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Marine Pasturel, Anne Alexandre, Alice Novello, Amadou M Dièye, Abdoulaye Wélé, et al.. Grass Physiognomic Trait Variation in African Herbaceous Biomes. *Biotropica*, 2016, 48 (3), pp.311 - 320. 10.1111/btp.12282 . hal-01909495

HAL Id: hal-01909495

<https://hal.science/hal-01909495>

Submitted on 14 Dec 2018

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Grass Physiognomic Trait Variation in African Herbaceous Biomes

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ABSTRACT

African herbaceous biomes will likely face drastic changes in the near future, due to climate change and pressures from increasing human activities. However, these biomes have been simulated only by dynamic global vegetation models and failing to include the diversity of C₄ grasses has limited the accuracy of these models. Characterizing the floristic and physiognomic diversity of these herbaceous biomes would enhance the parameterization of C₄ grass plant functional types, thereby improving simulations. To this end, we used lowermost and uppermost values of three grass physiognomic traits (culm height, leaf length, and leaf width) available in most floras to identify several grass physiognomic groups that form the grass cover in Senegal. We then checked the capacity of these groups to discriminate herbaceous biomes and mean annual precipitation domains. Specifically, we assessed whether these groups were sufficiently generic and robust to be applied to neighboring (Chad) and distant (South Africa) phytogeographic areas. The proportions of two physiognomic groups, defined by their lowermost limits, delineate steppe from savanna and forest biomes in Senegal, and nama-karoo, savanna, and grassland biomes in South Africa. Proportions of these two physiognomic groups additionally delineate the mean annual precipitation domains <600 mm and >600 mm in Senegal, Chad, and South Africa, as well as the <250 mm and >1000 mm domains in South Africa. These findings should help to identify and parameterize new C₄ grass plant functional types in vegetation models applied to West and South Africa.

Key words: Africa; cluster analysis; culm height; grasses; mean annual precipitation; physiognomic trait.

HERBACEOUS BIOMES ARE AMONG THE MOST VULNERABLE ECOSYSTEMS TO CLIMATE CHANGE AND TO increasing human pressure (Sala *et al.* 2000, Parr *et al.* 2014). They occupy a fifth of the global terrestrial surface and are as widespread in the tropics as tropical forests (Scurlock & Hall 1998). In continental Africa, where they can be categorized as savanna, steppe, and high-altitude grassland (Yangambi classification: CSA 1956, Mucina & Rutherford 2006), they cover half of the continent's surface and support a large proportion of its human population (Scholes & Archer 1997). These herbaceous biomes are dominated by grasses, representing up to 75–90 percent of the aboveground biomass (Garnier & Dajoz 2001), and are characterized by high floristic and physiognomic diversity (CSA 1956, Mucina & Rutherford 2006).

Dynamic Global Vegetation Models (DGVMs) [e.g., CARAIB (François *et al.* 1998), ORCHIDEE (De Noblet-Ducoudre *et al.* 2004), and LPJ-GUESS (Smith *et al.* 2001)] are state-of-the-art tools for producing simulations of vegetation dynamics to aid

land management decisions. However, as DGVMs were first developed with an emphasis on global, boreal, and temperate regions, they do not adequately represent tropical grass diversity. Only two tree and one C₄ grass plant functional type (PFT) were parameterized for tropical regions. Additionally, human impacts were not included in early versions of the models (Smith *et al.* 2001, Sitch *et al.* 2003). As a result, simulated limits of tropical herbaceous biomes, distinguished by changes in dominant natural PFTs (Prentice *et al.* 1992, Jolly *et al.* 1998, Harrison & Prentice 2003, Hély *et al.* 2006), matched vegetation maps poorly (Gaucherel *et al.* 2008). This mismatch, in turn, weakened our appreciation of ecosystem degradation in tests of past and future effects of climate change (Hély *et al.* 2009, O'ishi & Abe-Ouchi 2013). Efforts are thus needed to enhance the C₄ grass PFTs parameterization in vegetation models. Specifically, the floristic and physiognomic diversities of the tropical herbaceous biomes need to be characterized, and the relationship between grass cover and bioclimatic constraints needs to be assessed (Jackson *et al.* 2002, Sankaran *et al.* 2004, Parr *et al.* 2014).

