finer scale than the strict physiognomic classification, but the coarse scale of the Yangambi categories is also meaningful with respect to species composition.

In this study, classification of the tree layer data revealed less distinct groups than the classification of the herb layer data. This is not surprising as Hall & Jenik (1968) pointed out that West African tree species are not useful as solitary criteria for floristic classification approaches as their overall species number is low and most species show both a wide distribution range and a large ecological amplitude. Floristic blocks of the tree layer classified by phytosociological criteria coincide with the floristic blocks of the herb layer mainly for the *Bas fonds* plots and the open savannas. For the more dense savannas and woodlands, tree species did not differentiate much and therefore do not coincide with the classification of herb layer. However, an independence of herb and tree layer especially for intermediate sites which are neither open savannas nor dense forests as thoroughly discussed by Menaut (1983) and Hahn (1996), can not be confirmed for the study site. This might be due to the local scale, but also Houinato (2001) found on a larger scale in proximity to the study area of the present thesis a good agreement of floristic tree and herb layer classification.

In summary, it can be stated that it is possible in the studied area to link physiognomic characteristics with vegetation composition on a local to regional scale, if azonal sites and zonal sites are distinguished. Nevertheless, such relation can only be expected, if processes are absent that uncouple structure and species composition. Crop cultivation followed by fallows is a frequently occurring process in West Africa. Young fallows, for examples, must be classified after the physiognomic Yangambi categories as shrub savannas, but they differ to a great extent in their species composition from undisturbed shrub savannas.

In order to elaborate vegetation and land-cover maps by means of remote sensing techniques, physiognomic classification of vegetation is of great advantage as a matter of its general compatibility with remote sensing data, despite the general problem of small-scale patchy distribution of vegetation types. However, to parameterise these classes with information on ecological and floristic properties as well as with information on land use, a strict physiognomic approach is by far not sufficient. In order to distinguish azonal and zonal sites as well as fallows and arable land, multitemporal approaches are frequently applied (Reed *et al.* 1994, Hahn-Hadjal & Schmid 1999, Schmid 1999). These demand detailed knowledge e.g.

on phenological characteristics of vegetation but seem to be challenging (Mistry 2000b, Roehrig *et al.* 2005). The possibility to link physiognomic vegetation types with species composition – as shown in this study and those cited above – suggests that also floristic information may be incorporated in remote sensing maps. However, much further research will be needed in order to increase the quantity and quality of ground data as well as the knowledge of ecological processes. Despite of its intrinsic value, the elaboration of a phytosociological system of West Africa – in combination with the comparison of such a system with a physiognomic classification – would also be of much help in this context. On the one hand, a phytosociological system would facilitate the categorization of results of local studies. On the other hand, a phytosociological system could help to interpret classes in remote sensing maps and could especially improve the set up of knowledge based decision trees for remote sensing algorithms.

5.2 Structural characteristics of vegetation types

Tree data

The parameters woody biomass, tree cover, and composition of tree-size classes revealed a gradual change from open savannas to woodlands. Woody biomass ranged from about 90 t ha⁻¹ for the woodlands and about 40 t ha⁻¹ for the savanna types *SM*, *ST*, and *SW* to below 10 t ha⁻¹ for the open savanna in the *Bas fond*. The same tendency was found for tree cover with high values in the woodlands (about 70%) and low values in the *Bas fonds* (below 10%). Tree-size class-composition concerning height classes showed much more distinct groups than classification based on diameter classes. In general, woodlands were characterized by a higher total number of individuals than the savannas. In savannas (*SB*, *SM*, *ST*), mostly less than 200 individuals with a diameter larger than 10 cm dbh were counted per hectare. For woodlands and the wooded savanna, this value was about 350 individuals ha⁻¹. In addition, tree-size class composition of woodlands showed a higher number of larger tree individuals for both height and diameter classes than savannas.

In West Africa, detailed analysis of tree-size classes and biomass were frequently carried out in closed and mainly in moist forests formations (Ghana: Hall & Swaine 1981, Lawson 1986, Swaine *et al.* 1987, Swaine *et al.* 1990; Liberia and Ivory Coast: van Rompaey 1993 and national forest inventories cited in Bongers *et al.* 1999; Benin: Nansen *et al.* 2001, Sokpon *et al.* 2001). In contrast, for savannas and woodlands such data are sparse. However, for woodlands, Monnier (1981) and Menaut *et al.* (1995) integrated several data collected in West Africa. For tree density, Monnier (1981) presented values of about 250 individuals ha⁻¹ for woodlands in northern Ivory Coast. With regard to woody above-ground biomass, Menaut *et al.* (1995) estimated a value of 100 t ha⁻¹ for West African woodlands. Monnier (1981, northern Ivory Coast) gave a value of 92 t ha⁻¹.

With respect to savannas, Keay (1949) measured for trees larger 10 cm dbh values from 62 to 185 individuals ha^{-1} for different savanna types in the Sudanian zone of Nigeria. Hennenberg (*unpublished data*, compare Hennenberg *et al.* 2005) counted for the same size class about 110 individuals ha^{-1} for a tree savannas in the Comoé National Park in northeastern Ivory Coast. Lawson *et al.* (1956) measured in the Mole game reserve in northwestern Ghana for a wooded savanna a mean tree density of about 300 individuals ha^{-1} larger 10 cm dbh. Monnier (1981) found 80 to 350 and 250 to 400 individuals ha^{-1} for Guinea and Sudanian savannas, where woody biomass values were given to be about 30 and 10 t ha^{-1} , respectively.

In addition, the subdivision of tree-size classes is very inconsistent and often the derivation of tree densities is impossible from existing studies. For example, Couteron & Kokou (1997) counted all tree individuals larger 1.5 m in height, Hovestadt (1997) measured the density of trees larger 2 m and shrubs larger 1 m in height, Sobey (1978) included only selected species, and PAMF (1996) focused on valuable timber species for presentation. Even though each of the mentioned studies is of high value of its own, the necessity to establish standardized tree inventories for savannas and woodlands in West Africa is to be stressed to enhance comparability of individual studies. The absence of these inventories might be a result of higher commercial values found in closed forest formations based on timber exploitation than in savannas and woodlands (compare Brown & Gaston 1996).

However, the cited values are of the same orders of magnitude as those measured in the present study indicating an overall comparability of the studied savannas and woodlands with those in other areas of the Sudanian and Guinea zone in West Africa. The presented structural data of woody species for different vegetation types, however, contribute and help to complete the low number of existing data. These data are additionally valuable, e.g. for the interpretation of remote sensing data, as key parameters for meteorological and hydrological modelling, and especially as a base for the development of forest management plans. In addition, the applied vegetation types, that are primarily based on the physiognomic Yangambi categories, proved to be well related to structural parameters of the tree layer as recorded in this thesis. The most differentiating parameters have been the distribution of height classes of trees and tree cover.

Herb data

Biomass of grasses was highest in the *Bas fonds* with mean values of 8 t ha^{-1} and maximum values of about 12 t ha^{-1} (*SB*-plots). In contrast, in the woodlands about 2 t ha^{-1} of grass biomass were measured. Both, the biomass of herbs and litter were very low in the open savannas ($< 0.5 \text{ t ha}^{-1}$), but for the woodlands, these fractions were in the same range as the grass biomass.

In contrast to the low number of studies on woody biomass of savannas and woodlands and due to the importance of herb biomass as pasture, many studies deal with biomass of the herb

layer of these vegetation types in West Africa, especially in Ivory Coast and Burkina Faso. Biomass values for the herb layer range from about 2 t ha⁻¹ in woodlands to 14 t ha⁻¹ in grass savannas in depressions (Menaut & César 1979, 1982, Villecourt *et al.* 1979, 1980, César 1981, 1992, Monnier 1981, Fournier 1983, Menaut *et al.* 1987, 1991, 1995). From studies on the pasture value of different vegetation types in central-eastern Benin near Parakou (Ferme d'Elevage de l'Okpara), Sinsin (2003) gives biomass values of the herb layer for *Bas fonds* of 7.0 and 7.9 t ha⁻¹ for 2001 and 2002, respectively. These values measured for the same years as those of the present thesis are in the same order of the data presented here. Similar values of 7.2 and 6.2 t ha⁻¹ in 1996 and 1997 were also measured by Houinato (2001) for *Bas fonds* in central-western Benin (region of Monts Kouffé). For savannas similar to *ST* and *SW*, Sinsin (2003) found 4.8 and 4.3 t ha⁻¹ in 2001 and 2002. These values were similar to the studied *ST* plots of this study with about 4.2 t ha⁻¹ in 2001, but *ST* plots in 2002 (about 3.4 t ha⁻¹) and *SW* plots in 2001 and 2002 (about 2.3 and 3.4 t ha⁻¹) showed lower biomass values of the herb layer. This difference can be explained by grazing impact that was not excluded in this study but in Sinsin (2003). For an *Isoberlinia* dominated woodland, Sinsin (2003) gives biomass values for the herb layer of 4.5 and 3.1 t ha⁻¹ (2001/2002, no grazing impact), and Houinato (2001) measured for a woodland dominated by *Isoberlinia doka* and *Uapaca togoensis* a herb biomass of 3.2 t ha⁻¹ (low grazing impact). Again, the values are in the same order as those measured in the Aguima catchment for comparable vegetation types. In northern Benin (Péhunco near Natitingou), Sturm (1993) measured in 1990 biomass values of the herb layer of 6.4 t ha⁻¹ for grass savannas in depressions, 2.9 t ha⁻¹ for tree savannas, 1.7 t ha⁻¹ for wooded savannas, and 1.8 t ha⁻¹ for woodlands. These values are in general lower as those mentioned above which might have been caused by the low annual rainfall of 995 mm in 1990 (see discussion below). In total, it can be concluded that the biomass values of the herb layer measured in the Aguima catchment are representative for central Benin and comparable to those of the southern Sudanian and Guinean zone in West Africa.

Annual litter data are quite sparse again. Devineau (1982) gives values from 4.7 to 6.8 t ha⁻¹ for annual leaf litter fall for different forest formations from Guinea to Sudanian zone. The biomass of litter of the studied woodlands was dominated by leaf litter and took values of about 2 t ha⁻¹, whereas grass litter was dominant in the savannas. As additional leaf fall occurred after the date of sampling at the beginning of the dry season these values are underestimated. Hennenberg (2005 *unpublished dissertation*) found in savanna and forest system in northern Ivory Coast a doubling of the leaf litter fraction from the end of the rainy season to the end of the dry season.

Considering all studied plots, the transfer of structural data (cover, height and volume), from small plots (1 m x 1 m) to larger ones (5 m x 15 m) proved to be satisfying for grasses, but limited for herbs and litter. The main reason for the latter might be the rather sparse and heterogeneous occurrence of herbs and litter. Correlation analyses between structural

parameters and biomass values (1 m x 1 m plots) revealed strong correlations, again especially with respect to grasses (mass of grasses versus volume of grasses: $r > 0.9$). Also Fournier (1991) and Hennenberg (2005 *unpublished dissertation*) found that the maximum grass height was strongly correlated with grass biomass. Thus, such correlations may be used in future studies to reduce the labour required for sampling, as measuring structural parameters is less time consuming than measuring biomass.

Interannual differences between the two measured years for the three considered biomass fractions of the herb layer were rather low. This is probably a result of similar rain fall regimes in the two studied years (see Chapter 2.1). However, differences in rainfall can lead to strong differences in biomass production of the herb layer in savannas and woodlands (César 1992, Sturm 1993, van de Vijver 1999). For the example of a grass savanna on shallow soil in Péhunco (northern Benin), Sturm (1993) measured for a year of low rainfall (995 mm a⁻¹) a herb biomass of 3.5 t ha⁻¹, whereas in the following year with a high annual rainfall (1,484 mm) this value was 5.9 t ha⁻¹. Le Houérou *et al.* (1988) found a good relation for variability of annual precipitation to herbaceous biomass production on a global level. Nevertheless, annual biomass production appears to be much more variable than variability in the sum of annual rainfall. César (1981, 1992) pointed out in regional studies, that the variation of the biomass production of the herb layer in the Sudanian Zone is much better correlated with the duration of the rainy season than with the sum of annual rainfall. In the Guinea zone sum of rainfall during the second peak of rainy season correlated best (César 1981, 1992).

Not only annual rainfall but a complex interaction of biotic and abiotic parameters has influence on the herb biomass at one site. Especially competition of trees and grasses for resources (e.g. light, nutrients, and soil water) is of high importance (Walker & Noy-Meir 1982, Scholes & Archer 1997, Higgins *et al.* 2000). A negative relation between tree cover and herb biomass has often been described (review in Scholes & Archer 1997). For the Sudanian zone, Fournier (1987), César (1992) and Sturm (1993) found a threshold value of about 25% tree cover to strongly reduce grass biomass production, whereas César (1992) revealed 40% tree cover for the Guinea zone. In this study, a significant decrease in grass biomass compared to the open savanna sites in the *Bas fonds* occurred for *ST* plots that were characterized by a tree cover of about 20%. Beside light conditions, patterns of nutrient availability and water supply are to be discussed with respect to herb biomass. For the Sahel and the Sudanian zone, Breman & de Wit (1983) found a strong increase in herb biomass due to fertilization. Such effect, however, was much lower in the Guinea zone (César 1992). Data of Menaut & César (1982) and Sturm (1993) indicate the effect of water availability on herb biomass. Especially the relation of nutrient availability and water supply with topography may play a role for the densities of grasses and trees in the studied system. This aspect will be stressed in the following chapter.

5.3 Environmental parameters and vegetation

5.3.1 Vegetation types

In the present study, a wide number of different environmental parameters were recorded. For most of these parameters, significant differences were found between the applied vegetation types that are in first order based on the physiognomic Yangambi categories.

Microclimate

Especially microclimatic parameters such as visible sky (*VS*) and vapour pressure deficit (*VPD*) revealed clear gradual and significant differences from open savannas to woodlands. The general course of microclimate was, of course, driven by macroclimate. Open sites were influenced by higher insolation and extremer conditions for air temperature (*T*), humidity (*H*) and vapour pressure deficit (*VPD*) than closed sites. Microclimatic conditions were found to be strongly correlated with tree cover. During the rainy season microclimate differed to a greater extent between vegetation types than during the dry season.

The effect of tree cover on insolation and in consequence on microclimate is well known in ecology and was described, e.g. on a regional scale in Zaïre for a gradient from dry forest over woodland to savanna by Freson *et al.* (1974), and on a local scale in Kenya from forest over savanna to grassland (Belsky & Amundson 1992). Studies on microclimate on a local scale are rare for West Africa and do not focus on the comparison of vegetation types (e.g. Lawson *et al.* 1956, 1970, Hopkins 1965b). Lawson *et al.* (1970) pointed out, that microclimate mostly affects species of the lower strata such as herbs, grasses and seedlings and saplings of trees. With regards to tree individuals of the upper strata, microclimatic conditions – measured in a height of 1.3 m above the ground – must be interpreted rather as the cause of those conditions than being influenced by them.

Soil parameters and topographical position

In contrast, to microclimatic parameters, other parameters such as soil parameters can be assumed to be much more and relative topographic height (*TopH*) to be completely independent from tree cover. Also for these parameters significant differences were found from open savannas in the *Bas fonds* to woodlands. These differences were less pronounced than those for microclimatic parameters. Soil conditions of the study area were in general rather similar. For physical soil properties, significant differences between vegetation types occurred, but not gradually along the vegetation types. Chemical soil parameters showed slight gradual differences between vegetation types with most pronounced changes between open savannas in the *Bas fonds* and savannas and woodlands on the slopes. With respect to relative topographic height, vegetation types also showed a gradual change with open savannas located at the deepest position in the *Bas fonds* and woodlands on the upper slopes.

The overall similarity of soil parameters in the study area was also stressed by Junge (2004) for the study region and is confirmed for many other regions in West African savanna systems (e.g. Menaut & César 1982, Hahn 1996). Menaut & César (1982) pointed out, that with regards to chemical properties, seasonal variations are often higher than spatial differences. Junge (2004) based her classification of soil types of the study region on the topographic position and differences were found for both chemical and physical soil parameters. Ground water influence in the depression was the most differentiating factor for all soil types considered in the present thesis (Junge 2004). Along the topographical gradient, long-term erosion as well as lateral transport of fine material due to water flow led to a gradual differentiation of soil types resulting, e.g. in less profound soil profiles on hilltops or in elevated potassium and sodium concentration in the *Bas fonds* (Junge 2004). Similar differentiation of soil types along topographical gradients were found in many other West African regions in the Sudanian and Guinea zone (e.g. Faust 1989, Swoboda 1992) and vegetation types were described to occur along these gradients (Aubréville 1965, Schmidt 1973, Spichiger 1975, Menaut & César 1982, Fournier 1991, Menaut *et al.* 1995, Devineau *et al.* 1997, Diatta *et al.* 1998, Devineau 2001). Comparable toposesquences were also mentioned, e.g. the miombo vegetation in southern Africa (Chidumayo 1997) and moist forests in West Africa (van Rompaey 1993).

The topographic gradient at the study site can be characterized overall by a clay/sand opposition, a gradient in exchangeable cation richness and in hydric conditions (compare Devineau 2001). Soil texture at the study site is rather homogeneous with slightly elevated clay and silt contents in the *Bas fonds*. Nevertheless, the sum of basic cations as well as pH and C/N ratio showed a gradual decrease from the hilltop where the woodlands are situated into the depression with open savannas. This and the strong correlations of soil parameters with each other stresses the interdependence of physical and chemical soil properties due to the described processes which led to the topographic gradient.

Termite mounds, fire and grazing

The edaphic topographic gradient can be strongly influenced by termite activity which might superimpose the strict gradual change from hilltop to depression. With the exception of the ground water influenced sites in the *Bas fonds*, termite mounds are evenly dispersed at the study site (Junge 2004). The influence of termite activity on chemical and physical soil properties leading to microsites differing from the overall edaphic properties is described by many authors (Trapnell *et al.* 1976, Montgomery & Askew 1983, Swoboda 1992, Menaut *et al.* 1995, Korb 1997, Konaté *et al.* 1999, Bloesch 2002). Junge (2004) found that the influence of termite mounds on soil profiles at the study site led to a transport of clay to upper horizons, to a base saturation near 100%, and to the only occurrences of carbonate in the soil at the study region. Despite the patchy distribution of termite mounds, an overall accordance

of vegetation type with topographic position and edaphic parameters was observed in the present thesis.

Beside termite activity, also fire and grazing may cause patchiness of vegetation (Backéus 1992, Binkley *et al.* 1993, Christensen 1993, van Langevelde *et al.* 2003). The occurrence of both fire and grazing is nowadays mainly driven by humans (Menaut *et al.* 1991, Goldammer 1993b, Dwyer *et al.* 1998, Roberts 2000). Hunters and herdsmen frequently light fires and herdsmen conduct their cattle herds to attractive pastures. This led to an intense discussion whether savannas and woodlands evolved exclusively under human influence and if the exclusion of human-made fires and grazing would bring back the dominance of natural forests in the Sudanian and Guinea zone (Keay 1959b, Walter 1971, Knapp 1973, Anhuf & Frankenberg 1991, Anhuf 1994, 1997). Many authors reject this view because fires also occurred without the impact of humans, and today's impact of cattle herds substitute former impact of large herbivores though frequency, spatial patterns, and intensity might be different (Gillon 1983, Trollope 1984, Weiss *et al.* 1996, Roberts 2000, Salzmann 2000, Stott 2000, Salzmann *et al.* 2002, Neumann *et al.* 2004).

In the study area, fire is frequently lit by farmers and herdsmen. In 2001 and 2002, fires started in December at already desiccated sites (compare Chapter 2.4.2). The intensity of surface fires in savannas is known to be strongly related to the amount of fuel, but also its moisture content is of importance as well as other factors, e.g. velocity and direction of wind, air humidity and time of the day (Gillon 1983, Goldammer 1993a, 1993b, Whelan 1995, DeBano *et al.* 1998, Stott 2000, van Langevelde *et al.* 2003). Also in the study area, fire temperature was strongly and positively correlated with the amount of biomass of the herb layer. Fire temperature was with 100 to 600 °C in the same range as cited in the review of Ramsey & Rose-Innes (1963) and measured by Hopkins (1965a). The rise in temperature during fire is with four to five minutes very brief and the highest temperatures do not persist for more than a few seconds (Gillon 1983). Higher temperatures and longer burning duration will be achieved by the burning of trunks and other large woody compartments which are frequently found at the study site but which are spatially restricted (Stott 2000, Bloesch 2002). The moisture content of fuel generally declines as the dry season proceeds, resulting in hotter and more uniform late fires, and a more complete combustion (Hopkins 1965a, Afolayan 1978, Gillon 1983, Montgomery & Askew 1983, Trollope 1984, Goldammer 1993b, Grenz 1998, Sinsin & Saidou 1998, Houinato *et al.* 2001). This relation could not be confirmed for the studied plots over all vegetation types, probably due to the high variability in fuel loads in combination with the high man-made stochastic of date of fire.

With regards to the studied vegetation types, open savannas tend to be influenced by higher fire temperatures than woodlands. The date of fire occurrence in the studied plots was quite variable and differed only slightly between vegetation types with a tendency for woodlands and sites in the *Bas fonds* to burn later than other savannas. On the one hand, this might be a

result of the water content of the material and its drying behaviour in dependence to site conditions (compare Gillon 1983, Biddulph & Kellman 1998, Stott 2000). On the other hand, ignition by humans is highly stochastic which may explain the variability of the date of fire. Anderson (1982) stated that the amount of fuel fractions with a high volume-to-area ratio such as grasses and herbs is of importance for the ignition of fires and, thus, for the spread of fires. This might explain the low occurrences of fires in the *Uapaca* dominated woodlands, as the leaves of *Uapaca togoensis* are thick and not easy flammable. Fuls (1992) showed that the spread of fire can be limited by a reduction of grassy biomass. In the latter study, patchy grazing of herbivores led to a patchy occurrence of fire (see also Adler *et al.* 2001). Thus, the high variability of the fire-temperature data in the present thesis may also be a result of the patchiness of grazing.

Grazing intensity – estimated as grazing impact and trampling damage – was rather similar for all vegetation types considered in the present thesis, except plots in the *Bas fonds* that were rarely visited by cattle herds until the date of sampling at the end of the rainy season due to the high water table at these sites. However, grazing intensity was much higher in 2002 than in 2001. This is in accordance with the general increase in cattle density in the study region due to the arrival of many new herds in 2002 (Wotto 2003). The impact of grazing on savanna systems can act both positively and negatively (Jeltsch *et al.* 2000, van Langevelde *et al.* 2003, Neumann *et al.* 2004). In a direct manner plant species that are sensible to grazing and trampling may be reduced in abundance or even eliminated (César 1982, 1992, Sturm 1993, Hahn 1996). Indirectly reduced fire intensity as a result of a reduced herb biomass by grazing (see above) may promote the establishment of fire-sensitive plant species (Scholes & Archer 1997, Neumann *et al.* 2004). Long-term monitoring of the permanent plots installed during the present thesis may clarify the effect of the increase of the grazing intensity in the study area. However, grazing and fire intensity – in interrelationship with herb biomass production – tend to show a gradual change from open savannas in the *Bas fonds* to the woodlands, but this gradient is strongly superimposed by the stochastic occurrence of these two parameters.

5.3.2 Vegetation composition

Above the relation of vegetation types with environmental parameters has been discussed, this chapter will focus on the relation of species composition and environmental parameters, and the power of the latter in order to explain floristic variability.

Environmental parameters

Canonical correspondence analyses (CCA) was carried out for species composition of the herb and the tree layer, both *Bas fonds* plots included and excluded, versus environmental parameters. The applied forward selection procedure (Chapter 3.5.2.2) revealed that for each

dataset only two up to four of the considered environmental parameters had to be included into the models. With respect to the large species number and the low number of environmental parameters considered in each *CCA*, the amount of floristic variability of 20-26% explained by environmental parameters is very high (compare ter Braak & Smilauer 2002, Lepš & Smilauer 2003). Økland (1999) demonstrated that the ratio of constrained to unconstrained total inertia alone is no valuable proof in order to state the degree of explained floristic variability. He suggested that only via comparison of the explained floristic variability from different environmental datasets knowledge can be gained on the response of species data to particular environmental data, what was done in this study (see discussion below). The reason why only a low number of environmental parameters could be significantly included into the models is that many environmental parameters are highly inter-correlated (compare A-Table 8 and 9 in the Appendix). Thus, single parameters included in a *CCA* can be interpreted to represent a group of parameters that explain a similar part of the floristic variability of a data set.

For the data set of the herb layer, visible sky (*VS*), sand fraction (*S*) and magnesium (*Mg*), and grazing impact (*GI-M*) could be significantly included into the model. These parameters may represent microclimatic parameters (*VS* \cong light, temperature, humidity), soil conditions (*S* \cong soil texture and soil moisture s.l.; *Mg* \cong chemical soil properties) and the impact of cattle herds. The parameter visible sky (*VS*), depending directly on tree cover, showed the highest explanation of floristic variability of the species composition of the herb layer. This parameter as well as in a broader sense herb layer composition must be interpreted as a result of tree cover and can neither be the cause for tree layer composition nor for the structural vegetation types. For the tree data sets, also soil parameters explained a large amount of the floristic variability beside the biomass of grasses (*G_{B-M}*) which is strongly related to fire intensity. Thus, especially for the tree, but also for the herb layer, soil parameters were the most important parameters to explain the variability of species composition in the studied savanna and woodland systems.

Sinsin (1993) analysed herb layer data in combination with soil data for savanna formations in Benin and found likewise that the chemical properties showed significant differences between vegetation types, but that the sand-fraction explained highest amounts of floristic variability. This was also confirmed by Sturm (1993) who states that species show a rather indifferent pattern with regards to differences in chemical soil properties. For southwestern Burkina Faso Hahn (1996) found – except for the fine-material richer and therefore nutrient richer soils in the depressions – only slight differences in soil nutrient content and emphasized the role of soil moisture availability, depending mainly on the physical properties. Schmidt (1973) stresses in a study in the Ivory Coast that the occurrences of one vegetation type on soils with different physical properties, either sand-dominated or clay-dominated sites, gives a strong hint on the importance of soil moisture availability. This most important role of soil moisture

availability and its vertical distribution is stressed by many studies for the different savanna regions (Frost *et al.* 1986; Ivory Coast and Burkina Faso: Fournier 1991, Menaut *et al.* 1995, Hahn 1996; Kenya: Ludwig *et al.* 2004).

From both the results of the present thesis and those of the cited studies it can be concluded that water availability as a result of physical soil properties and topographical position is a central parameter for the species composition and vegetation type distribution in West African savannas. Already Morison *et al.* (1948) described the process chain of high soil moisture availability leading to an increased herb biomass production, causing higher fire temperatures which result in elevated mortality rates, especially of young tree individuals. This results in more open vegetation formations, while low soil moisture availability, leads to more closed stands. Such process chains often used to explain the coexistences of trees and grasses in savanna systems (see also reviews: Scholes & Archer 1997, Higgins *et al.* 2000, Jeltsch *et al.* 2000, Sankaran *et al.* 2004) show a high potential to be used to explain species composition of vegetation types in West Africa.

However, the measurement of plant relevant soil-water availability is rather sophisticated and not yet sufficiently solved. The problems range from high measurement uncertainties in times of low soil-water contents to strongly heterogeneous capabilities of species and individuals to deal with water stress (Larcher 2001). At the study site, spatial patchiness of soil moisture content is caused by microrelief, termite activity as well as clufts in the ferricretes which enables a faster water transport from upper soil layers under the ferricrete as well as to preferential pathways for roots. Though Giertz (2004) observed in the study area a general trend in the soil moisture content with lower values in hill tops and higher ones in the *Bas fonds*, she showed that the variability of soil moisture content at the same topographic position can be as high as between different topographic positions. This does not hinder generalizations being of good use in terms of e.g. water-runoff models (Giertz 2004) but it does not lead to reliable and spatially explicit data, relevant for the presence of single plant individuals at particular sites.

Vegetation types versus environmental parameters

Parameters measured on an ordinal or relative scale can usually explain a higher amount of floristic variability than nominal parameters due to the explanation of higher amounts of small-scale variability. But with respect to uncertainties to measure plant-relevant environmental parameters of the studied system as discussed above, nominal parameters that integrate plant-relevant parameters should explain a higher amount of floristic variability than those measured on an ordinal or relative scale. Thus, in the present thesis, the nominal key parameter vegetation type was compared with measured parameters with regard to the amount of explained floristic variability and the amount of shared floristic variability. This was done for groups of parameter that were included into models by the model-selection procedure as

well as for the measured key parameters visible sky and topographical height. Visible sky was strongly related to tree cover and should represent the nominal variable vegetation type on a relative scale. Topographic height was chosen in accordance with its importance in the conceptual vegetation models for savanna systems (e.g. Morison *et al.* 1948, Spichiger 1975, Menaut *et al.* 1995, Scholes & Archer 1997, Higgins *et al.* 2000).

For the herb layer data set, the upper assumption seems to be correct comparing vegetation type (*Vegtyp*) and environmental parameters of the selected model, *VS* and *S*. *Vegtyp* explained a much higher amount of floristic variability than the environmental parameters. In addition, most of the floristic variability explained by the environmental parameters was also explained by *Vegtyp*. In contrast, for the other three approaches (herb layer without *Bas fond* plots, tree layer with and without *Bas fond* plots), a similar amount of the floristic variability was explained by the environmental parameters of the respective selected model and *Vegtyp*. The amount of shared floristic variability between environmental parameters and *Vegtyp* was very low for these three approaches. Thus, the nominal variables vegetation type (*Vegtyp*) and the environmental parameters included into the respective selected models explained different aspects of the floristic variability.

A central point leading to these results might be the dominant gradient of the first axis for the data set of the herb layer (*Bas fonds* included) that comprised 23% of the floristic variability. This gradient is dominated by the abrupt change in species composition from the temporal inundated *Bas fonds* to all other vegetation types. As the included environmental parameters as well as *Vegtyp* followed this gradient, a high amount of the floristic variability was shared between both. For the herb layer data without *Bas fond* plots, no dominating floristic gradient could be found, and environmental parameters and *Vegtyp* were less directed. This is – not at least – a result of the generally high patchiness of savannas and woodlands (Braithwaite 1996). Results concerning the tree layer data without *Bas fonds* may be explained in the same manner. But also for the tree data set *Bas fonds* included, this explanation may be consistent due to the absence of an obvious gradient towards the *Bas fonds* sites.

The analyses for the parameter visible sky (*VS*) revealed that the explained floristic variability for this parameter is always considerably below the explained variability by the nominal parameter *Vegtyp*. Thus, though *VS* is recorded on a higher scale than *Vegtyp*, it is not appropriate to substitute the nominal variable *Vegtyp*. Shared variability between the two parameters was only high for the herb layer data set including *Bas fonds*, and again the dominating gradient of the first axis and the abrupt species turnover along this axis can be cited as explanation.

Topography, a parameter often stressed to be responsible for the distribution of the vegetation in many regions of West Africa (e.g. Aubréville 1965, Schmidt 1973, Spichiger 1975, Fournier 1991, Menaut *et al.* 1995, Devineau 2001, see above), only explained low amounts

of floristic variability and was not suitable to substitute *Vegtyp*. For this parameter, however, it has to be taken into account that it was interpolated from digital elevation model derived from satellite images. Thus, resolution in both height and position was limited and the parameter relative topographic height (*TopH*) has to be considered as rough approximation. As a matter of the high patchiness of parameters related to soil moisture content found in the study area (compare Giertz 2004, Junge 2004) it is questionable if a higher resolution could improve the analysis.

In the present study, measured key parameters *VS* and *TopH* as well as environmental parameters included into selected models were limited to substitute the nominal variable *Vegtyp* and vice versa. Thus the importance to consider both integrating nominal variables and measured environmental parameters as well as their relation has to be stressed in order to explain floristic compositions of West African woodlands and savannas.

5.4 Impact of selective logging on the woodland-savanna mosaic

Environmental parameters and species data of the herb layer

The gap plots, that were included in this study, originated from single logging events in *Isoberlinia doka* woodlands. With respect to environmental parameters and especially for microclimatic parameters, these gap plots appeared to be more similar to wooded savanna (*SW*) and tree savanna (*ST*) than to *Isoberlinia* woodlands (*WI*). This was also true for grass biomass, whereas soil parameters were rather unaffected from gap creation.

In tropical forests, gap creation has immediate impacts on PAR interception, latent and sensible heat fluxes, water stress and plant productivity (Bongers & Popma 1988, Whitmore 1996, Asner *et al.* 2004). Sterck (1997) summarizes for tropical rain forests that closed canopies may intercept 99% of the incident light, whereas the light levels may reach up to 50% in gaps. In the studied *Isoberlinia* woodlands (*WI*), intercepted light was about 75% in undisturbed plots and about 55% after gap creation. Therefore, changes in microclimatic parameters show the same trend as in closed forests but more moderate (compare McGuire *et al.* 2001). Grass biomass production increased, following the pattern of insolation. This might be additionally favoured by reduced competition for soil water due to the absence of the felled tree individual (compare Sawadogo *et al.* 2005), an aspect demonstrated for gaps in moist forests in Ghana (Veenendaal *et al.* 1995).

Species data (composition and abundance) of the herb layer of the gap plots – two and four years after gap creation – differed from all other vegetation types. In the *DCA* diagram (Fig. 4.22, *Bas fonds* excluded), however, species data of gap plots were most similar to those in plots of *Isoberlinia* woodlands (*WI*), though gap creation within *WI* led to significant changes in several environmental parameters, particularly microclimate, towards conditions

typical for *SW* and *ST*. This is not surprising because the establishment of species being characteristic for more open savannas as well as the disappearance of perennial species being present before gap creation may take longer (compare Connell 1989, Costa & Magnusson 2002, 2003, Sawadogo *et al.* 2005). In fact, changes mainly occurred on the level of species abundances, e.g. decrease of cover values for *Andropogon tectorum* and *Aframomum alboviolaceum* in gap plots and increase of cover values for *Cassia mimosoides*. These changes in abundance might be the result of a high phenotypic plasticity of many species as a reaction on the change in environmental parameters (Obot 1988, Ludwig *et al.* 2004, see also Popma & Bongers 1991, Sterck *et al.* 1999, Marod *et al.* 2004). In this context, grass-biomass production – and therefore growth of several grass species that occur in *Isobertinia* woodlands – can be interpreted as an increase of fitness, e.g. due to higher insolation and soil moisture (see Chapter 5.2).

Recruitment of woody species in vegetation types after selective logging

With respect to recruitment of woody species, seedlings and saplings were sampled in all relevé and gap plots from 2001 until 2004. Total species number and density of seedlings differed strongly and simultaneously between the years across all vegetation types and gaps. This showed that some years were in general favourable and others were unfavourable for tree recruitment. In favourable years for recruitment (particularly 2001) characterized by a high species number and density of seedlings, differences between vegetation types and gaps were much more obvious than in the most unfavourable year (2004). Saplings, however, appeared to be mainly influenced by the density of seedlings of the former year. This was especially apparent for the peak of species number and density of saplings in 2002 that followed the respective peaks of seedlings in 2001. In general, it can be assumed that higher recruitment of seedlings should occur in wetter years. However, the pattern found was the inverse. In 2001, when highest seedling recruitment occurred, annual rainfall was lowest. One explanation of this relation could be that lower rainfall would reduce competition between seedlings and e.g. grasses due to reduced grass growth (compare Jeltsch *et al.* 2000, Witkowski & Garner 2000). Also periods of drought are known to be of high importance for the survival of seedlings and saplings (Swaine 1996, Veenendaal *et al.* 1996). Another reason for the observed pattern might be the direct impact of cattle pasture (Sturm 1993, Weber *et al.* 1998, Schwartz & Caro 2003) that strongly increased after 2001 (Wotto 2003). Also the fire regime of the previous year could have strongly influenced the amount of seeds being available for recruitment of seedlings (Gillon 1983). This impact could provoke both, an increase in recruitment due to fire-induced germination, or a decrease in recruitment due to a higher mortality rate in seeds (Gillon 1983, Swaine 1992, Witkowski & Garner 2000). As no information is available on the reaction of the studied species to the above mentioned parameters, detailed studies on single species would be helpful to clarify these aspects (compare Gignoux *et al.* 1997).

Several aspects are known to play an important role in the dynamics of tree establishment in gap plots such as environmental conditions, seed bank, seed input, and the survival of species that already occurred before gap creation (Connell 1989, Garwood 1989, Schupp *et al.* 1989, Lieberman & Li 1992). For tropical forests, Swaine & Whitmore (1988) proposed a classification of tree species in pioneers and non-pioneers. Beside others, a central aspect of this classification is the ability of species to regenerate under full-light conditions (pioneers) or in the shade of a closed canopy (non-pioneers). The dichotomous pioneer/climax framework has often been criticised as simplistic classification (e.g. Martinez-Ramos *et al.* 1989, Agyeman *et al.* 1999, Brokaw & Busing 2000, Baker *et al.* 2003). For the studied woodland-savanna system, this classification is a priori limited as canopy conditions are much more open (compare Chapter 4.3.1, and discussion above). Nevertheless, many species demonstrated clear preferences. For example, *Pterocarpus erinaceus*, *Daniellia oliveri*, and *Terminalia macroptera* regenerated in more open savannas and e.g. *Uapaca togoensis* and *Uvaria chamae* in more closed woodlands. For gap plots, especially the high density of seedlings and sapling of *Isoberlinia doka*, the dominant tree species of the initial vegetation type (*WI*), is to be stressed. This species appeared to regenerate well in the gaps during favourable years (seedlings), and additionally may have the potential to close the stand again due to the high survival rates of saplings. Even though species composition of both seedlings and saplings of the gap plots was similar to *WI* plots, it was also similar to *ST* and *SW* plots. Thus, gap plots may also have the potential to develop towards more open savanna types. Assuming the possibility of multiple pathways of succession, i.e. towards *WI*, *SW*, and *ST*, the question arises which factors favour a particular successional pathway (e.g. Gibson 1996, Łaska 2001). As outlined above, gaps exhibit higher grass-biomass production than the woodland stands and are therefore probably affected by an increase in fire risk and intensity (Sawadogo *et al.* 2005). Though the effect of fire on the recruitment of the species in the studied gaps is not known, a general suppression of trees by frequent and especially late fires is well studied for West Africa (Aubréville 1953, Hopkins 1963, 1965a, Ramsey & Rose-Innes 1963, Afolayan 1978, Swaine *et al.* 1992, Louppe *et al.* 1995, Ola-Adams & Ojo 1999, Houinato *et al.* 2001). Thus, a higher fire risk and intensity would favour the succession towards more open savannas. Succession towards open savannas may also be supported by a high trampling damage by grazers due to an increased mortality rate of seedlings and saplings (compare discussion above). But in contrast, grazing may also reduce the fire risk (see Chapter 5.3.1). However, if the impact of fire and grazers will not increase excessively and disturbance will be restricted to single gaps, the succession towards *Isoberlinia* woodland seems to be the most probable pathway as seed input is still available and soil parameters are hardly influenced by gap creation.