Received 26 October 2014; revision accepted 18 August 2015.

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Plant specialization leads to a trade-off between physiological and physiognomic traits, inducing high rates of resource acquisition under non-limiting conditions and retention of resource capital under limiting conditions (Grime *et al.* 1997). This was recently expressed by statistical relationships established between grass physiognomic traits and biomass (Georgiadis 1989, Guevara *et al.* 2002), leaf area index (Lang & Xiang 1986), and climate (Skarpe 1996, Devineau & Fournier 2005, Schmidt *et al.* 2011) in tropical areas. Here, we used three grass physiognomic traits commonly described in floras (culm height, leaf length, and leaf width) to identify several grass physiognomic groups in Senegal. The objective was to identify relationships required for creating new C_4 grass plant functional types in vegetation models. To account for the range of trait values observed for each species across its ecological niche, the values of the uppermost and lowermost limits of the three traits were taken into account. We checked the capacity of the defined physiognomic groups to discriminate herbaceous biomes and mean annual precipitation (MAP) domains. We also assessed if the groups were sufficiently generic and robust to be applied to a neighboring phytogeographic area (Chad) and to the austral area (South Africa) where different climatic, topographic, and anthropic constraints explain the spatial distribution of grasses. We initially focused on Senegal, as the floristic composition of the Senegalese herbaceous biomes clearly varies latitudinally across a MAP gradient and has been inventoried in detail.

METHODS

GRASS SPECIES DATASETS.—In West Africa, grass cover increases in abundance and continuity from North to South, and from the steppe to the savanna and forest biomes (CSA 1956), distributed along a MAP gradient of 200–1800 mm. Here, we define steppe as dry tropical grasslands at low elevation.

Floras of the Sahelo-Sudanian area include a great number of grass species (Poilecot 1999, Thiombiano *et al.* 2012, Brundu & Camarda 2013), most of the species being non-dominant (CSA 1956, Mbow *et al.* 2013). We chose to limit our investigation to dominant grass species, which are more relevant for describing the grass cover physiognomy, using the vegetation map of Senegal and of Gambia (based on ground surveys, Stancioff *et al.* 1986) for dominant grass species selection. The extent of tree cover and the dominant natural tree, shrub, grass, and other herbaceous species were used to identify the forest, savanna, and steppe biomes (Fig. 1A), themselves divided into vegetation types and subtypes. Vegetation subtypes were mapped as polygons ranging from 0.16 to 5586 km², and 1–3 dominant grass species were listed per subtype (Stancioff *et al.* 1986). We did not include vegetation subtypes *a priori* assessed as edaphic rather than climatic, such as wetlands, valleys, and gallery forests (~25% of the investigated area). A total of 32 grass species from 28 subtypes of steppe, 75 subtypes of savanna, and 7 subtypes of forest made up the Senegal dataset (Table S1). To account for grass species characterizing areas in West Africa which are drier than in Senegal (<200 mm of MAP), we included nine grass species inventoried from two sites in south-

ern Mauritania (Naegelé 1958, Assemien 1971) in the dataset (Table S1). However, due to the lack of accurate coordinates and associated biome description, we did not include Mauritanian sites when assessing the statistical relationships between grass physiognomic groups, biomes, and precipitations (see below).

In Chad, a grass species inventory was conducted in 2010 at 2 steppe, 25 savanna, and 3 forest (palm groves) sites (Fig. 1B; Novello 2012, Novello *et al.* 2012). The MAP at the sampled sites ranged from 282 to 989 mm (Hijmans *et al.* 2005). To match the Senegal dominant grass species dataset, we extracted the two most abundant grass species per site from this inventory. The final dataset from Chad included 41 species (Table S1).