Intensive selective logging and recommendation for management

At the site for the study on intensive selective logging (Fig. 3.1), in total about 7% of the upper tree layer was removed by selective logging. Though this amount clearly exceeded the amount of natural disturbance in forests of approximately 1% (Hartshorn 1990, Jans *et al.* 1993, van der Meer & Bongers 1996), many of the aspects measured in the gap plots in the Upper Aguima catchment – and already discussed above – may be transferable. However, two additional aspects may be of importance. First, distance between logged individuals was often smaller than 60 m what could lead to additive effects with regards to microclimate, insolation as well as related parameters such as grass-biomass production (Popma *et al.* 1988, van der Meer *et al.* 1994). Second, for the tree species of interest, most tree individuals with a size above 45 cm were felled. Thus, recruitment of these species may be strongly limited due to a reduction of seed rain, as all logged species enter their fertile phase with diameters above 45 cm dbh (unpublished data Orthmann). This aspect is strengthened by the absence of a soil seed bank of the logged tree species (unpublished data Orthmann, compare Hall & Swaine 1981, Garwood 1989). However, these two aspects may raise the probability of successional pathways towards more open stands.

With regards to management plans, Hartshorn (1989) proposed the incorporation of insights of ecological gap research in forestry. In accordance with studies from other regions (Hawthorne 1993, Sist *et al.* 2003), it can be concluded from this study, that parent trees with an ecological meaningful minimum diameter must be retained evenly dispersed throughout a stand in order to guarantee seed dispersal and sufficient seed rain. In the study area, this was not respected during the logging history of *Azelia africana* and *Khaya senegalensis*, nowadays reflected by very low densities of young tree individuals of these species. Both species as well as *Pterocarpus erinaceus* are furthermore used by herdsman that cut the young leaves as fodder during the time of fruiting (Sturm 1993, Sieglstetter 2002, Wotto 2003). This aspect leads to an additional decline in available seeds for recruitment and should be taken into account for management plans to avoid conflicts of interest between herdsman and forest management. In addition, Hawthorne (1993) and Sist *et al.* (2003) strongly emphasize the need for further criteria such as a maximum number of tree individuals allowed for cutting, reduced-impact logging practices (minimizing size and connectivity of gaps, avoidance of understorey clearings), and reasonable felling cycles. For the study region, a growth model based on tree-ring analysis of *Isobertinia doka* revealed a cutting cycle of once every 20 years with a minimum logging diameter of 48 cm to be economically reasonable (Schöngart *et al.* unpublished data). Thus, for management plans of selective logging of *Isobertinia doka*, economical and ecological recommendations coincide. A more efficient usage of logged tree individuals, however, could lead to an important reduction of logging requirements in the study area as nowadays only 10% of the logged individual is taken out of the systems as timber boards, whereas about 90% is left as woody debris in the field (compare Abebe &

Holm 2003a, Abebe & Holm 2003b). Nevertheless, apart from these ecological and silvicultural concerns, it has to be stressed that the clarification of land properties is most essential in order to translate into action any management strategies (Doevenspeck 2004).

Summary

Worldwide, mankind is facing the negative repercussions of global change. A main consequence of global change is an increasing shortage of natural resources, especially the resource freshwater, but also a threat to biodiversity. In the Sudanian zone of West Africa, land use change strongly increased during the last 30 years caused by an increase in population due to population growth and immigration as well as the improvement of infrastructure.

Fieldwork was conducted in the Upper Aguima catchment near the village Doguè (Upper Ouémé Valley, central Benin). Here, a woodland-savanna mosaic which is typical for the Sudanian zone in West Africa was studied within the interdisciplinary research project IMPETUS (Integratives Management Projekt für den effizienten und tragfähigen Umgang mit der Ressource Süßwasser) to gain knowledge on ecosystems with low human impact. Most important human impacts on natural vegetation are cattle grazing, annual burning, and selective logging of valuable tree species such as *Isobertinia doka*, *Pterocarpus erinaceus*, *Azelia africana*, and *Khaya senegalensis*.

Classification of vegetation at the study site followed in a first step the physiognomic categories defined at the Yangambi conference in 1956 and a separation of zonal and azonal sites. In a second step, woodlands were subdivided according to dominant tree species. Seven vegetation types were differentiated wherein 35 relevé plots were studied from 2001 to 2004: savanna in inland valleys (*Bas fonds*) (*SB*), savanna at the *Bas fonds* margin (*SM*), tree savanna (*ST*), savanna woodland (*SW*), and woodlands dominated by *Isobertinia doka* (*WI*), *Uapaca togoensis* (*WU*), and *Anogeissus leiocarpus* (*WA*). Within *WI*, 14 gap plots were installed in gaps created by felling of one single tree individual of *Isobertinia doka* with a dbh larger 45 cm and with a distance of at least 60 m to the next felled tree. As logging activity was comparably sparse in the Upper Aguima catchment, one additional *Isobertinia doka* dominated woodland (*WI*) near Doguè characterized by a high logging intensity was chosen for comparison.

The present thesis comprises two main topics. The first topic deals with the ecosystem analysis of the woodland-savanna mosaic of the Upper Aguima catchment, focussing on the analysis of species composition, structural parameters, and the relation of environment and vegetation. Vegetation composition showed a gradual species turnover from open savannas in the *Bas fonds* to woodlands for both tree and herb layer, though many species occurred in all vegetation types. Tabular comparison based on strict phytosociological criteria revealed more

distinct species groups than classification following the stratified vegetation types based on extended Yangambi categories. Pairwise comparison of species data revealed significant differences between savanna types and woodlands but also within woodlands. Thus, the linkage between physiognomic characteristics and species composition was possible. Structural data of the tree and herb layer showed gradual changes from open savanna to woodlands with high grass biomass in open savannas and in particular high densities of trees of medium diameter and height classes in woodlands. The differentiation within woodlands was not significant for most structural parameters. As studies on structural data of the tree layer in woodlands and savannas in West Africa are sparse, this study expands the knowledge on these formations. For the studied environmental parameters, clear differences between stratified vegetation types following the gradient from open savanna to woodlands were found for microclimatic parameters, whereas for soil and fire related parameters as well as for grazing impact differences were less distinct. However, many environmental parameters showed inter-correlations. With regard to the species composition of the herb layer, canonical correspondence analysis revealed that light conditions explained most of the floristic variability followed by soil conditions. For tree species composition, also soil parameters were of prominent importance. Variance partitioning revealed that in order to explain floristic variability single key parameters such as vegetation type, topographical position, and visible sky were limited to substitute measured environmental parameters.

The second topic addresses the impact of selective logging on *Isoberlinia* dominated woodlands (*WI*). Here, the logging history and intensity, the impact of gap creation on micro-environment and floristic properties, and the recruitment of woody species in gaps were studied. Concerning the microclimatic parameters and biomass of the herb layer, gaps were more similar to savannas (mainly *SW* and *ST*) than to woodlands, but soil parameters did not differ. Species composition of the herb layer of the gap plots was most similar to those of *WI* plots. Recruitment of seedlings and saplings of woody species in gaps was comparable to those in *WI*, *SW*, and *ST*. Due to unchanged soil conditions and if seed input is guaranteed, succession towards *WI* appears most likely. But intensive selective logging and changes in grazing intensity may favour succession towards more open stands.

The detailed ecosystem analysis of the present thesis contributes to a better understanding of the woodland-savanna mosaic in central Benin and the findings can now be incorporated into modelling approaches of IMPETUS. Studies on the impact of selective logging may help to set up plans for silvicultural management of savannas and woodlands in Benin.

Zusammenfassung

Weltweit wird die Menschheit mit den negativen Folgen des globalen Wandels konfrontiert. Zu den wichtigsten Auswirkungen zählt die Verknappung von Ressourcen, wie etwa Süßwasser, aber auch die Bedrohung der Biodiversität. In der Sudanzone in Westafrika ist in den letzten 30 Jahren eine starke Intensivierung der Landnutzung zu beobachten. Dies resultiert aus einer Verbesserung der Infrastruktur, sowie der Zunahme der Bevölkerung durch Bevölkerungswachstum und Immigration.

Die Datenerhebung zur vorliegenden Arbeit wurde im Oberen Aguima Einzugsgebiet in der Nähe des Dorfes Doguè (Oberes Ouémé Einzugsgebiet, Zentral-Benin) durchgeführt, welches durch ein für die Sudanzone typisches Mosaik aus lichten Trockenwäldern und Savannentypen charakterisiert ist. Das interdisziplinäre Forschungsprojekt IMPETUS (Integratives Management Projekt für den effizienten und tragfähigen Umgang mit der Ressource Süßwasser) untersucht hier Ökosysteme mit geringem menschlichen Einfluss. Die wichtigsten Einflüsse sind Rinderbeweidung, jährliche Brände und selektiver Einschlag von Wertholzarten wie *Isobertinia doka*, *Pterocarpus erinaceus*, *Azelia africana* und *Khaya senegalensis*.

Die Vegetation des Untersuchungsgebietes wurde nach den physiognomischen Kategorien der Yangambi Konferenz (1956) und durch eine Trennung von zonalen und azonalen Standorten klassifiziert. Lichte Trockenwälder wurden zudem nach dominanten Baumarten unterteilt. In den sieben stratifizierten Vegetationstypen – Savanne in feuchten Senken (*Bas fonds*) (*SB*), Savanne am Rande der *Bas fonds* (*SM*), Baumsavanne (*ST*), Waldsavanne (*SW*) und lichte Trockenwälder mit Dominanzen von *Isobertinia doka* (*WI*), *Uapaca togoensis* (*WU*) und *Anogeissus leiocarpus* (*WA*) – wurden von 2001 bis 2004 in 35 Flächen Daten erhoben. Zudem wurden in *WI* 14 Lückenflächen untersucht, die durch Einzelbaumentnahme von *Isobertinia doka* mit einem dbh von mindestens 45 cm entstanden waren. In einem *WI*-Bestand mit starkem selektiven Holzeinschlag fanden weitere Untersuchungen statt.

Die vorliegende Arbeit gliedert sich in zwei Themenbereiche. Der erste Themenbereich umfasst eine Ökosystemanalyse des Vegetationsmosaiks des Oberen Aguima Einzugsgebietes mit den Schwerpunkten Vegetationszusammensetzung, Vegetationsstruktur und dem Zusammenhang von Umweltparametern und Vegetation. Die Vegetationszusammensetzung zeigte in der Kraut- und Baumschicht einen graduellen Wechsel von offenen Savannen in den *Bas fonds* zu lichten Trockenwäldern, wobei viele Arten in allen Vegetationstypen anzutreffen waren. Tabellenarbeit nach strikten phytosoziologischen Kriterien ergab klarere Artengruppen als eine Sortierung basierend auf den erweiterten Yangambi Kategorien. Der

statistische Einzelvergleich der Artenzusammensetzung wies signifikante Unterschiede zwischen den Savanntentypen und lichten Trockenwäldern, aber auch innerhalb der lichten Trockenwälder auf. Somit war eine Verknüpfung von physiognomischen Charakteristiken und Artenzusammensetzung möglich. Die Vegetationsstruktur der Kraut- und Baumschicht zeigte eine graduelle Veränderung von offenen Savannen zu lichten Trockenwäldern mit hoher Grasbiomasse in offenen Savannen und insbesondere hohen Baumdichten mittlerer Durchmesser- und Höhenklassen in den lichten Trockenwäldern. Die meisten strukturellen Parameter unterschieden sich innerhalb der lichten Trockenwälder jedoch nicht signifikant voneinander. Da zur Struktur der Baumschicht lichter Trockenwälder und Savannen in Westafrika bislang wenige Daten vorliegen, verbessert diese Studie den Wissenstand zu diesen Formationen. Für die untersuchten Umweltparameter wurde eine besonders klare Differenzierung der Vegetationstypen entlang des Gradienten von offener Savanne zu lichten Trockenwäldern für mikroklimatische Parameter gefunden. Für Boden-, Feuer- und Beweidungsparameter war diese Differenzierung weniger deutlich. Viele Umweltparameter korrelierten signifikant miteinander. Für die Artenzusammensetzung der Krautschicht ergaben Kanonische Korrespondenzanalysen, dass Licht- gefolgt von Bodenbedingungen die meiste floristische Variabilität erklärten. Für die Baumartenzusammensetzung waren ebenfalls Bodenparameter von vorrangiger Bedeutung. Die Varianzpartizipation zeigte, dass zur Erklärung floristischer Variabilität gemessene Umweltparameter nur im begrenzten Maße durch einzelne Schlüsselparameter wie Vegetationstypen, topographische Lage oder Baumdeckung ersetzt werden konnten.

Der zweiten Themenbereich befasst sich mit dem Einfluss von selektivem Holzeinschlag auf *Isobertinia* dominierte lichte Trockenwälder (*WI*). Untersucht wurde die Geschichte und Intensität des Holzeinschlages und der Einfluss von Lückenbildung auf Umweltparameter, Ausprägung der Krautschicht sowie die Verjüngung von Baumarten. Die mikroklimatischen Parameter und die krautige Biomasse in den Lückenflächen zeigten größere Ähnlichkeit zu den Savanntentypen *SW* und *ST* als zu den lichten Trockenwäldern. Die Bodenparameter unterschieden sich nicht. Die Artenzusammensetzung der Lückenflächen ähnelte am meisten der von *WI* und die Verjüngung der Baumarten war vergleichbar mit der in *WI*, *SW*, and *ST*. Aufgrund der unveränderten Bodenbedingungen, bei vorhandenem Sameneintrag, erscheint eine Sukzession der Lückenflächen zu *WI* als wahrscheinlich. Eine Intensivierung von selektivem Holzeinschlag und Beweidung kann hingegen eine Sukzession zu Savannen fördern.

Die detaillierte Ökosystemanalyse der vorliegenden Arbeit trägt zu einem verbesserten Verständnis des untersuchten Mosaiks aus lichten Trockenwäldern und verschiedenen Savanntentypen in Zentral-Benin bei. Die Ergebnisse stehen zur Einarbeitung in Modellieransätze in IMPETUS zur Verfügung. Die Untersuchungen zum selektiven Holzeinschlag können als Unterstützung bei der Entwicklung von forstlichen Managementplänen in vergleichbaren Systemen in Westafrika dienen.

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Appendix

A-Table 1. List of abbreviations.

Chemical soil properties	
<i>Bas</i>	Sum of basic cations (<i>Ca</i> , <i>K</i> , <i>Mg</i>) (cmol _c kg ⁻¹)
<i>C</i>	Organic carbon (%)
<i>C/N</i>	C/N-ratio
<i>Ca</i>	Calcium (cmol _c kg ⁻¹)
<i>K</i>	Potassium (cmol _c kg ⁻¹)
<i>Mg</i>	Magnesium (cmol _c kg ⁻¹)
<i>N</i>	Nitrogen (%)
<i>Na</i>	Natrium (cmol _c kg ⁻¹)
<i>P</i>	Phosphate (ppm)
<i>pH</i>	Soil reaction
Physical soil properties	
<i>S</i>	Sand (%)
<i>Sdp</i>	Soil depth (cm)
<i>Sdp_{Ah}</i>	Depth of the Ah-horizon (cm)
<i>Sk</i>	Skeleton (%)
<i>T</i>	Clay (%)
<i>U</i>	Silt (%)
Topographic position	
<i>Exp</i>	Exposition (°)
<i>Inc</i>	Inclination (%)
<i>TopH</i>	Relative topographic height (m)
Microclimatic parameters	
<i>DSF</i>	Direct site factor - October 2002 (%)
<i>GSF</i>	Global site factor - October 2002 (%)
<i>H_{min}</i>	Mean of diurnal minimum of air humidity (25.09. - 05.10.2001) (%)
<i>ISF</i>	Indirect site factor - October 2002 (%)
<i>LAI</i>	Leaf area index - October 2002
<i>T_{amp}</i>	Mean of diurnal amplitude of air temperature (25.09. - 05.10.2001) (°C)
<i>VDP_{max}</i>	Mean of diurnal maximum of vapour pressure deficit (25.09. - 05.10.2001) (%)
<i>VS</i>	Visible sky - October 2002 (%)
Fire	
<i>DF-01, DF-02, DF-M</i>	Date of fire in 2001 and 2002, and the mean of two years
<i>FT-01, FT-02, FT-M</i>	Fire temperature in 2001 and 2002, and the mean of two years (°C)
Grazing	
<i>GI-01, GI-02, GI-M</i>	Grazing impact in 2001 and 2002, and the mean of two years (%)
<i>TD-01, TD-02, TD-M</i>	Trampling damage in 2001 and 2002, and the mean of two years
Structural properties	
<i>DWB_{C-01}, DWB_{C-02}, DWB_{C-M}</i>	Cover of dead woody biomass in 2001 and 2002, and the mean of two years (%)
<i>G_{B-01}, G_{B-02}, G_{B-M}</i>	Biomass of grasses in 2001 and 2002, and the mean of two years (t ha ⁻¹)
<i>G_{C-01}, G_{C-02}, G_{C-M}</i>	Cover of grasses in 2001 and 2002, and the mean of two years (%)
<i>G_{H-01}, G_{H-02}, G_{H-M}</i>	Height of grasses in 2001 and 2002, and the mean of two years (m)
<i>G_{Vol-01}, G_{Vol-02}, G_{Vol-M}</i>	Volume of grasses in 2001 and 2002, and the mean of two years (m ³ m ⁻²)
<i>HE_{B-01}, HE_{B-02}, HE_{B-M}</i>	Biomass of herbs in 2001 and 2002, and the mean of two years (t ha ⁻¹)
<i>HE_{C-01}, HE_{C-02}, HE_{C-M}</i>	Cover of herbs in 2001 and 2002, and the mean of two years (%)
<i>HE_{H-01}, HE_{H-02}, HE_{H-M}</i>	Height of herbs in 2001 and 2002, and the mean of two years (m)
<i>HEL_{B-01}, HEL_{B-02}, HEL_{B-M}</i>	Biomass of herbs and litter in 2001 and 2002, and the mean of two years (t ha ⁻¹)
<i>HE_{Vol-01}, HE_{Vol-02}, HE_{Vol-M}</i>	Volume of herbs in 2001 and 2002, and the mean of two years (m ³ m ⁻²)
<i>L_{B-01}, L_{B-02}, L_{B-M}</i>	Biomass of litter in 2001 and 2002, and the mean of two years (t ha ⁻¹)
<i>L_{C-01}, L_{C-02}, L_{C-M}</i>	Cover of litter in 2001 and 2002, and the mean of two years (%)
<i>LG_{C-01}, LG_{C-02}, LG_{C-M}</i>	Cover of grass litter 2001 and 2002, and the mean of two years (%)
<i>LNG_{C-01}, LNG_{C-02}, LNG_{C-M}</i>	Cover of non-grass litter 2001 and 2002, and the mean of two years (%)
<i>OG_{C-01}, OG_{C-02}, OG_{C-M}</i>	Cover of open ground 2001 and 2002, and the mean of two years (%)
<i>TC</i>	Tree cover estimated in 2001 (%)
<i>TM-01, TM-02, TM-M</i>	Cover of termite mounds 2001 and 2002, and the mean of two years (%)
Vegetation	
<i>Bas fonds</i>	Inland valley
<i>SB</i>	Savanna in the <i>Bas fonds</i>
<i>SM</i>	Savanna at the margin of the <i>Bas fonds</i>
<i>ST</i>	Tree savanna
<i>SW</i>	Savanna woodland
<i>WA</i>	Woodland dominated by <i>Anogeissus leiocarpus</i>
<i>WI</i>	Woodland dominated by <i>Isobertinia doka</i>
<i>WU</i>	Woodland dominated by <i>Uapaca togoensis</i>
<i>Vegtyp</i>	Vegetation types after extended Yangambi classification

A-Table 2. Cover of tree species larger 10 cm dbh in the relevé plots. Relevé plots were sorted according to vegetation types. Abbreviations of vegetation types are given in Table 3.2.

Cover of trees	1	2	0	2	10	2	10	15	2	18	20	15	20	35	45	48	35	45	45	45	60	70	55	65	55	55	60	55	65	75	65	75	70	65	50			
Floristic block	1	1	5	1	2	1	2	2	1	2	3	2	2	3	3	3	2	3	5	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	4	3	4	
Vegetation type	SB	SB	SB	SB	SB	SB	SM	SM	SM	ST	ST	ST	ST	SW	SW	SW	SW	SW	SW	SW	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WA	WA	WA		
Plot	R12	R14	R15	R17	R18	R29	R01	R07	R13	R11	R27	R35	R37	R02	R05	R08	R16	R19	R22	R23	R03	R04	R06	R10	R21	R32	R34	R39	R09	R24	R33	R38	R20	R25	R30			
Species																																						
<i>Isobertia doka</i>	.	.	.	7	9	.	.	7	4	.	11	12	24	19	34	28	34	32	56	.	.	.	8	.	.	.			
<i>Uapaca togoensis</i>	2	.	3	.	42	.	1	.	4	.	.	2	12	.	.	2	18	.	8	87	39	35	.	4	.	.			
<i>Anogeissus leiocarpus</i>	1	11	3	9	.	4	10	.	11	15	.	.	.	25	8	33			
<i>Terminalia macroptera</i>	3	.	.	1		
<i>Terminalia schimperiana</i>	.	2	.	1	.	.	3	28	1		
<i>Syzygium guineense</i>	.	.	.	1	1	1	
<i>Daniellia oliveri</i>	.	.	.	8	.	.	26	.	12	.	15	5	.	1	.	9	9	13	3	6		
<i>Vitellaria paradoxa</i>	2	.	.	3	1	7	6	7	3	9	9	14	1	6	5	11	4	4	1	4	4	2	4	7	23	4	12	2	4	3	10			
<i>Pterocarpus erinaceus</i>	.	.	.	4	1	.	.	.	1	.	1	4	.	2	1	7	3	7	5	7	1	3	10	1	10	.	6	12	1				
<i>Maranthes polyandra</i>	1	.	.	1	.	1	.	1	.	.	.	1	.	9	.	11	1	3	4	1	1	1	.	4	7	.	1	3	1	.	.			
<i>Terminalia avicennioides</i>	.	.	.	1	.	1	.	1	.	.	2	.	.	1	.	6	1	1	1	15	1	1		
<i>Cussonia arborea</i>	1	3	1	1	.	.	2	1	.	.	.			
<i>Lonchocarpus sericeus</i>	.	.	1	3	1		
<i>Pseudocedrela kotschy</i>	1	.	.	12	29		
<i>Acacia polyacantha</i>	2	8	4		
<i>Entada africana</i>	2	7		
<i>Monotes kerstingii</i>	2	.	4	.	3	15	.	1	.	4	1	.	2	.	1	.	.	.	2	.	1	.	1	.	.	.			
<i>Burkea africana</i>	9	3	.	.	6	.	7	2	15	6	.	11	4	7	2	6	11	1	8	4	.	13	1	.	7	7			
<i>Parinari curatellifolia</i>	3	.	1	.	1	.	40	.	1	2	2	6	.	2	.	7	3	1	.	1	5	1	.	1	.	.			
<i>Lannea acida</i>	1	2	1	2	.	.	3	1	1	2	.	1	.	1	1	8	.	1	.	2	1			
<i>Combretum molle</i>	2	.	1	.	.	.	1	.	.	2	2	2	.	1	1	.	3	.	1	.	7	.			
<i>Hymenocardia acida</i>	1	.	.	.	1	.	12	1	1		
<i>Detarium microcarpum</i>	1	.	.	.	2	1	4		
<i>Prosopis africana</i>	6	1	2		
<i>Trichilia emetica</i>	1	5	.	.	1	.	.	2		
<i>Bombax costatum</i>	7	6	1	
<i>Strychnos spinosa</i>	1	1	
<i>Crossopteryx febrifuga</i>	3	.	4	9	1	4	.	7		
<i>Bridelia ferruginea</i>	1	.	.	.	1	2	2	
<i>Vitex doniana</i>	9	3	
<i>Sarcocephalus latifolius</i>	7	5	2
<i>Albizia malacophylla</i>	2	7	
<i>Azela africana</i> Smith	4	1	
<i>Pericopsis laxiflora</i>	1	1	
<i>Swartzia madagascariensis</i>	1	.	.	1	.	1	.	1	.	1	.	1		
<i>Ficus sur</i>	2	1	.	2	.	.	.	1	1	1		
<i>Khaya senegalensis</i>	1	2	
<i>Piliostigma thonningii</i>	1	1
<i>Acacia sieberiana</i>	.	1	
<i>Pteleopsis suberosa</i>	1
<i>Securidaca longepedunculata</i>	2
<i>Ficus platyphylla</i>	3
<i>Diospyros mespiliformis</i>	11
<i>Sterculia setigera</i>	1
<i>Tamarindus indica</i>	4
<i>Ximenia americana</i>	1
<i>Xeroderris stuhlmannii</i>	1	.	.
<i>Lophira lanceolata</i>	8
<i>Parkia biglobosa</i>	4

Continuation of A-Table 3.

Cover of trees	1	2	0	2	10	2	10	15	2	18	20	15	20	35	45	48	35	45	45	45	60	70	55	55	55	55	55	60	55	65	75	65	75	70	65	50			
Floristic block	1	1	1	1	1	1	1	1	1	4	3	4	3	4	2	48	2	2	3	3	3	3	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5		
Vegetation type	SB	SB	SB	SB	SB	SB	SB	SM	SM	SM	ST	ST	ST	ST	SW	SW	SW	SW	SW	SW	SW	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WA	WA	WA		
Plot	R12	R14	R15	R17	R18	R29	R01	R07	R13	R11	R27	R35	R37	R02	R05	R08	R16	R19	R22	R23	R03	R04	R06	R10	R21	R32	R34	R39	R09	R24	R33	R38	R20	R25	R30				
Species																																							
Curculigo pilosa							1			1			1				1					1		1		1	1	1				1			1		1		
Crassocephalum togoense							1			1	1			1	1	1	1	1	1			1	1		1	1	1	1				1							
Parinari curatellifolia								1		1	1	1		1	1	1	1	1	1			1	1		1		1	1				1							
Isoberlinia doka							1			1	1	1		1	1	1	1	1	1			1	1	1		1	1	1											
Laggeta alata							1			1	1	1		1	1	1	1	1	1			1	1		1	1	1	1				1							
Vernonia purpurea								1		1	1	1		1	1	1	1	1	1			1	1		1	1	1	1				1							
Burkea africana								1		1	1	1		1	1	2	1	1	1					1	1	1	1	1				1							
Panicum strictissimum								1							1				4			2		2															
Schizachyrium brevifolium								1							1																								
Anogeissus leiocarpus								1		1									1			1		1															
Fimbristylis filamentosa							1								1									1				1											
Bulbostylis filamentosa								1			1														1														
Pteleopsis suberosa								1			1				1	1	1																						
Crossopteryx febrifuga								1								1			1																				
Ischaemum amethystinum							1			1	30	1					4						2		2								1	2		1	20		
Schizachyrium sanguineum							1	1		4		1		1	4					1		2		10	2	4								1					
Aframomum albobolaceum							1	1		1	2	1		2	2	1		2	10	20		20	1	10	2	2	4	4		10	30	2	1	4	2	2			
Hyparrhenia smithiana	1							1		10	10	10		2	4		2	10	20			1	2	1	10	10	4	1	1	20	2		10			1	1		
Aspilia helianthoides										1	1	1		1	1	1	1	1	1	1	1	1		2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Vigna racemosa										2		1		1	1	1	1	1	1	1	1	2	2	4	2	2	1	2	1	1	1	1	1	1	1	1	1	1	
Cissus populnea										1	2	1		1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Rourea coccinea							1			1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	
Trichilia emetica										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pandiaka involucrata										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Uapaca togoensis										1	1	1		1	1	1	1	2				1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1		
Desmodium gangeticum										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Commelina erecta										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Fadogia cienkowskii										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Combretum molle										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Stereospermum kunthianum										1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Annona senegalensis										1	1	1		1	1	1	1	1	2				1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	
Rottboellia cochinchinensis										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Amorphophallus flavovirens										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pulicaria incisa										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Keetia venosa										1	1	1		1	1	1	1	1	1	1	1	4	4	2	2	10			4	2	1	1	1	1	1	1	1	1	
Englerastrum gracillimum										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Smilax anceps										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Diospyros mespiliformis										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Maranthus polyandra										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Detarium microcarpum										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Alysicarpus glumaceus										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Combretum nigricans										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Mariscus cylindristachyus										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Triumfetta tomentosa										2	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Clematis hirsuta										2	1	1		1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Asparagus africanus										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Sarcocephalus latifolius										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Psorospermum glaberrimum										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Monotes kerstingii										2	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Strychnos sp.										1	1	1		1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Rhynchosia minima										1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Hymenocardia acida																																							

Continuation of A-Table 3.

Cover of trees	1	2	0	2	10	2	10	15	2	18	20	15	20	35	45	48	35	45	45	60	70	55	65	55	55	60	55	65	75	75	60	65	50						
Floristic block	1	1	1	1	1	1	2	1	2	4	3	4	3	2	2	2	2	2	3	3	3	5	5	4	5	5	5	5	5	5	5	5	5	5					
Vegetation type	SB	SB	SB	SB	SB	SB	SM	SM	SM	ST	ST	ST	ST	SW	SW	SW	SW	SW	SW	SW	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI	WI						
Plot	R12	R14	R15	R17	R18	R29	R01	R07	R13	R11	R27	R35	R37	R02	R05	R08	R16	R19	R22	R23	R03	R04	R06	R10	R21	R32	R34	R39	R09	R24	R33	R38	R20	R25	R30				
Species																																							
<i>Crotalaria microcarpa</i>										1					1								1																
<i>Haumaniastrum lilacinum</i>										1					1																								
<i>Vigna luteola</i>										1	1	1			1	1	2		1		1																		
<i>Echinops longifolius</i>										1							1	1																					
<i>Ipomoea coscinosperma</i>										1	1				1																								
<i>Indigofera geminata</i>										1					1			2																					
<i>Pericopsis laxiflora</i>											1					1				1																			
<i>Lippia rugosa</i>										1									1	1																			
<i>Andropogon tectorum</i>							1									4	1			10		2	10	4	10	4	10	4	1	30	10	4	2	20	20	4			
<i>Bridelia ferruginea</i>															1	1				1		1		1	1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>Justicia insularis</i>																				1			2		1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Imperata cylindrica</i>																		1	1			1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Combretum collinum</i>																	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Dioscorea praeensis</i>																1		1			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Encephalartos barteri</i>																		1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Pennisetum polystachion</i>																2									1			20									1		
<i>Azella africana</i>															1	1					1			1					1		1		1		1				
<i>Desmodium salicifolium</i>																				1								1		1		1		1		1		1	
<i>Allophylus africanus</i>																			1											1		1		2	4				
<i>Bombax costatum</i>																	1		1				1														1		
<i>Parkia biglobosa</i>																			1									1									1		
<i>Brachiaria brizantha</i>																				1		1													1				
<i>Cussonia arborea</i>															1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>Vigna reticulata</i>															1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Teramnus labialis</i>																	1					1			2										1				
<i>Ficus sur</i>																							1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Syzygium guineense</i>																1		1				1																	
<i>Hybanthus enneaspermus</i>																							1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Cissus sokodensis</i>																1	1																						
<i>Nervilia reniformis</i>																			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Hibiscus asper</i>																				1																			
<i>Cyperus incompressus</i>															1										1														
<i>Nervilia umbrosa</i>																1																							
<i>Hyparrhenia welwitschii</i>																						1				1													
<i>Hyperthelia dissoluta</i>															1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Cochlospermum planchonii</i>																	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Lophira lanceolata</i>																	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Chasmopodium caudatum</i>															1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Psychotria vogeliana</i>																	1		1			1	1	1	1	1	30			30	30				1	1			
<i>Nephrolepis biserrata</i>	1																						1	4						20					10				
<i>Uvaria chamae</i>																							1							1	2			1	1	2			
<i>Cissus aralioides</i>																							1																
<i>Margaritaria discoidea</i>																							1																
<i>Chlorophytum sp.</i>																																							
<i>Scrophulariaceae</i>																							1			1													
<i>Keetia cornelia</i>																									1	1													
<i>Ekebergia senegalensis</i>																								1	1														
<i>Triumfetta rhomboidea</i>																							1			1	1												
<i>Ochna schweinfurthiana</i>																							1			1	1												
<i>Khaya senegalensis</i>																								1	1		1	1											
<i>Saba senegalensis</i>																																							
<i>Paullinia pinnata</i>																																							

Abildgaardia hispida: R02 (1); Acacia polyacantha: R20 (1); Acacia sieberiana: R07 (1), R29 (1); Achyranthes aspera: R39 (1); Aeschynomene lateritia: R05 (1); Albizia malacophylla: R38 (1), R39 (1); Amorphophallus abyssinicus: R20 (1), R33 (1); Ampelocissus leonensis: R09 (1), R20 (1); Andropogon curvifolius: R16 (1); Aneilema paludosum: R01 (1), R35 (1); Antidesma venosum: R25 (1); Asystasia gangetica: R06 (1); Blumea aurita: R35 (1); Brachiaria lata: R35 (2); Bulbostylis sp.: R13 (1), R38 (1); Capronia serrata: R14 (1); Cissus palmatifida: R33 (1); Clerodendrum umbellatum: R33 (2), R38 (1); Corchorus tridens: R10 (1); Crotalaria ochroleuca: R27 (1); Caperion canescens: R02 (1); Cyperus haspani: R01 (1); Cyperus imbricatus: R12 (1); Cyphostemma sokodense: R06 (1); Desmodium tortuosum: R20 (4); Desmodium velutinum: R39 (1), R25 (1); Dichrostachys cinerea: R30 (1), R39 (1); Dicoma sessiliflora: R37 (1); Dicoma tomentosa: R10 (1), R11 (1); Digitaria leptorhachis: R35 (1); Dioscorea togoensis: R03 (1), R23 (1); Dioscorea tomentosa: R20 (1); Drosera indica: R18 (1), R29 (1); Ectadiopsis oblongifolia: R22 (1); Eleocharis dulcis: R12 (1), R29 (1); Entada africana: R23 (1); Eriocaulon jordanii: R01 (1); Eriocaulon sp.: R29 (1); Eriocaulon togoense: R01 (1); Eriosema glomeratum: R07 (1), R08 (1); Eriosema griseum: R13 (1), R27 (1); Eriosema psoraloides: R16 (1), R02 (1); Eriosema pulcherrimum: R11 (1); Eulophia horsfallii: R29 (1); Euphorbia convolvuloides: R35 (1); Euphorbia hirta: R35 (1); Euphorbiaceae: R04 (1); Fadogia agrestis: R02 (1), R24 (1); Ficus ingens: R19 (1); Fiacourtia flavescens: R30 (1); Flueggea virosa: R20 (1); Grewia flavescens: R09 (1), R20 (1); Grewia mollis: R27 (1), R30 (1); Hibiscus articulatus: R39 (1); Hibiscus squamosus: R12 (1); Hyparrhenia subplumosa x involucreta: R12 (1), R13 (10); Indigofera leptocladia: R32 (1); Indigofera hirsuta: R02 (1); Indigofera kerstinii: R02 (1), R08 (1); Indigofera macrocalyx: R13 (1), R11 (2); Indigofera polysphaera: R07 (1), R35 (1); Indigofera rhynchocarpa: R23 (1); Ipomoea eriocarpa: R25 (1); Ipomoea togoensis: R03 (1); Lagereria pterodontia: R03 (1); Lannea acida: R10 (1); R11 (1); Leersia hexandra: R12 (1); Liliaceae sp. 1: R08 (1), R23 (1); Liliaceae sp. 2: R01 (1), R02 (1); Liliaceae sp.

A-Table 4. Woody biomass (BM, t ha⁻¹), calculated cover of trees (Cov, %), and tree density (D, individuals ha⁻¹) for vegetation types (VT) (abbreviations are given in Table 3.2) according to diameter classes (all = all diameter classes together). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