The vegetation map of South Africa, Lesotho, and Swaziland (Mucina & Rutherford 2006) also presented biomes divided into vegetation types and subtypes (mapped as polygons of 0.01–43,818 km²) based on their floristic composition. We analyzed five biomes characterized by a significant or dominant grass layer (Mucina & Rutherford 2006): desert, nama-karoo, grassland, savanna, and Indian Ocean coastal belt (IOCB) (Fig. 1C). These biomes had MAP values of 45 to more than 2500 mm. The nama-karoo biome is physiognomically close to the semiarid steppe biome in West Africa although its floristic composition is different (Cordova *et al.* 2013). The IOCB is a mosaic of grassland, savanna, and forest units. Mucina and Rutherford (2006) listed from 0 to 24 dominant grass species per subtype. In the absence of any arguments to justify selecting some dominant species rather than others, they were all included in the analysis. The final dataset from South Africa constituted 164 grass species from 15 desert, 14 Nama-Karoo, 72 grassland, 87 savanna, and 5 IOCB subtypes (Table S1).

GRASS TRAITS AND PRECIPITATION DATASETS.—For each grass species, we extracted the uppermost and lowermost limits of culm height, leaf length, and leaf width from regional and global grass data bases (Poilecot 1999, Clayton *et al.* 2006). When the two sources disagreed on the trait in question, we used the extreme values (Table S1). We additionally assigned grass species (Table S1) three biological and taxonomical characteristics (Poilecot 1999, Clayton *et al.* 2006, Linder *et al.* 2010, Peterson *et al.* 2011): grass subfamily (Pooideae, Bambusoideae, Ehrhartoideae, Chloridoideae, Aristidoideae, Danthonioideae, and Panicoideae), photosynthetic pathway (C_3 vs. C_4), and life cycle (annual vs. perennial). We ascribed a perennality proportion of 1, 0.75, 0.25, or 0 to each species, according to its description as ‘perennial’, ‘perennial sometimes annual’, ‘annual sometimes perennial’, or ‘annual’ in floras.

We extracted terrestrial MAP values from the WORLDCLIM data base (Hijmans *et al.* 2005) at coordinates of the Chadian sites and at coordinates of the centroid of every digitized polygon of the Senegal and South Africa maps. We computed polygon centroids using the Centroid function from the ArcMAP 10.0 software (ESRI 2010), with the INSIDE option selected. As several centroids (15 Senegalese and 2 South African coastal polygons) fell outside of the continental climate pixels, we manually reassigned them to the nearest continental climate pixel.