VT	Plot	1 - <5 cm			5 - <10 cm			10 - <20 cm			20 - <45 cm			≥45cm			all		
		BM	Cov	D	BM	Cov	D	BM	Cov	D	BM	Cov	D	BM	Cov	D	BM	Cov	D
SB	R12	0.05	0.21	167	0.11	0.17	33	0.93	1.62	33	4.84	4.67	22	0.00	0.00	0.00	5.93	6.26	256
SB	R14	0.02	0.08	22	0.00	0.00	0	0.52	0.89	11	3.20	1.67	11	0.00	0.00	0.00	3.74	2.39	44
SB	R15	0.01	0.02	11	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0.00	0.01	0.02	11
SB	R17	0.03	0.11	56	0.40	0.68	89	0.91	1.86	33	0.00	0.00	0	0.00	0.00	0.00	1.34	2.60	178
SB	R18	0.00	0.00	0	0.00	0.00	0	0.85	0.67	11	4.01	2.33	11	21.15	9.45	22.22	26.01	11.81	44
SB	R29	0.21	0.80	522	0.55	0.86	133	1.91	3.04	67	3.78	4.44	11	0.00	0.00	0.00	6.45	7.73	733
SM	R01	0.04	0.20	56	0.18	0.28	33	0.00	0.00	0	5.96	5.97	44	52.71	25.56	33.33	58.90	29.29	167
SM	R07	0.02	0.11	67	0.14	0.07	11	3.48	4.63	67	27.77	26.39	122	0.00	0.00	0.00	31.40	30.22	267
SM	R13	0.06	0.64	189	0.54	1.28	89	1.51	1.61	22	13.01	11.06	33	0.00	0.00	0.00	15.12	12.88	333
ST	R11	0.12	0.59	189	0.89	2.05	156	4.73	11.44	89	28.04	28.18	89	0.00	0.00	0.00	33.79	34.10	522
ST	R27	0.04	0.22	144	0.49	1.02	89	4.67	8.92	133	19.53	19.95	67	13.96	8.67	11.11	38.70	33.75	444
ST	R35	0.05	0.21	100	0.15	0.16	56	0.00	0.00	0	17.88	12.07	33	12.46	11.67	11.11	30.54	23.69	200
ST	R37	0.04	0.31	133	0.57	1.43	111	7.41	9.65	156	13.26	6.00	33	22.55	5.00	11.11	43.83	20.05	444
SW	R02	0.21	1.06	200	2.20	3.85	311	11.03	18.27	233	27.38	16.48	100	0.00	0.00	0.00	40.82	37.06	844
SW	R05	0.25	1.57	500	1.15	2.25	178	20.79	37.36	322	11.95	17.90	78	0.00	0.00	0.00	34.15	50.02	1078
SW	R08	0.07	2.16	189	1.01	7.05	211	9.40	27.41	278	44.93	52.81	189	0.00	0.00	0.00	55.41	66.01	867
SW	R16	0.03	0.31	111	0.62	1.77	100	5.08	3.61	122	16.71	10.63	89	43.01	13.72	22.22	65.45	28.97	444
SW	R19	0.06	0.43	89	0.50	1.20	67	6.53	8.77	156	70.18	47.52	200	0.00	0.00	0.00	77.26	56.27	511
SW	R22	0.21	1.49	367	2.05	4.26	311	9.47	15.08	244	25.35	14.75	122	0.00	0.00	0.00	37.08	32.39	1044
SW	R23	0.10	0.87	133	1.14	2.39	178	14.82	45.20	411	13.99	24.47	78	0.00	0.00	0.00	30.05	61.13	800
WI	R03	0.08	0.89	67	0.56	1.74	89	16.60	26.42	278	53.13	31.30	144	0.00	0.00	0.00	70.36	52.48	578
WI	R04	0.14	0.95	222	0.75	1.80	144	11.64	19.03	278	70.21	35.27	144	0.00	0.00	0.00	82.74	51.19	789
WI	R06	0.03	0.20	89	0.69	10.34	122	6.69	10.34	122	53.12	18.32	111	45.89	17.72	33.33	105.73	42.38	356
WI	R10	0.38	1.91	433	3.62	7.25	522	2.22	2.72	44	60.71	35.74	189	13.37	8.33	11.11	80.31	51.65	1200
WI	R21	0.09	0.51	144	0.34	1.10	67	5.19	9.84	133	76.96	38.03	122	0.00	0.00	0.00	82.58	45.67	467
WI	R32	0.38	3.52	467	1.12	5.24	167	11.78	23.09	278	64.69	35.73	178	0.00	0.00	0.00	77.98	55.94	1089
WI	R34	0.05	0.32	89	0.80	1.67	133	14.15	21.69	278	74.38	38.79	178	0.00	0.00	0.00	89.37	55.67	678
WI	R39	0.13	2.10	222	1.57	5.29	144	11.30	17.15	233	60.14	38.45	144	7.43	5.50	11.11	80.56	57.49	756
WU	R09	0.05	0.66	122	0.59	2.06	111	13.52	18.82	256	36.76	26.93	133	26.78	21.78	22.22	77.71	56.10	644
WU	R24	0.06	0.48	78	0.64	1.52	89	9.23	27.26	211	40.47	57.86	178	9.24	10.83	11.11	59.65	73.57	567
WU	R33	0.08	0.40	144	0.96	2.02	156	12.58	32.31	178	48.26	44.93	178	21.07	10.00	11.11	82.95	75.25	667
WU	R38	0.07	1.28	200	1.78	4.66	189	25.49	23.14	378	26.44	20.28	111	0.00	0.00	0.00	53.78	44.79	878
WA	R20	0.18	0.80	233	1.06	1.65	133	4.10	11.30	111	44.66	36.32	89	27.14	8.28	22.22	77.13	50.46	589
WA	R25	0.01	0.07	33	0.46	0.64	56	3.89	8.97	100	60.74	31.81	133	35.49	10.72	22.22	100.60	46.35	344
WA	R30	0.02	0.11	56	0.34	0.21	22	10.37	17.94	156	45.09	32.96	100	44.55	16.25	33.33	100.36	53.23	367
SB	Med	0.02 ^b	0.10 ^e	39 ^a	0.06 ^d	0.09 ^e	17 ^e	0.88 ^e	1.26 ^c	22 ^d	3.49 ^a	2.00 ^c	11 ^d	0.00 ^b	0.00 ^b	0.00 ^b	4.83 ^c	4.43 ^c	111 ^d
SM	Med	0.04 ^{ab}	0.20 ^{ce}	67 ^a	0.18 ^d	0.28 ^e	33 ^{de}	1.51 ^{de}	1.61 ^c	22 ^{cd}	13.01 ^d	11.06 ^{bc}	44 ^{bc}	0.00 ^{ab}	0.00 ^{ab}	0.00 ^{ab}	31.40 ^b	29.29 ^{bc}	267 ^d
ST	Med	0.05 ^{ab}	0.27 ^{be}	139 ^a	0.53 ^{bcd}	1.22 ^{bce}	100 ^{ae}	4.70 ^{de}	9.28 ^{bc}	111 ^{cd}	18.70 ^{cd}	16.01 ^b	50 ^{cd}	13.21 ^{ab}	6.83 ^{ab}	11.11 ^{ab}	36.24 ^b	28.72 ^b	444 ^d
SW	Med	0.10 ^a	1.06 ^a	189 ^a	1.14 ^a	2.39 ^a	178 ^a	9.47 ^{ab}	18.27 ^a	244 ^a	25.35 ^{cd}	17.90 ^{ab}	100 ^{ab}	0.00 ^b	0.00 ^b	0.00 ^b	40.82 ^b	50.02 ^a	844 ^a
WI	Med	0.11 ^a	0.92 ^a	183 ^a	0.77 ^{ac}	1.77 ^{acd}	139 ^{abcd}	11.47 ^{ac}	18.09 ^a	256 ^{ab}	62.70 ^a	35.73 ^a	144 ^a	0.00 ^b	0.00 ^{ab}	0.00 ^b	81.57 ^a	52.07 ^a	717 ^{ab}
WU	Med	0.06 ^{ab}	0.57 ^{abcd}	133 ^a	0.80 ^{ab}	2.04 ^{ab}	133 ^{ab}	13.05 ^a	25.20 ^a	233 ^a	38.62 ^{bc}	35.93 ^a	156 ^a	15.16 ^{ab}	10.42 ^{ab}	11.11 ^{ab}	68.68 ^a	64.83 ^a	656 ^{ac}
WA	Med	0.02 ^{ab}	0.11 ^{de}	56 ^a	0.46 ^{ad}	0.64 ^{de}	56 ^{bce}	4.10 ^{bcd}	11.30 ^{ab}	111 ^{bc}	45.09 ^{ab}	32.96 ^a	100 ^{ac}	35.49 ^a	10.72 ^a	22.22 ^a	100.36 ^a	50.46 ^a	367 ^{bcd}

A-Table 5. Woody biomass (BM, t ha⁻¹), calculated cover of trees (Cov, %), and tree density (D, individuals ha⁻¹) for vegetation types (VT) (abbreviations are given in Table 3.2) according to height classes (all = all diameter classes together). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

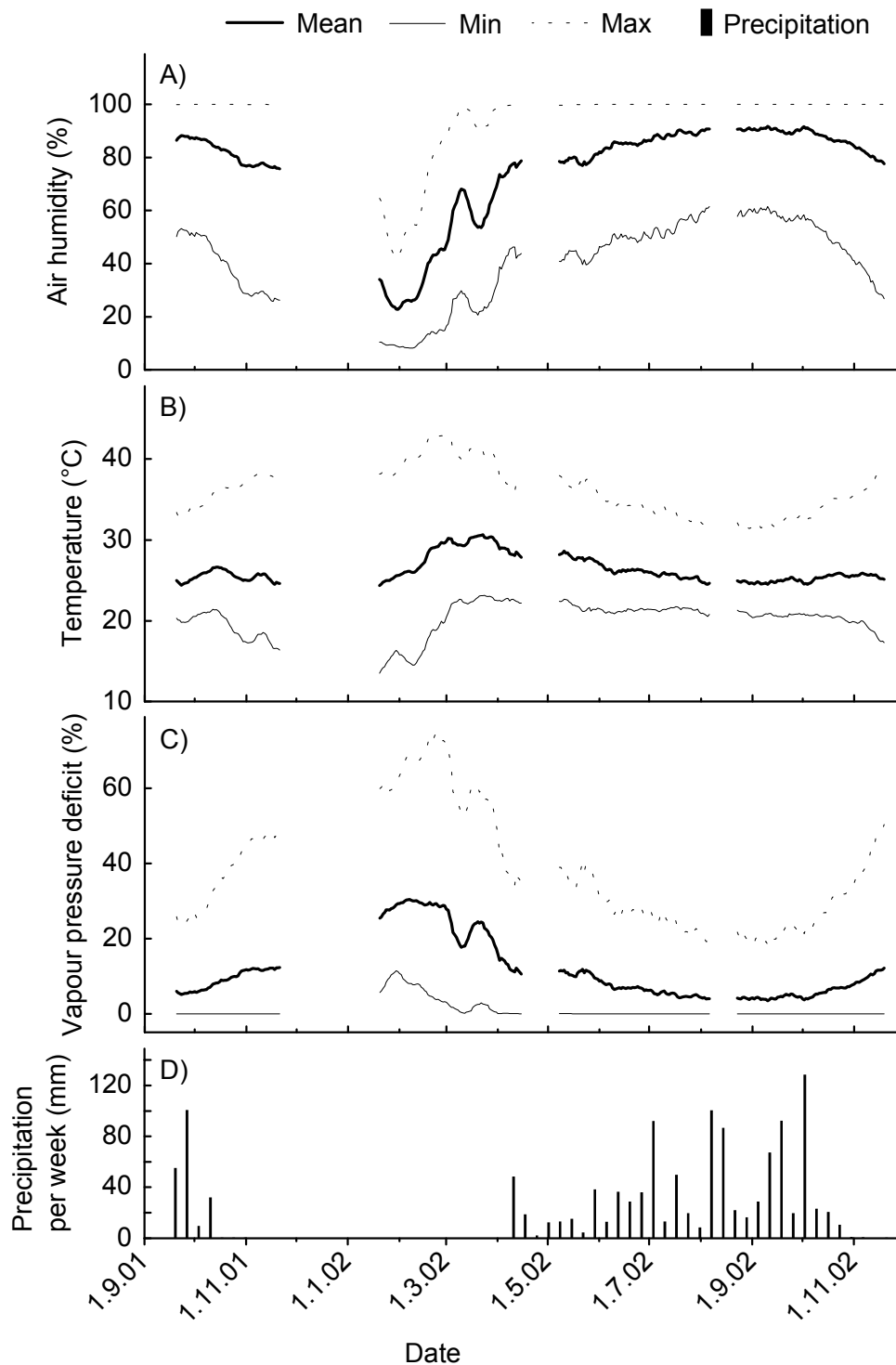
VT	Plot	<2 m			2 - <5 m			5 - <10 m			≥10 m			all		
		BM	Cov	D	BM	Cov	D	BM	Cov	D	BM	Cov	D	BM	Cov	D
SB	R12	0.06	0.19	167	0.51	0.70	56	0.53	1.11	11	4.84	4.67	22	5.93	6.26	256
SB	R14	0.00	0.03	11	0.01	0.05	11	0.52	0.89	11	3.20	1.67	11	3.74	2.39	44
SB	R15	0.01	0.02	11	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.01	0.02	11
SB	R17	0.01	0.06	33	0.43	0.73	111	0.91	1.86	33	0.00	0.00	0	1.34	2.60	178
SB	R18	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0	26.01	11.81	44	26.01	11.81	44
SB	R29	0.08	0.37	344	1.48	3.21	356	1.11	1.11	22	3.78	4.44	11	6.45	7.73	733
SM	R01	0.00	0.10	33	1.57	3.33	67	1.08	1.83	22	56.24	26.94	44	58.90	29.29	167
SM	R07	0.01	0.01	33	0.24	0.77	44	6.49	6.25	89	24.66	24.17	100	31.40	30.22	267
SM	R13	0.01	0.22	89	0.25	0.86	156	2.32	2.23	56	12.55	11.28	33	15.12	12.88	333
ST	R11	0.04	0.18	100	0.71	2.08	233	3.70	9.39	78	29.34	29.08	111	33.79	34.10	522
ST	R27	0.01	0.08	100	0.99	3.00	167	2.39	4.89	78	35.31	30.81	100	38.70	33.75	444
ST	R35	0.02	0.06	56	0.18	0.30	100	0.84	1.11	11	29.50	22.62	33	30.54	23.69	200
ST	R37	0.02	0.18	111	0.37	1.52	100	6.19	10.32	178	37.24	10.82	56	43.83	20.05	444
SW	R02	0.03	0.25	56	1.52	3.99	378	12.09	20.78	311	27.17	14.62	100	40.82	37.06	844
SW	R05	0.02	0.19	144	0.54	2.23	433	11.82	24.45	300	21.77	32.04	200	34.15	50.02	1078
SW	R08	0.03	0.52	100	1.97	10.65	333	23.19	41.59	333	30.23	30.63	100	55.41	66.01	867
SW	R16	0.02	0.21	89	0.73	1.90	111	8.09	5.85	156	56.61	21.97	89	65.45	28.97	444
SW	R19	0.01	0.14	44	0.19	0.61	67	7.62	11.96	200	69.44	45.78	200	77.26	56.27	511
SW	R22	0.04	0.37	178	2.26	4.55	433	11.40	14.50	311	23.39	16.87	122	37.08	32.39	1044
SW	R23	0.02	0.05	67	1.45	6.27	233	12.59	39.20	378	16.00	33.27	122	30.05	61.13	800
WI	R03	0.00	0.00	0.00	0.29	1.84	100	9.63	20.64	256	60.43	38.55	222	70.36	52.48	578
WI	R04	0.16	0.19	133	0.66	1.91	222	9.42	16.00	256	72.50	38.14	178	82.74	51.19	789
WI	R06	0.10	0.10	44	0.01	0.12	56	2.08	0.65	56	103.54	41.65	200	105.73	42.38	356
WI	R10	0.03	0.18	100	1.96	5.36	600	5.95	8.14	300	72.38	42.36	200	80.31	51.65	1200
WI	R21	0.00	0.05	44	0.43	1.57	167	5.52	13.17	122	76.62	39.95	133	82.58	45.67	467
WI	R32	0.04	0.61	167	1.24	7.03	411	8.68	19.77	278	68.02	38.61	233	77.98	55.94	1089
WI	R34	0.01	0.10	33	0.57	1.47	144	8.02	15.48	244	80.79	41.68	256	89.37	55.67	678
WI	R39	0.03	0.76	111	0.43	3.08	156	12.95	19.75	256	67.15	43.37	233	80.56	57.49	756
WU	R09	0.03	0.65	89	1.01	3.78	167	13.38	20.95	222	63.29	41.59	167	77.71	56.10	644
WU	R24	0.00	0.02	11	0.81	2.46	156	11.03	34.73	211	47.81	52.72	189	59.65	73.57	567
WU	R33	0.00	0.08	44	0.37	1.12	167	5.61	11.61	178	76.97	72.42	278	82.95	75.25	667
WU	R38	0.01	0.27	78	0.25	2.81	156	10.22	15.89	333	43.30	32.76	311	53.78	44.79	878
WA	R20	0.02	0.21	100	0.61	3.23	144	4.54	10.25	233	71.96	43.46	111	77.13	50.46	589
WA	R25	0.00	0.04	22	0.19	0.46	44	6.25	14.03	144	94.16	36.76	133	100.60	46.35	344
WA	R30	0.01	0.08	44	0.41	3.37	44	3.76	11.37	67	96.18	45.51	211	100.36	53.23	367
SB	Med	0.01 ^a	0.05 ^a	22 ^a	0.22 ^b	0.38 ^b	33 ^e	0.52 ^f	1.00 ^d	11 ^e	3.49 ^d	3.06 ^c	11 ^d	4.83 ^c	4.43 ^c	111 ^e
SM	Med	0.01 ^a	0.10 ^a	33 ^a	0.25 ^{ab}	0.86 ^{ab}	67 ^{bce}	2.32 ^{df}	2.23 ^{cd}	56 ^{de}	24.66 ^c	24.17 ^{bc}	44 ^{cd}	31.40 ^b	29.29 ^{bc}	267 ^{de}
ST	Med	0.02 ^a	0.13 ^a	100 ^a	0.54 ^{ab}	1.80 ^{ab}	133 ^{ae}	3.05 ^{ef}	7.14 ^{bd}	78 ^{de}	32.40 ^c	25.85 ^b	78 ^c	36.24 ^b	28.72 ^b	444 ^d
SW	Med	0.02 ^a	0.21 ^a	89 ^a	1.45 ^a	3.99 ^a	333 ^a	11.82 ^a	20.78 ^a	311 ^a	27.17 ^c	30.63 ^b	122 ^b	40.82 ^b	50.02 ^a	844 ^c
WI	Med	0.03 ^a	0.14 ^a	72 ^a	0.50 ^{ab}	1.87 ^a	161 ^{ab}	8.35 ^{bc}	15.74 ^a	256 ^{ac}	72.44 ^{ab}	40.80 ^a	211 ^a	81.57 ^a	52.07 ^a	717 ^b
WU	Med	0.00 ^a	0.17 ^a	61 ^a	0.59 ^{ab}	2.64 ^a	161 ^{acd}	10.62 ^{ab}	18.42 ^a	217 ^{ab}	55.55 ^b	47.15 ^a	233 ^a	68.68 ^a	64.83 ^a	656 ^a
WA	Med	0.01 ^a	0.08 ^a	44 ^a	0.41 ^{ab}	3.23 ^{ab}	44 ^{de}	4.54 ^{cde}	11.37 ^{abc}	144 ^{bcd}	94.16 ^a	43.46 ^a	133 ^{ab}	100.36 ^a	50.46 ^a	367 ^{ab}

A-Table 6. Median and quartile of structural and grazing parameters sampled in 2001 and 2002 for vegetation types (abbreviations for vegetation types and the parameters (Par) are given in A-Table 1). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by small letters. For the correlations between 2001 and 2002, the correlation coefficient after Spearman (r_s) and the significance level (P) are given. Med = median, Q25 = lower quartile, Q75 = upper quartile.

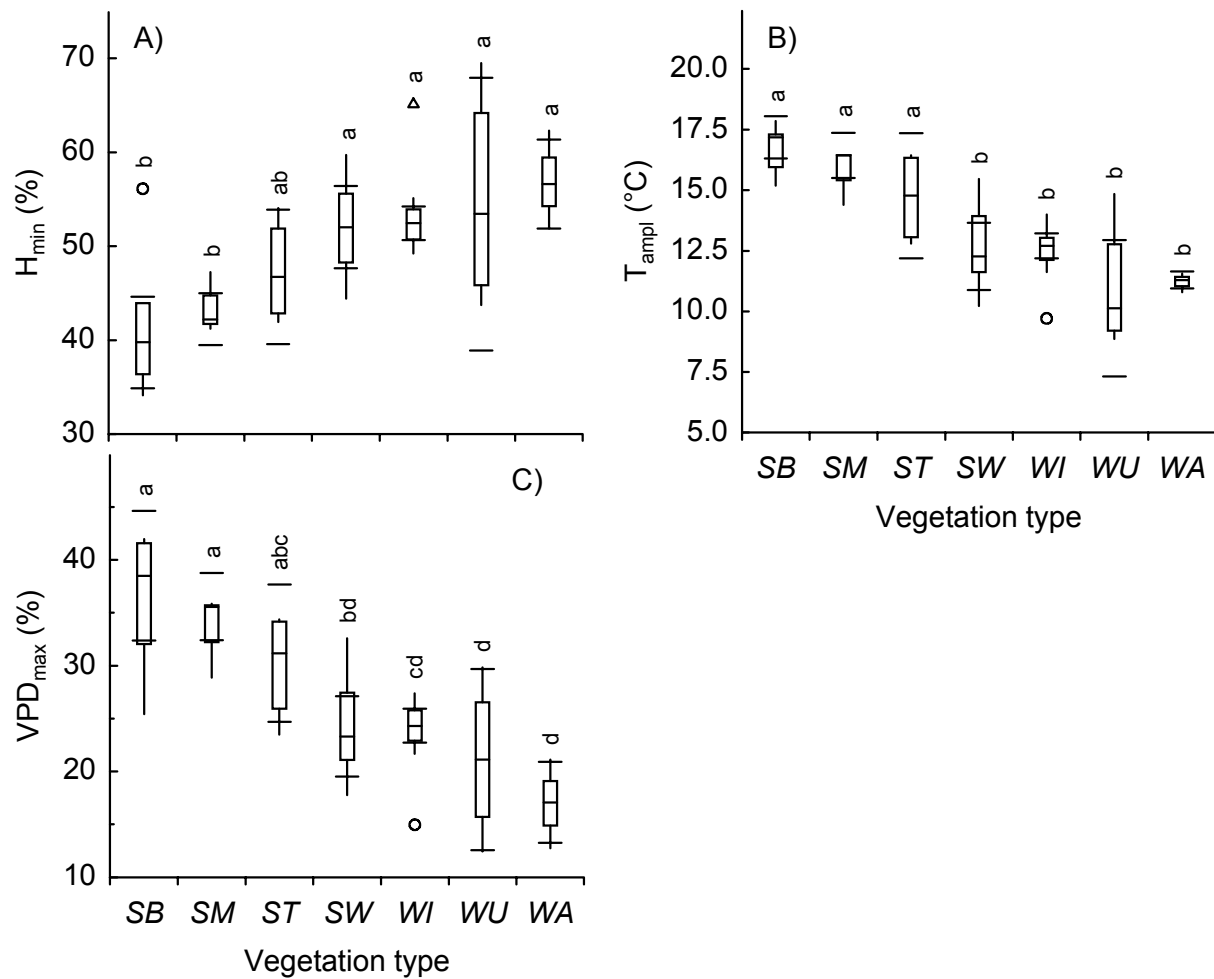
Par	r_s	P	SB			SM			ST			SW			WI			WU			WA		
			Q25	Med	Q75	Q25	Med	Q75	Q25	Med	Q75	Q25	Med	Q75	Q25	Med	Q75	Q25	Med	Q75	Q25	Med	Q75
G_C-01 (%)	0.88	0.0001	(93)	95 ^a	(95)	(83)	85 ^a	(88)	(36)	55 ^b	(71)	(50)	60 ^b	(73)	(19)	25 ^c	(25)	(20)	20 ^c	(25)	(15)	20 ^c	(25)
G_C-02 (%)			(90)	92 ^a	(95)	(83)	85 ^a	(85)	(49)	53 ^{bc}	(56)	(50)	60 ^b	(68)	(39)	40 ^{cd}	(50)	(19)	23 ^d	(35)	(33)	35 ^d	(35)
G_H-01 (cm)	0.49	0.0029	(263)	290 ^a	(310)	(278)	315 ^a	(358)	(238)	330 ^a	(428)	(220)	250 ^a	(290)	(210)	220 ^a	(263)	(245)	275 ^a	(348)	(245)	280 ^a	(350)
G_H-02 (cm)			(243)	250 ^a	(288)	(250)	260 ^a	(285)	(218)	235 ^{ab}	(250)	(205)	240 ^{ab}	(245)	(190)	210 ^b	(215)	(195)	210 ^b	(218)	(160)	210 ^b	(215)
G_{Vor-01} (m ³ m ⁻²)	0.82	0.0001	(2.48)	2.71 ^a	(2.98)	(2.44)	2.84 ^{ab}	(3.02)	(1.4)	1.74 ^{abc}	(2.14)	(1.08)	1.54 ^b	(2.02)	(0.39)	0.59 ^d	(0.66)	(0.49)	0.55 ^{cd}	(0.94)	(0.42)	0.42 ^d	(0.63)
G_{Vor-02} (m ³ m ⁻²)			(2.26)	2.3 ^a	(2.76)	(2.13)	2.21 ^a	(2.35)	(1.19)	1.26 ^{bc}	(1.29)	(1.06)	1.44 ^b	(1.62)	(0.71)	0.86 ^{cd}	(1.07)	(0.31)	0.46 ^d	(0.79)	(0.53)	0.74 ^d	(0.75)
HE_C-01 (%)	0.65	0.0001	(3)	4 ^b	(4)	(10)	10 ^a	(15)	(10)	10 ^a	(18)	(10)	15 ^a	(20)	(10)	18 ^a	(31)	(18)	25 ^a	(30)	(15)	20 ^a	(25)
HE_C-02 (%)			(3)	5 ^d	(5)	(8)	10 ^{bcd}	(10)	(20)	23 ^{ac}	(25)	(20)	25 ^a	(35)	(24)	25 ^a	(26)	(16)	23 ^{ab}	(33)	(25)	30 ^a	(35)
HE_H-01 (cm)	0.69	0.0001	(60)	63 ^f	(69)	(95)	100 ^{bcd}	(120)	(118)	120 ^{ae}	(125)	(100)	120 ^{ad}	(150)	(128)	150 ^a	(170)	(143)	150 ^{ab}	(153)	(135)	150 ^{ac}	(150)
HE_H-02 (cm)			(70)	70 ^d	(78)	(70)	70 ^{bcd}	(90)	(110)	115 ^{ab}	(125)	(115)	120 ^a	(160)	(115)	140 ^a	(153)	(138)	145 ^a	(153)	(110)	110 ^{ac}	(120)
HE_{Vor-01} (m ³ m ⁻²)	0.73	0.0001	(0.02)	0.03 ^b	(0.03)	(0.1)	0.1 ^{ab}	(0.19)	(0.11)	0.13 ^a	(0.23)	(0.15)	0.18 ^a	(0.21)	(0.13)	0.31 ^a	(0.5)	(0.26)	0.33 ^a	(0.39)	(0.23)	0.3 ^a	(0.33)
HE_{Vor-02} (m ³ m ⁻²)			(0.02)	0.03 ^c	(0.04)	(0.05)	0.07 ^{bc}	(0.09)	(0.24)	0.26 ^{ab}	(0.29)	(0.3)	0.38 ^a	(0.41)	(0.29)	0.34 ^a	(0.42)	(0.23)	0.34 ^a	(0.51)	(0.28)	0.33 ^a	(0.43)
L_C-01 (%)	0.53	0.0007	(2)	2 ^d	(3)	(2)	2 ^d	(3)	(3)	3 ^{bcd}	(3)	(4)	10 ^{ac}	(13)	(10)	10 ^a	(10)	(5)	8 ^{ab}	(15)	(8)	10 ^a	(15)
L_C-02 (%)			(3)	7 ^e	(10)	(8)	10 ^e	(10)	(15)	18 ^d	(20)	(18)	20 ^{cd}	(23)	(25)	30 ^a	(30)	(19)	23 ^{bd}	(26)	(23)	30 ^{abc}	(33)
LG_C-01 (%)	0.08	0.6486	(2)	2 ^a	(2)	(1)	1 ^a	(1.5)	(1.75)	2 ^a	(2)	(1.5)	2 ^a	(7.5)	(1)	2 ^a	(2.25)	(2)	2 ^a	(2.5)	(2)	2 ^a	(10)
LG_C-02 (%)			(1.25)	3.5 ^c	(5)	(5)	5 ^{bc}	(5)	(10)	10 ^a	(10)	(5)	10 ^{ab}	(10)	(5)	5 ^{ac}	(6.25)	(5)	7.5 ^{ac}	(10)	(5)	5 ^{ac}	(17.5)
LNG_C-01 (%)	0.78	0.0001	(0)	0.5 ^d	(1)	(0.5)	1 ^d	(1)	(1)	1.5 ^{bcd}	(2)	(2)	5 ^{ac}	(5)	(5.75)	8 ^a	(8.25)	(2.75)	4.5 ^a	(11.5)	(2.5)	3 ^{ab}	(5.5)
LNG_C-02 (%)			(1.25)	2 ^e	(4.25)	(3)	5 ^e	(5)	(5)	7.5 ^{bcd}	(10)	(10)	10 ^{ac}	(12.5)	(18.75)	22.5 ^a	(26.25)	(10)	15 ^{ab}	(20)	(7.5)	10 ^{ad}	(17.5)
OG_C-01 (%)	0.59	0.0002	(8)	8.5 ^d	(9.75)	(16)	20 ^{cd}	(22.5)	(15)	25 ^{bc}	(46.25)	(15)	20 ^c	(40)	(47.5)	60 ^a	(71.25)	(23.75)	32.5 ^{ac}	(43.75)	(45)	50 ^{ab}	(55)
OG_C-02 (%)			(2)	3.5 ^f	(5)	(7.5)	10 ^{bcd}	(10)	(13.75)	17.5 ^a	(22.5)	(10)	10 ^{ae}	(10)	(10)	12.5 ^{ac}	(20)	(10)	12.5 ^{ad}	(16.25)	(12.5)	15 ^{ab}	(15)
DWB_C-01 (%)	0.72	0.0001	(0)	0 ^c	(0)	(0.5)	1 ^{bc}	(1)	(2)	2.5 ^a	(3.5)	(1)	1 ^b	(1.5)	(1)	1 ^{ab}	(2.75)	(1)	1 ^b	(1)	(1)	1 ^{ab}	(2)
DWB_C-02 (%)			(0)	0 ^e	(0)	(0)	0 ^{bcd}	(0.5)	(2.75)	4.5 ^a	(7)	(1)	3 ^{ac}	(3.5)	(0)	2 ^{ad}	(5.25)	(0)	0 ^{bcd}	(0.5)	(1.5)	2 ^{ab}	(2.5)
$TM-01$ (%)	0.49	0.0029	(0)	0 ^a	(0)	(0)	0 ^a	(0)	(0)	0 ^a	(0)	(0)	0 ^a	(0)	(0)	0 ^a	(2.25)	(0)	0 ^a	(1.5)	(0)	0 ^a	(0)
$TM-02$ (%)			(0)	0 ^a	(0)	(0)	0 ^a	(0.5)	(0)	0 ^a	(0.25)	(0)	0 ^a	(0)	(0)	0 ^a	(0.25)	(0)	0 ^a	(1.25)	(0)	0 ^a	(0)
$TD-01$	0.24	0.1668	(2)	2 ^b	(2.75)	(2.5)	3 ^{ab}	(3)	(2)	2 ^b	(2.5)	(2)	3 ^{ab}	(4)	(2)	3 ^{ab}	(3.25)	(2.75)	3.5 ^{ab}	(4)	(4)	4 ^a	(4)
$TD-02$			(2)	2 ^f	(2)	(2.5)	3 ^{bcd}	(3)	(3.75)	4 ^a	(4)	(3)	3 ^{ae}	(3.5)	(3)	3 ^{ab}	(4)	(2.75)	3.5 ^{ad}	(4)	(3)	3 ^{ac}	(3.5)
$GI-01$ (%)	0.62	0.0001	(0)	0 ^f	(0)	(0)	0 ^{ef}	(1)	(2)	11 ^{ad}	(21)	(2)	5 ^{bcd}	(7)	(7)	10 ^a	(30)	(7)	13.5 ^{ac}	(20)	(15)	20 ^{ab}	(20)
$GI-02$ (%)			(0)	1.5 ^d	(8)	(8)	10 ^{bcd}	(20)	(46)	65 ^{ab}	(73)	(27)	50 ^{ac}	(70)	(50)	55 ^a	(90)	(73)	85 ^a	(90)	(60)	70 ^a	(83)

A-Table 7. Pearson's correlation coefficients (r) for cover of trees larger than 10 cm dbh and visible sky correlated with microclimatic parameters.

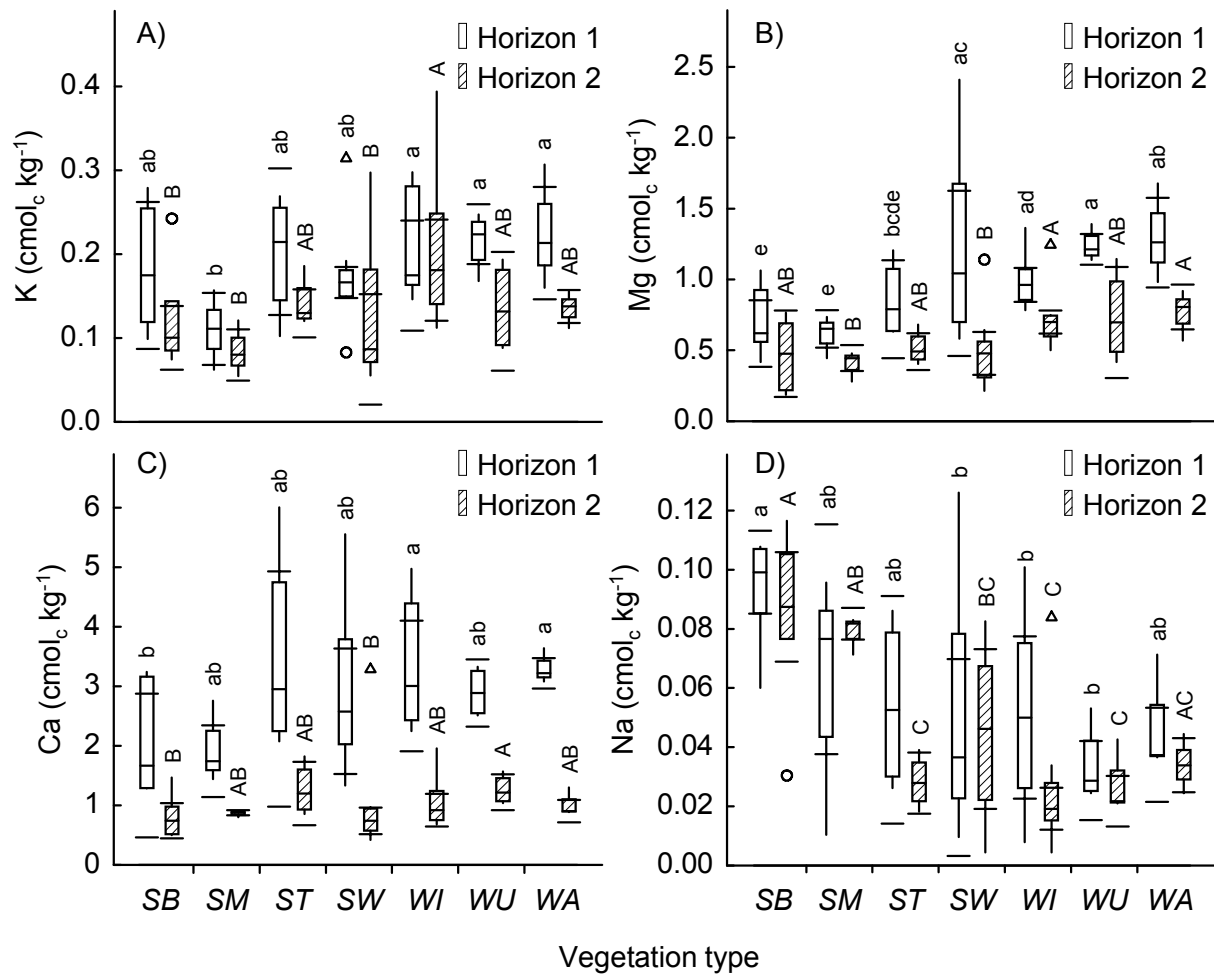
Parameter	Tree cover (%)	Visible sky
	r	r
Visible sky (VS)	0.916 ***	--
Indirect site factor (ISF)	0.918 ***	0.993 ***
Direct site factor (DSF)	0.887 ***	0.970 ***
Global site factor (GSF)	0.891 ***	0.973 ***
Leave area index (LAI)	0.933 ***	0.976 ***
Minimum air humidity (%) H_{min}	0.630 ***	0.665 ***
Amplitude of air temperature (°C) T_{ampl}	0.786 ***	0.823 ***
Maximum of VPD (%) VPD_{max}	0.722 ***	0.759 ***



A-Fig. 1. 10-day-moving average based on the mean of diurnal minimum, mean, and maximum for air humidity (A), air temperature (B), and vapour pressure deficit (C) measured in all relevé plots. Interruptions of the graphs resulted from periods needed for data download and logger maintenance. At the beginning of the measurement period, data from all relevé plots were considered. As a matter of a continuous loss of data loggers, at the end of the measurement period only 60% of the relevé plots were still considered. Panel D shows the precipitation measured at the meteorological station in Doguè (precipitation data from Giertz 2004).



A-Fig. 2. Boxplots of the 10-day-mean of the diurnal minimum of air humidity (H_{min}) (A), the diurnal amplitude of air temperature (T_{ampl}) (B), and diurnal maximal vapour pressure deficit (VPD_{max}) for vegetation types (abbreviations are given in Table 3.2). During the 10-day-period from 25.9. to 5.10.2001 for all relevé plots data were available (compare A-Fig. 1 and Fig. 4.12). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.



A-Fig. 3. Boxplots of selected parameters of soil chemistry (A: potassium; B: magnesium; C: calcium; D: sodium) of the two upper horizons for vegetation types (abbreviations are given in Table 3.2). Statistically significant groups computed by pairwise comparison between vegetation types are indicated by letters.

A-Table 10. Amount of explained floristic variability (eFV) and significance levels (P) for each environmental parameter (Par) from CCA revealed within the model-selection procedure and different variance partitioning approaches (*Vegtyp*, *TopH*) for the herb-layer data-set including *SB* and *SM* relevé plots. Cov = Covariate. Abbreviations of environmental parameters (Par) are given in A-Table 1.