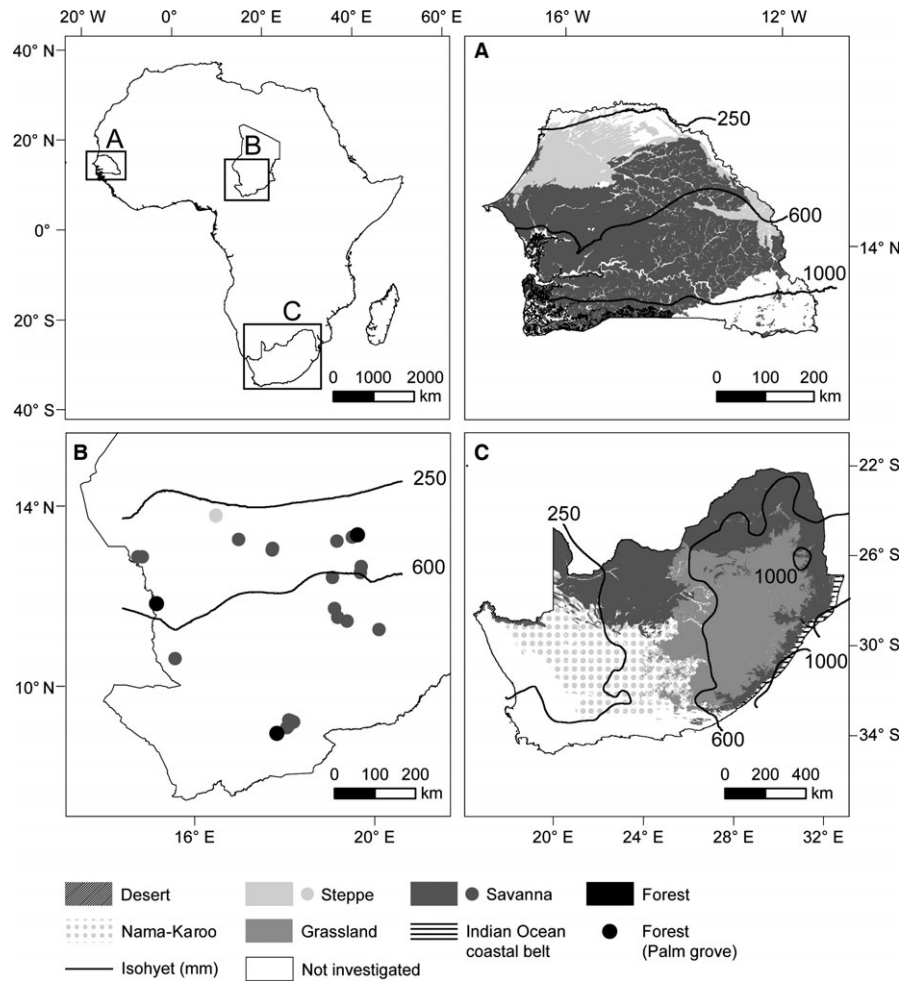


FIGURE 1. Location of the three African study areas (top left box), spatial distribution of biomes, and mean annual precipitation (MAP; Hijmans *et al.* 2005) domains delimited by the isohyets 250 mm, 600 mm, and 1000 mm in (A) Senegal, (B) Chad, and (C) South Africa. Senegal and South Africa biome maps were adapted from digitized maps from Stancioff *et al.* (1986) and Mucina and Rutherford (2006), respectively. Chad biome map was based on 30 sites described in Novello (2012) and Novello *et al.* (2012).

STATISTICAL ANALYSES.—We carried out statistical and spatial distribution analyses using the R 3.0.1 software (R Development Core Team 2013) and the ArcMap 10.0 software, respectively. We considered a *P*-value lower than 0.05 significant for all tests.

STEP 1: DEFINITION AND SPATIAL DISTRIBUTION OF PHYSIOGNOMIC GROUPS.—To identify physiognomic groups relevant for future *C*₄ grass PFTs definition, we performed two cluster analyses separately on uppermost and lowermost values of culm height, leaf length, and leaf width of the Senegal grass species. We chose the Partition Around Medoid (PAM) method (Kaufman & Rousseeuw 1990) to cluster the trait dataset into *k* groups (cluster R package, Maechler *et al.* 2013). This method has the advantage of selecting an existing individual for each *k* group centroid (medoid). A second advantage is that an average silhouette (AS) value indicates the significance of each *k* built group, as well as of the overall grouping (good if AS > 0.5). Among distance com-

putation choices, the Manhattan distance provided the best AS and was selected for the two cluster analyses, whereas we tested the best number of grass groups (*k*) to be built from the trait dataset for *k* values ranging from 2 to 11 groups, based on the best AS result.

We quantified the representation of grass subfamily, life cycle, and photosynthetic pathways in each physiognomic group *a posteriori*. We characterized each vegetation subtype by the groups with which dominant species were affiliated, using matrix multiplication between the subtype/species and the species/group matrices. We report the results as proportions assigned to every digitized polygon of the Senegal map.

Physiognomic groups could not be directly defined from the South African dominant grass species (AS < 0.5). The large number of species (up to 24) listed per vegetation subtype (Mucina & Rutherford 2006) potentially explains this absence of dominant physiognomy. In Chad, we considered the local grass species

inventory as not representative of the regional vegetation. Finally, we separately assigned grass species from Chad and South Africa to the physiognomic groups previously defined from the Senegal grasses, based on their shortest trait value distance to a group medoid. We assessed the biological and taxonomical characteristics and the spatial distributions of Chadian and Southern African groups using the same methods as for Senegal.

STEP 2: MAP DOMAINS AND BIOMES ASSOCIATED WITH PHYSIOGNOMIC GROUPS.—In Africa the 600 and 1000 mm isohyets are captured by changes in tree cover density (Sankaran *et al.* 2005, Staver *et al.* 2011), whereas the 250 mm isohyet is characterized by changes in tree floristic composition (e.g., White 1983). Here, we aimed to assess if the MAP domains <250, 250–600, 600–1000, and >1000 mm are reflected in grass cover physiognomy.