Cov: none			Cov: VS			Cov: VS, S			Cov: <i>Vegtyp</i>			Cov: <i>TopH</i>		
Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)
VS	0.0001	19.15	S	0.0002	4.65	<i>Inc</i>	0.0430	3.09	<i>H_{min}</i>	0.0374	2.83	VS	0.0001	13.11
<i>G_B-M</i>	0.0001	18.18	<i>T</i>	0.0026	4.06	<i>GI-M</i>	0.0594	3.03	<i>GI-M</i>	0.0508	2.80	<i>G_B-M</i>	0.0001	12.12
<i>TC</i>	0.0001	15.39	<i>U</i>	0.0042	4.04	<i>TC</i>	0.0786	2.97	<i>VPD_{max}</i>	0.0486	2.79	<i>TC</i>	0.0001	10.42
<i>U</i>	0.0001	14.29	<i>DF-M</i>	0.0038	3.94	<i>Mg</i>	0.0884	2.96	<i>T</i>	0.1144	2.63	<i>U</i>	0.0001	9.70
<i>GI-M</i>	0.0001	13.04	<i>GI-M</i>	0.0428	3.27	<i>VPD_{max}</i>	0.0870	2.94	<i>T_{ampl}</i>	0.1056	2.63	<i>HEL_B-M</i>	0.0001	9.38
<i>T_{ampl}</i>	0.0001	12.57	<i>K</i>	0.0444	3.25	<i>DF-M</i>	0.0960	2.90	<i>S</i>	0.1322	2.61	<i>GI-M</i>	0.0001	9.06
<i>pH</i>	0.0001	12.57	<i>TC</i>	0.0564	3.23	<i>Sdp</i>	0.1252	2.85	<i>K</i>	0.1228	2.58	<i>pH</i>	0.0001	8.42
<i>S</i>	0.0002	12.16	<i>VPD_{max}</i>	0.1296	2.91	<i>H_{min}</i>	0.1462	2.77	<i>TD-M</i>	0.1502	2.54	<i>S</i>	0.0001	8.17
<i>VPD_{max}</i>	0.0001	12.01	<i>Inc</i>	0.1556	2.91	<i>T_{ampl}</i>	0.1560	2.76	<i>DF-M</i>	0.1848	2.51	<i>T_{ampl}</i>	0.0001	7.81
<i>HEL_B-M</i>	0.0001	11.25	<i>Mg</i>	0.1420	2.91	<i>TD-M</i>	0.1802	2.70	<i>FT-M</i>	0.2318	2.44	<i>VPD_{max}</i>	0.0002	7.31
<i>H_{min}</i>	0.0001	9.66	<i>G_B-M</i>	0.1470	2.88	<i>Sdp_{Ah}</i>	0.2062	2.67	<i>VS</i>	0.2464	2.43	<i>CN</i>	0.0002	6.73
<i>TD-M</i>	0.0004	8.77	<i>T_{ampl}</i>	0.1516	2.85	<i>G_B-M</i>	0.2338	2.65	<i>HEL_B-M</i>	0.2480	2.41	<i>TD-M</i>	0.0044	6.01
<i>TopH</i>	0.0004	8.75	<i>H_{min}</i>	0.1860	2.79	<i>TopH</i>	0.2464	2.63	<i>Sk</i>	0.3034	2.36	<i>H_{min}</i>	0.0040	5.70
<i>FT-M</i>	0.0032	7.25	<i>TD-M</i>	0.2076	2.77	<i>HEL_B-M</i>	0.2464	2.63	<i>TopH</i>	0.2990	2.36	<i>Mg</i>	0.0122	5.05
<i>Sdp</i>	0.0040	7.07	<i>TopH</i>	0.2436	2.71	<i>Sk</i>	0.3716	2.47	<i>Mg</i>	0.3100	2.35	<i>Na</i>	0.0132	4.85
<i>Na</i>	0.0174	5.73	<i>pH</i>	0.2726	2.66	<i>FT-M</i>	0.3772	2.47	<i>Inc</i>	0.3126	2.34	<i>Sdp</i>	0.0240	4.59
<i>Sdp_{Ah}</i>	0.0218	5.55	<i>HEL_B-M</i>	0.3778	2.52	<i>K</i>	0.4224	2.41	<i>G_B-M</i>	0.3494	2.31	<i>Ca</i>	0.0248	4.53
<i>CN</i>	0.0268	5.26	<i>FT-M</i>	0.4196	2.49	<i>P</i>	0.5346	2.30	<i>TC</i>	0.3822	2.28	<i>DF-M</i>	0.0870	3.74
<i>Mg</i>	0.0330	5.04	<i>Sk</i>	0.4494	2.44	<i>pH</i>	0.6476	2.20	<i>Sdp</i>	0.4464	2.23	<i>T</i>	0.0904	3.72
<i>Sk</i>	0.0392	4.80	<i>Sdp</i>	0.4734	2.42	<i>Ca</i>	0.6832	2.16	<i>Sdp_{Ah}</i>	0.4590	2.22	<i>FT-M</i>	0.1030	3.63
<i>T</i>	0.0416	4.73	<i>Sdp_{Ah}</i>	0.5920	2.31	<i>T</i>	0.7464	2.10	<i>U</i>	0.4612	2.21	<i>Sdp_{Ah}</i>	0.1134	3.58
<i>Inc</i>	0.0628	4.41	<i>P</i>	0.5600	2.31	<i>U</i>	0.7482	2.10	<i>P</i>	0.5156	2.14	<i>K</i>	0.1274	3.47
<i>Ca</i>	0.0788	4.28	<i>Na</i>	0.6524	2.24	<i>Na</i>	0.7710	2.09	<i>Ca</i>	0.6902	2.00	<i>Sk</i>	0.2256	3.17
<i>DF-M</i>	0.1404	3.76	<i>Ca</i>	0.9384	1.88	<i>CN</i>	0.9378	1.85	<i>Na</i>	0.7226	1.98	<i>Inc</i>	0.3198	2.93
<i>K</i>	0.1474	3.71	<i>CN</i>	0.9432	1.87				<i>CN</i>	0.7444	1.94	<i>P</i>	0.7746	2.24
<i>P</i>	0.9250	2.04							<i>pH</i>	0.8230	1.85			

A-Table 11. Amount of explained floristic variability (eFV) and significance levels (P) for each environmental parameter (Par) from CCA revealed within the model-selection procedure and different variance partitioning approaches (*Vegtyp*, *TopH*) for the herb-layer data-set excluding *SB* and *SM* relevé plots. Abbreviations of environmental parameters (Par) are given in A-Table 1. Cov = Covariate.

Cov: none			Cov: VS			Cov: VS, <i>GI-M</i>			Cov: VS, <i>GI-M</i> , <i>Mg</i>			Cov: VS, <i>GI-M</i> , <i>Mg</i> , <i>S</i>			Cov: <i>Vegtyp</i>			Cov: <i>TopH</i>		
			eFV (%) = 8.25			eFV (%) = 13.87			eFV (%) = 19.24			eFV (%) = 24.44			eFV (%) = 24.02			eFV (%) = 4.88		
Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)
<i>TC</i>	0.0004	8.26	<i>GI-M</i>	0.0148	5.62	<i>Mg</i>	0.0218	5.37	<i>S</i>	0.0166	5.20	<i>VPD_{max}</i>	0.1186	4.43	<i>H_{min}</i>	0.0284	4.93	<i>TC</i>	0.0004	8.16
<i>VS</i>	0.0002	8.25	<i>Mg</i>	0.0552	5.01	<i>DF-M</i>	0.0718	4.81	<i>DF-M</i>	0.0812	4.72	<i>Sk</i>	0.1602	4.33	<i>GI-M</i>	0.0512	4.71	<i>VS</i>	0.0006	7.98
<i>G_B-M</i>	0.0018	7.38	<i>DF-M</i>	0.0710	4.87	<i>TopH</i>	0.1048	4.59	<i>Sk</i>	0.0964	4.57	<i>Inc</i>	0.1478	4.33	<i>VPD_{max}</i>	0.0696	4.60	<i>G_B-M</i>	0.0038	7.05
<i>DF-M</i>	0.0034	6.88	<i>Inc</i>	0.1014	4.74	<i>VPD_{max}</i>	0.1088	4.58	<i>U</i>	0.1190	4.46	<i>H_{min}</i>	0.1480	4.31	<i>T_{ampl}</i>	0.1078	4.42	<i>DF-M</i>	0.0040	6.74
<i>VPD_{max}</i>	0.0140	6.21	<i>Sdp_{Ah}</i>	0.1088	4.65	<i>Inc</i>	0.1132	4.57	<i>VPD_{max}</i>	0.1154	4.45	<i>TopH</i>	0.1706	4.26	<i>S</i>	0.1376	4.35	<i>T_{ampl}</i>	0.0140	6.21
<i>T_{ampl}</i>	0.0156	6.10	<i>G_B-M</i>	0.1138	4.63	<i>H_{min}</i>	0.1694	4.36	<i>Sdp</i>	0.1316	4.45	<i>DF-M</i>	0.2034	4.16	<i>TD-M</i>	0.1406	4.34	<i>VPD_{max}</i>	0.0134	6.18
<i>GI-M</i>	0.0176	5.96	<i>TopH</i>	0.1108	4.61	<i>T_{ampl}</i>	0.1754	4.35	<i>Sdp_{Ah}</i>	0.1576	4.36	<i>TD-M</i>	0.2036	4.16	<i>HEL_B-M</i>	0.1544	4.27	<i>GI-M</i>	0.0200	5.96
<i>H_{min}</i>	0.0206	5.96	<i>TD-M</i>	0.1390	4.51	<i>Sdp_{Ah}</i>	0.1882	4.30	<i>H_{min}</i>	0.1730	4.27	<i>Sdp_{Ah}</i>	0.2590	4.04	<i>VS</i>	0.1826	4.23	<i>H_{min}</i>	0.0282	5.73
<i>HEL_B-M</i>	0.0736	5.12	<i>VPD_{max}</i>	0.1692	4.46	<i>Sk</i>	0.1974	4.28	<i>TopH</i>	0.1752	4.27	<i>G_B-M</i>	0.4426	3.66	<i>DF-M</i>	0.1776	4.21	<i>HEL_B-M</i>	0.0552	5.31
<i>FT-M</i>	0.1012	4.92	<i>HEL_B-M</i>	0.1642	4.42	<i>Sdp</i>	0.2184	4.21	<i>TD-M</i>	0.2056	4.18	<i>FT-M</i>	0.4522	3.64	<i>G_B-M</i>	0.2430	4.09	<i>K</i>	0.1232	4.84
<i>TopH</i>	0.1168	4.88	<i>H_{min}</i>	0.1900	4.36	<i>TD-M</i>	0.2362	4.16	<i>K</i>	0.2390	4.13	<i>Sdp</i>	0.4850	3.61	<i>Sdp_{Ah}</i>	0.2514	4.06	<i>TD-M</i>	0.1468	4.68
<i>Mg</i>	0.1310	4.80	<i>T_{ampl}</i>	0.1996	4.32	<i>S</i>	0.2730	4.12	<i>G_B-M</i>	0.3524	3.89	<i>T_{ampl}</i>	0.5326	3.50	<i>FT-M</i>	0.2574	4.05	<i>Sdp_{Ah}</i>	0.1654	4.67
<i>Sdp</i>	0.1424	4.79	<i>Sdp</i>	0.2484	4.21	<i>G_B-M</i>	0.2978	4.08	<i>FT-M</i>	0.4030	3.79	<i>K</i>	0.5532	3.47	<i>TopH</i>	0.2534	4.03	<i>S</i>	0.1636	4.66
<i>K</i>	0.1296	4.77	<i>S</i>	0.2748	4.21	<i>U</i>	0.3014	4.03	<i>T_{ampl}</i>	0.4128	3.77	<i>HEL_B-M</i>	0.6094	3.40	<i>U</i>	0.2568	4.02	<i>FT-M</i>	0.1590	4.63
<i>TD-M</i>	0.1666	4.67	<i>U</i>	0.2602	4.20	<i>K</i>	0.3370	3.97	<i>T</i>	0.4328	3.74	<i>T</i>	0.6148	3.35	<i>Sk</i>	0.2874	3.96	<i>Sdp</i>	0.1726	4.60
<i>Sdp_{Ah}</i>	0.1664	4.60	<i>Sk</i>	0.3138	4.10	<i>FT-M</i>	0.3472	3.93	<i>Inc</i>	0.5192	3.61	<i>U</i>	0.6216	3.35	<i>Mg</i>	0.2988	3.95	<i>Mg</i>	0.1970	4.56
<i>S</i>	0.1970	4.57	<i>FT-M</i>	0.3804	3.96	<i>T</i>	0.4524	3.73	<i>P</i>	0.6250	3.41	<i>Na</i>	0.6482	3.33	<i>Sdp</i>	0.3386	3.88	<i>U</i>	0.2786	4.31
<i>Sk</i>	0.2888	4.32	<i>K</i>	0.3910	3.95	<i>Na</i>	0.5774	3.57	<i>HEL_B-M</i>	0.6476	3.40	<i>pH</i>	0.6544	3.28	<i>K</i>	0.3408	3.86	<i>T</i>	0.3388	4.24
<i>T</i>	0.3352	4.24	<i>TC</i>	0.4022	3.94	<i>HEL_B-M</i>	0.6124	3.52	<i>pH</i>	0.6686	3.35	<i>TC</i>	0.6652	3.26	<i>P</i>	0.3488	3.85	<i>Sk</i>	0.3732	4.12
<i>U</i>	0.3256	4.22	<i>Na</i>	0.4642	3.81	<i>pH</i>	0.6622	3.43	<i>Na</i>	0.6708	3.35	<i>CN</i>	0.6974	3.23	<i>T</i>	0.3430	3.83	<i>Inc</i>	0.4252	4.01
<i>Inc</i>	0.3340	4.22	<i>T</i>	0.5098	3.71	<i>P</i>	0.7562	3.25	<i>Ca</i>	0.6770	3.34	<i>P</i>	0.7368	3.10	<i>Na</i>	0.5260	3.58	<i>Na</i>	0.5960	3.68
<i>Na</i>	0.5374	3.83	<i>pH</i>	0.6960	3.47	<i>TC</i>	0.8034	3.18	<i>CN</i>	0.7616	3.18	<i>Ca</i>	0.7788	3.05	<i>TC</i>	0.5776	3.48	<i>pH</i>	0.6490	3.61
<i>pH</i>	0.7024	3.56	<i>P</i>	0.7422	3.34	<i>CN</i>	0.8258	3.14	<i>TC</i>	0.7820	3.14				<i>Inc</i>	0.6086	3.39	<i>CN</i>	0.6820	3.57
<i>P</i>	0.8240	3.31	<i>CN</i>	0.7614	3.33	<i>Ca</i>	0.8988	2.93							<i>pH</i>	0.6884	3.29	<i>P</i>	0.8876	3.06
<i>CN</i>	0.8744	3.22	<i>Ca</i>	0.9346	2.92										<i>Ca</i>	0.7212	3.24	<i>Ca</i>	0.9754	2.67
<i>Ca</i>	0.9700	2.88													<i>CN</i>	0.7454	3.18			

A-Table 12. Amount of explained floristic variability (eFV) and significance levels (P) for each environmental parameter (Par) from CCA revealed within the model-selection procedure and different variance partitioning approaches (*Vegtyp*, *TopH*) for the tree-layer data-set including *SB* and *SM* relevé plots. Abbreviations of environmental parameters (Par) are given in A-Table 1. Cov = Covariate.

Cov: none			Cov: S eFV (%) = 7.47			Cov: S, U eFV (%) = 12.57			Cov: S, U, G _B -M eFV (%) = 16.92			Cov: S, U, G _B -M, Mg eFV (%) = 21.21			Cov: Vegtyp eFV (%) = 25.30			Cov: VS eFV (%) = 7.16			Cov: TopH eFV (%) = 4.63		
Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)
<i>U</i>	0.0001	8.05	<i>VS</i>	0.0001	6.19	<i>VS</i>	0.0006	5.43	<i>VS</i>	0.0032	5.09	<i>VS</i>	0.0048	4.99	<i>S</i>	0.0022	6.03	<i>S</i>	0.0004	6.50	<i>U</i>	0.0001	7.28
<i>S</i>	0.0002	7.47	<i>TC</i>	0.0002	5.42	<i>TC</i>	0.0014	5.08	<i>Mg</i>	0.0700	4.29	<i>TC</i>	0.0394	4.07	<i>U</i>	0.0050	5.15	<i>U</i>	0.0002	5.98	<i>S</i>	0.0002	6.62
<i>VS</i>	0.0001	7.16	<i>U</i>	0.0292	5.10	<i>Inc</i>	0.0178	4.49	<i>Na</i>	0.0270	4.10	<i>Inc</i>	0.0526	3.95	<i>T</i>	0.0496	5.14	<i>T</i>	0.0464	5.58	<i>VS</i>	0.0001	6.25
<i>G_B-M</i>	0.0014	6.31	<i>T</i>	0.0302	5.10	<i>G_B-M</i>	0.0188	4.34	<i>TC</i>	0.0396	4.07	<i>Sdp</i>	0.0630	3.94	<i>Mg</i>	0.1062	3.91	<i>Mg</i>	0.0600	4.74	<i>TC</i>	0.0010	5.64
<i>TC</i>	0.0002	6.24	<i>Mg</i>	0.0122	5.09	<i>Sdp</i>	0.0360	4.19	<i>Sdp</i>	0.0586	3.98	<i>Sdp_{Ah}</i>	0.0884	3.70	<i>Na</i>	0.0814	3.79	<i>Inc</i>	0.0942	4.33	<i>G_B-M</i>	0.0054	5.18
<i>T</i>	0.1028	4.89	<i>G_B-M</i>	0.0048	4.80	<i>pH</i>	0.0500	4.17	<i>Inc</i>	0.0640	3.91	<i>pH</i>	0.2284	3.23	<i>G_B-M</i>	0.1310	3.72	<i>G_B-M</i>	0.0720	4.07	<i>CN</i>	0.0146	4.72
<i>Inc</i>	0.0632	4.87	<i>Sdp</i>	0.0386	4.26	<i>Sdp_{Ah}</i>	0.0474	4.01	<i>Sdp_{Ah}</i>	0.0690	3.86	<i>CN</i>	0.2684	3.08	<i>Inc</i>	0.1430	3.70	<i>TopH</i>	0.1394	3.72	<i>T</i>	0.1188	4.62
<i>pH</i>	0.0450	4.63	<i>Inc</i>	0.0468	4.22	<i>TopH</i>	0.0920	3.76	<i>CN</i>	0.1246	3.55	<i>TopH</i>	0.4184	2.80	<i>Ca</i>	0.1126	3.69	<i>Na</i>	0.1164	3.68	<i>pH</i>	0.0890	4.23
<i>TopH</i>	0.0282	4.63	<i>pH</i>	0.0612	4.20	<i>Mg</i>	0.1562	3.69	<i>Ca</i>	0.2122	3.31	<i>Na</i>	0.4214	2.78	<i>Sdp</i>	0.2288	3.29	<i>Sdp</i>	0.1680	3.65	<i>Inc</i>	0.1192	4.19
<i>Mg</i>	0.1040	4.32	<i>Ca</i>	0.0436	4.18	<i>Na</i>	0.0980	3.66	<i>TopH</i>	0.2232	3.25	<i>Sk</i>	0.4008	2.78	<i>TopH</i>	0.2298	3.21	<i>Ca</i>	0.2090	3.48	<i>Mg</i>	0.1040	4.08
<i>CN</i>	0.1092	3.95	<i>CN</i>	0.0814	3.88	<i>Sk</i>	0.1752	3.62	<i>pH</i>	0.2508	3.22	<i>H_{min}</i>	0.4596	2.71	<i>VS</i>	0.3148	3.01	<i>TC</i>	0.2598	3.34	<i>HEL_B-M</i>	0.0980	3.78
<i>GI-M</i>	0.0836	3.85	<i>Na</i>	0.0752	3.87	<i>CN</i>	0.1246	3.61	<i>H_{min}</i>	0.3610	2.95	<i>VPD_{max}</i>	0.5230	2.61	<i>CN</i>	0.3538	2.96	<i>CN</i>	0.3278	3.13	<i>Sdp</i>	0.1598	3.77
<i>Sdp</i>	0.1560	3.82	<i>TopH</i>	0.1042	3.77	<i>Ca</i>	0.2072	3.35	<i>VPD_{max}</i>	0.3914	2.88	<i>DF-M</i>	0.5016	2.61	<i>K</i>	0.3588	2.94	<i>TD-M</i>	0.4152	2.97	<i>Na</i>	0.1310	3.68
<i>T_{ampl}</i>	0.1150	3.79	<i>HEL_B-M</i>	0.1150	3.67	<i>FT-M</i>	0.2398	3.29	<i>Sk</i>	0.3962	2.83	<i>TD-M</i>	0.5696	2.50	<i>TC</i>	0.4730	2.73	<i>Sdp_{Ah}</i>	0.4054	2.97	<i>Ca</i>	0.1898	3.58
<i>Na</i>	0.1250	3.77	<i>Sk</i>	0.1998	3.65	<i>H_{min}</i>	0.3866	2.93	<i>HEL_B-M</i>	0.4808	2.70	<i>Ca</i>	0.5462	2.48	<i>HEL_B-M</i>	0.4848	2.68	<i>pH</i>	0.4520	2.85	<i>GI-M</i>	0.1606	3.55
<i>VPD_{max}</i>	0.1404	3.72	<i>Sdp_{Ah}</i>	0.1332	3.64	<i>T_{ampl}</i>	0.4054	2.89	<i>T_{ampl}</i>	0.5306	2.66	<i>T_{ampl}</i>	0.6218	2.44	<i>P</i>	0.4562	2.67	<i>HEL_B-M</i>	0.4860	2.82	<i>Sdp_{Ah}</i>	0.2994	3.29
<i>Ca</i>	0.1742	3.67	<i>VPD_{max}</i>	0.1272	3.60	<i>VPD_{max}</i>	0.4328	2.85	<i>P</i>	0.5006	2.54	<i>HEL_B-M</i>	0.6472	2.40	<i>TD-M</i>	0.5092	2.63	<i>K</i>	0.5628	2.74	<i>T_{ampl}</i>	0.3178	3.19
<i>HEL_B-M</i>	0.1820	3.56	<i>T_{ampl}</i>	0.1240	3.59	<i>DF-M</i>	0.4276	2.85	<i>DF-M</i>	0.6082	2.50	<i>FT-M</i>	0.6428	2.40	<i>GI-M</i>	0.5226	2.62	<i>Sk</i>	0.4782	2.69	<i>TD-M</i>	0.3700	3.11
<i>FT-M</i>	0.2532	3.43	<i>H_{min}</i>	0.1976	3.44	<i>HEL_B-M</i>	0.6080	2.53	<i>TD-M</i>	0.6936	2.35	<i>P</i>	0.5404	2.37	<i>FT-M</i>	0.6062	2.45	<i>P</i>	0.5208	2.57	<i>VPD_{max}</i>	0.3892	3.07
<i>Sdp_{Ah}</i>	0.2686	3.41	<i>FT-M</i>	0.2958	3.20	<i>P</i>	0.5374	2.47	<i>FT-M</i>	0.7884	2.21	<i>GI-M</i>	0.9138	1.90	<i>Sdp_{Ah}</i>	0.6954	2.34	<i>GI-M</i>	0.6892	2.51	<i>K</i>	0.4264	3.02
<i>H_{min}</i>	0.3272	3.23	<i>K</i>	0.2846	3.18	<i>TD-M</i>	0.6868	2.40	<i>GI-M</i>	0.9650	1.71	<i>K</i>	0.9858	1.43	<i>H_{min}</i>	0.6922	2.27	<i>DF-M</i>	0.6302	2.50	<i>Sk</i>	0.3904	2.95
<i>TD-M</i>	0.3704	3.18	<i>DF-M</i>	0.3954	2.98	<i>K</i>	0.8690	2.10	<i>K</i>	0.9678	1.68	<i>T</i>	1.0000	0.00	<i>DF-M</i>	0.7888	2.13	<i>H_{min}</i>	0.7126	2.37	<i>H_{min}</i>	0.4876	2.86
<i>Sk</i>	0.3508	3.14	<i>TD-M</i>	0.4670	2.86	<i>GI-M</i>	0.9188	1.97	<i>T</i>	1.0000	0.00	<i>VPD_{max}</i>	0.8288	2.08	<i>FT-M</i>	0.8268	2.18	<i>DF-M</i>	0.8268	2.18	<i>DF-M</i>	0.5352	2.75
<i>K</i>	0.4588	3.01	<i>GI-M</i>	0.6420	2.61	<i>T</i>	1.0000	0.00	<i>VPD_{max}</i>	0.8288	2.08	<i>pH</i>	0.8098	2.08	<i>VPD_{max}</i>	0.8876	2.08	<i>FT-M</i>	0.7178	2.51			
<i>DF-M</i>	0.5430	2.76	<i>P</i>	0.5602	2.51				<i>Sk</i>	0.7486	2.06	<i>Sk</i>	0.7486	2.06	<i>T_{ampl}</i>	0.9758	1.72	<i>P</i>	0.6568	2.27			
<i>P</i>	0.5598	2.55							<i>T_{ampl}</i>	0.8774	1.91	<i>T_{ampl}</i>	0.8774	1.91									

A-Table 13. Amount of explained floristic variability (eFV) and significance levels (P) for each environmental parameter (Par) from CCA revealed within the model-selection procedure and different variance partitioning approaches (*Vegtyp*, *TopH*) for the tree-layer data-set excluding *SB* and *SM* relevé plots. Abbreviations of environmental parameters (Par) are given in A-Table 1. Cov = Covariate.

Cov: none			Cov: S			Cov: S, U			Cov: S, U, G _B -M			Cov: S, U, G _B -M, Mg			Cov: Vegtyp			Cov: VS			Cov: TopH		
Par	P	eFV(%)	Par	P	eFV(%)	Par	p	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)	Par	P	eFV(%)
S	0.0030	7.86	TC	0.0012	7.15	TC	0.0004	7.35	Mg	0.0208	5.99	TC	0.0236	5.38	S	0.0020	8.39	S	0.0002	8.65	S	0.0056	7.40
U	0.0024	7.27	VS	0.0022	6.91	VS	0.0002	7.06	TC	0.0188	5.46	VS	0.0280	5.21	T	0.0346	7.44	T	0.0342	7.99	U	0.0026	7.10
T	0.0576	7.11	T	0.0108	6.34	G _B -M	0.0092	5.93	VS	0.0250	5.37	Inc	0.0986	4.72	U	0.0066	7.14	Mg	0.0106	7.61	T	0.0648	6.75
Mg	0.0252	6.68	U	0.0106	6.34	TopH	0.0234	5.56	Na	0.0666	4.97	CN	0.1638	4.38	Mg	0.0296	6.11	U	0.0024	7.29	TC	0.0028	6.66
TC	0.0036	6.66	Inc	0.0166	5.98	Mg	0.0564	5.53	TopH	0.0876	4.87	TopH	0.3390	3.87	Na	0.0222	5.89	Inc	0.0794	5.94	Sdp	0.0314	6.03
G _B -M	0.0162	6.18	Mg	0.0252	5.97	Inc	0.0638	5.13	Inc	0.0888	4.84	H _{min}	0.3400	3.84	Ca	0.0332	5.71	Sdp	0.0518	5.83	VS	0.0206	5.89
VS	0.0196	6.13	G _B -M	0.0170	5.92	Na	0.1304	4.75	CN	0.1996	4.40	Sdp	0.3584	3.82	Inc	0.0790	5.53	TopH	0.0364	5.79	G _B -M	0.0590	5.43
Sdp	0.0372	6.02	TopH	0.0360	5.56	FT-M	0.1410	4.70	Sdp	0.2714	4.23	HEL _B -M	0.4288	3.64	Sdp	0.0542	5.50	G _B -M	0.0550	5.74	Inc	0.1536	5.32
TopH	0.0264	6.02	Sdp	0.1622	4.78	CN	0.2198	4.43	Ca	0.2434	4.23	Ca	0.4294	3.62	G _B -M	0.0870	5.30	Na	0.0582	5.48	Mg	0.1196	5.18
Inc	0.1216	5.64	Sk	0.2488	4.62	DF-M	0.2664	4.29	H _{min}	0.3958	3.82	T _{ampl}	0.4752	3.52	VS	0.0778	5.17	Ca	0.0622	5.48	Sdp _{Ah}	0.1444	4.97
Ca	0.0684	5.50	pH	0.2042	4.62	Sdp	0.2926	4.27	HEL _B -M	0.4380	3.70	P	0.4446	3.50	TopH	0.0774	5.17	TC	0.1068	5.42	pH	0.2130	4.75
Na	0.0630	5.36	CN	0.2156	4.51	Ca	0.3106	4.15	T _{ampl}	0.4906	3.62	Na	0.5046	3.47	CN	0.1476	4.73	Sdp _{Ah}	0.1432	4.99	DF-M	0.2408	4.53
Sdp _{Ah}	0.1634	4.98	FT-M	0.2470	4.42	Sk	0.3764	4.04	Sdp _{Ah}	0.4722	3.60	Sdp _{Ah}	0.4814	3.47	K	0.2134	4.44	CN	0.1574	4.83	Na	0.2554	4.48
CN	0.1686	4.87	Sdp _{Ah}	0.2970	4.31	pH	0.4518	3.81	VPD _{max}	0.5034	3.57	VPD _{max}	0.4994	3.46	P	0.2656	4.33	pH	0.2828	4.45	Ca	0.2860	4.41
pH	0.2556	4.60	DF-M	0.3132	4.27	T _{ampl}	0.4684	3.73	DF-M	0.5178	3.53	DF-M	0.5858	3.28	Sdp _{Ah}	0.2758	4.26	HEL _B -M	0.2872	4.38	TD-M	0.3020	4.33
DF-M	0.2822	4.49	Na	0.3088	4.24	P	0.4940	3.63	P	0.4864	3.52	pH	0.5936	3.25	TC	0.2816	4.20	TD-M	0.2930	4.37	Sk	0.3146	4.30
Sk	0.3440	4.36	TD-M	0.3134	4.19	Sdp _{Ah}	0.5246	3.58	pH	0.5468	3.43	FT-M	0.6420	3.17	HEL _B -M	0.2842	4.19	K	0.2670	4.37	CN	0.3222	4.26
TD-M	0.3242	4.33	Ca	0.4242	3.93	H _{min}	0.5676	3.50	K	0.6878	3.19	K	0.6736	3.10	GI-M	0.2924	4.16	Sk	0.3708	4.15	K	0.5068	3.84
FT-M	0.3510	4.27	T _{ampl}	0.4868	3.78	VPD _{max}	0.6184	3.44	FT-M	0.6928	3.18	Sk	0.6632	2.91	FT-M	0.3474	4.01	P	0.4092	3.99	FT-M	0.5444	3.76
P	0.3698	4.17	HEL _B -M	0.5690	3.61	HEL _B -M	0.6900	3.25	Sk	0.6972	2.98	TD-M	0.7994	2.62	TD-M	0.3808	3.91	H _{min}	0.5656	3.61	HEL _B -M	0.5718	3.70
HEL _B -M	0.4286	4.08	VPD _{max}	0.6080	3.54	GI-M	0.8796	2.76	GI-M	0.9228	2.49	GI-M	0.9182	2.44	DF-M	0.5490	3.50	GI-M	0.6202	3.59	P	0.5056	3.65
K	0.4608	4.01	P	0.5624	3.53	K	0.9122	2.63	TD-M	0.9180	2.32	T	1.0000	0.00	H _{min}	0.5608	3.45	FT-M	0.6756	3.40	GI-M	0.6202	3.61
GI-M	0.6644	3.57	H _{min}	0.6358	3.45	TD-M	0.9376	2.31	T	1.0000	0.00	T	1.0000	0.00	Sk	0.6648	3.15	DF-M	0.7540	3.04	H _{min}	0.6444	3.43
H _{min}	0.6770	3.43	GI-M	0.7388	3.24	T	1.0000	0.00				pH	0.7246	3.10	VPD _{max}	0.8332	3.01	T _{ampl}	0.7064	3.37			
T _{ampl}	0.7366	3.40	K	0.8778	2.84							T _{ampl}	0.7118	3.07	T _{ampl}	0.9686	2.44	VPD _{max}	0.7688	3.21			
VPD _{max}	0.7736	3.26										VPD _{max}	0.7526	3.02									

A-Table 14. Environmental parameters measured for gap-plots (G). Given are the minimum (Min), the maximum (Max), the quartiles (Q25, Q75), and median (Med). * mark significant differences of gap plots and relevé plots of different vegetation types (pairwise comparison). Abbreviation of environmental parameters and vegetation types are given in A-Table 1.

Parameter	G (Min)	G (Q25)	G (Med)	G (Q75)	G (Max)	Significance level of pairwise comparison of G versus						
						SB	SM	ST	SW	WI	WU	WA
<i>K</i> (cmol _c kg ⁻¹)	0.09	0.15	0.19	0.22	0.36	-	-	-	-	-	-	-
<i>Na</i> (cmol _c kg ⁻¹)	0.02	0.02	0.02	0.03	1.07	*	-	-	-	-	-	-
<i>Ca</i> (cmol _c kg ⁻¹)	1.43	1.94	2.31	3.79	11.06	-	-	-	-	-	-	-
<i>Mg</i> (cmol _c kg ⁻¹)	0.38	0.67	0.90	1.13	3.44	-	-	-	-	-	-	-
<i>Bas</i> (cmol _c kg ⁻¹)	2.08	3.00	3.27	5.11	13.05	-	-	-	-	-	-	-
<i>P</i> (ppm)	0.44	0.59	0.62	0.78	8.49	-	*	-	-	*	-	-
<i>N</i> (%)	0.03	0.04	0.05	0.07	0.09	*	-	-	-	-	-	-
<i>C</i> (%)	0.24	0.62	0.82	1.17	1.58	-	-	-	-	-	-	-
<i>C/N</i>	9.3	13.8	15.5	16.5	17.9	-	-	-	-	-	-	-
<i>Sk</i> (%)	0.52	0.90	2.49	5.80	27.11	*	*	-	-	-	-	*
<i>pH</i>	5.26	5.71	5.77	5.97	7.33	*	*	-	*	-	-	-
<i>S</i> (%)	71.0	72.4	74.8	76.4	79.4	*	-	-	-	-	-	-
<i>U</i> (%)	14.6	15.1	16.4	18.4	20.2	*	-	-	-	-	-	*
<i>T</i> (%)	5.9	6.9	8.6	9.8	10.8	-	-	-	-	-	-	-
<i>Sdp</i> (cm)	35.0	42.5	55.0	73.0	84.0	*	*	-	*	-	-	*
<i>Sdp_{Ab}</i> (cm)	8.5	10.8	16.3	19.4	20.0	*	*	-	*	*	-	*
<i>VS</i> (%)	0.25	0.31	0.34	0.36	0.50	*	*	-	-	*	*	*
<i>ISF</i> (%)	0.34	0.43	0.46	0.49	0.68	*	*	-	-	*	*	*
<i>DSF</i> (%)	0.38	0.47	0.56	0.57	0.82	*	*	-	-	*	*	*
<i>GSF</i> (%)	0.38	0.46	0.55	0.56	0.80	*	*	-	-	*	*	*
<i>LAI</i>	0.58	0.92	1.00	1.12	1.39	*	*	-	-	*	*	*
<i>H_{min}</i> (%)	41.1	42.1	43.1	47.2	51.0	-	-	-	*	*	*	*
<i>T_{ampl}</i> (°C)	12.7	14.6	15.3	15.8	16.3	*	-	-	*	*	*	*
<i>VDP_{max}</i> (%)	25.0	30.2	32.3	35.3	36.5	-	-	-	*	*	*	*
<i>DF-01</i>	04.01.02	05.01.02	05.01.02	18.02.02	04.04.02	-	-	*	-	*	-	-
<i>DF-02</i>	01.01.03	01.01.03	04.01.03	11.03.03	30.03.03	-	-	-	-	-	-	-
<i>FT-01</i> (°C)	0	365	435	505	600	-	-	-	*	*	-	*
<i>FT-02</i> (°C)	0	324	413	505	600	-	-	-	-	-	-	-
<i>TopH</i> (m)	11	13	15	17	26	*	*	*	*	*	-	-
<i>Inc</i> (%)	1	1	1	1	3	*	*	-	*	-	*	-
<i>Exp</i> (°)	30	62	117	216	390	-	-	-	-	-	-	-
<i>G_{B-01}</i> (t ha ⁻¹)	1.33	1.78	2.28	2.48	3.30	*	*	*	-	*	-	*
<i>G_{B-02}</i> (t ha ⁻¹)	0.44	1.84	2.49	3.18	4.53	*	*	-	-	*	-	*
<i>G_{C-01}</i> (%)	15	26	30	58	75	*	*	-	*	*	-	*
<i>G_{C-02}</i> (%)	40	45	53	64	70	*	*	-	-	*	*	*
<i>G_{H-01}</i> (cm)	210	220	235	288	350	-	-	-	-	-	-	-
<i>G_{H-02}</i> (cm)	180	195	210	220	260	*	-	-	-	-	-	-
<i>G_{Vol-01}</i> (m ³ m ⁻²)	0.32	0.62	0.83	1.42	1.65	-	-	-	-	-	-	-
<i>G_{Vol-02}</i> (m ³ m ⁻²)	0.72	0.92	1.20	1.27	1.54	-	-	-	-	-	-	-

Continuation of A-Table 14.

Parameter	G (Min)	G (Q25)	G (Med)	G (Q75)	G (Max)	Significance level of pairwise comparison of G versus						
						SB	SM	ST	SW	WI	WU	WA
<i>HE_B-01</i> (t ha ⁻¹)	0.00	0.24	0.38	0.67	1.31
<i>HE_B-02</i> (t ha ⁻¹)	0.39	0.52	0.71	0.97	1.52	*	*
<i>HE_C-01</i> (%)	3	10	15	24	40	*	*	*	*	.	.	.
<i>HE_C-02</i> (%)	15	20	25	39	45	*	*	.	.	*	*	*
<i>HE_F-01</i> (cm)	40	120	135	160	200	*	*
<i>HE_F-02</i> (cm)	50	120	120	140	190	*	*	*	.	*	.	.
<i>HE_{Vol}-01</i> (m ³ m ⁻²)	0.01	0.11	0.22	0.44	0.56	*
<i>HE_{Vol}-02</i> (m ³ m ⁻²)	0.08	0.26	0.31	0.46	0.76	*	*
<i>L_B-01</i> (t ha ⁻¹)	0.57	0.67	0.93	1.44	1.63	*
<i>L_B-02</i> (t ha ⁻¹)	0.22	0.63	0.92	1.64	2.71	*	*
<i>L_C-01</i> (%)	5	9	12	17	20	*
<i>L_C-02</i> (%)	15	20	20	24	35	*	*
<i>LG_C-01</i> (%)	2	2	3	4	5	*	*	.	*	.	.	.
<i>LG_C-02</i> (%)	5	5	5	5	10	*	*
<i>LNG_C-01</i> (%)	3	5	9	13	16	*	*	*
<i>LNG_C-02</i> (%)	7	11	15	19	30	*	*	.	.	*	.	.
<i>DWB_C-01</i> (%)	0	1	2	7	12	.	*	*	.	*	.	.
<i>DWB_C-02</i> (%)	0	2	4	9	15	.	.	*
<i>OG_C-01</i> (%)	5	11	15	15	25	*	*	*	*	.	.	.
<i>OG_C-02</i> (%)	5	10	10	14	15	*	*	*
<i>TM-01</i> (%)	0	0	0	0	3	*
<i>TM-02</i> (%)	0	0	0	0	0	*	*	.	.	.	*	.
<i>GI-01</i> (%)	30	40	50	58	60	*	.	*	*	*	*	*
<i>GI-02</i> (%)	5	13	50	64	95	*	.	*
<i>TD-01</i>	2	2	2	3	4
<i>TD-02</i>	2	3	3	3	4

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- July 13, 1972 Born in Paderborn, Germany
- 1978-1982 Primary school, Wachenheim
- 1982-1991 Werner-Heisenberg-Gymnasium, Bad Dürkheim (Abitur)
- 1991-1992 assistant collaborator in projects on nature protection (ADENEX – association for the protection of nature and resources in the Extremadura), Mérida, Spain
- 1992-1994 Studies in biology at the University of Mainz (Vordiplom)
- 1994-1998 Studies in biology at the University of Göttingen (Diploma), subjects: botany, zoology, soil science
- Diploma thesis: Studies on vegetation of dry grasslands and soil conditions on Andesit- and Rhyolit-outcrops along a climatic gradient in the Nahe-valley, Rheinland-Pfalz
- 1995-1999 Student and graduate assistant at the Department of Botany, University of Göttingen
- 1999-2000 Scientific collaborator at the Department of Botany, University of Kaiserslautern: Feasibility study for the experimental station of silviculture in Trippstadt
- 2000-2005 Scientific employee in the BMBF-project IMPETUS (Integratives Management Projekt für den effizienten und tragfähigen Umgang mit der Ressource Süßwasser), Department of Botany, University of Rostock

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