For Senegal and South Africa, a MAP domain was attributed to each polygon centroid, in addition to physiognomic group composition and biome type. We tested if the proportion of a given grass group was different among the four delimited MAP domains using Kruskal–Wallis tests (Siegel & Castellan 1988), and pinpointed significant differences using the ‘kruskalmc’ R function (pgirmess package, Giraudoux 2013). We used the Wilcoxon test (Gehan 1965) for the Chad dataset as it covered only two MAP domains (<600 and >600 mm). We used a similar approach to test if the proportion of a given grass group differed among different biomes.

RESULTS

CHARACTERIZATION AND SPATIAL DISTRIBUTION OF PHYSIOGNOMIC GROUPS.—The cluster analyses run on the grass physiognomic trait data base from Senegal revealed three groups based on trait uppermost limits, and five groups based on lowermost limits (Table S2). We named these groups according to their culm height medoid, (e.g., up100 for ‘uppermost height limit of 100 cm’ group and low10 for ‘lowermost height limit of 10 cm’ group). AS values of 0.72 and 0.62, obtained for groups based on uppermost and lowermost limit value, respectively, showed that the definition of each group and the total number of groups were relevant. Groups obtained through cluster analyses varied similarly on grass culm height, leaf length, and leaf width. Among the three groups identified based on trait uppermost limit values, the short-grass group up100 included 33 species, the medium-sized-grass group up360 included 7 species, and the tall-grass group up1000 included a single species of bamboo (*Oxytenanthera abyssinica*; Table S1). Among the five groups identified based on the lowermost trait limit values, the short-grass group low10 contained 18 species, the medium-sized grass group low30 contained 15 species, the tall-grass group low100 contained 6 species, and the tall-grass groups low200 and low300 contained 1 species each (*Andropogon tectorum* and *O. abyssinica*, respectively; Table S1). Allocation of all grass species from Chad and South Africa to these groups (Table S1) showed that the majority of the South African grass species (>66%) belonged to the low30 and up100 groups. No species

from Chad or South Africa were assigned to the tall-grass groups up1000 and low300.

As expected, in the three regions, species included in the short-, medium-sized-, or tall-grass groups defined according to the lowermost limit of physiognomic traits also belonged to the short, medium-sized, or tall groups defined according to the uppermost limit of physiognomic traits (Table S3). Therefore, we chose to focus on the groups based on the lowermost values of traits. Statistical results obtained for the groups based on the uppermost values are presented in Supporting Information (Figs S1 and S2; Tables S4 and S5). The up1000 and low300 groups were discarded from the analysis as they represented only a single species in Senegal.

Regarding grass subfamilies, the Panicoideae and Chloridoideae were the main subfamilies represented in the grass datasets (>70%). In the three regions, all groups were dominated by Panicoideae species, except the shortest group low10, which was dominated by Chloridoideae species.

In Senegal and Chad, annual grass species dominated the short-grass group low10 (Fig. S1). Annual and perennial grass species were mixed in medium-sized and tall-grass groups low30 and low100. Perennial grass species dominated the tall-grass group low200. The tall-grass group low300, only composed of the bamboo species, were perennial, as expected. In South Africa, perennial species dominated all groups (>90% of perennials).

In Senegal, Chad, and South Africa, the C₄ photosynthetic pathway represented 95, 100, and 92 percent of the dominant grass species, respectively. All 15 C₃ species were perennial and most of them (13 of 15) belonged to the medium-sized-grass group low30 (Table S1).

The spatial distribution of low10 and low30 groups highlighted several regional patterns (Fig. 2). The short-grass group low10 was present in the driest northern part of Senegal (>14°N) and its proportion decreased from north to south. It was widespread in South Africa where its proportion decreased from east to west. The medium-sized-grass group low30 was widespread in the three regions. Its proportion varied in the opposite direction as the low10 group. The tall-grass groups low100, low200, and low300 presented localized occurrences in coastal areas and valleys with high local water availability (Fig. 2). In South Africa, the low100 group also characterized the Kalahari and occurred in few sites with specific edaphic characteristics or disturbed environments, such as rich clay soils or overgrazed areas.

PHYSIOGNOMIC GROUP PROPORTIONS DISTINCTIVE OF MAP DOMAINS.—Within short- and medium-sized grass groups, opposite proportions of low10 and low30 distinguished the <600 mm and >600 mm MAP domains in Senegal (Table 1), with the highest proportion of low10 (>55 ± 35%) at <600 mm and the highest proportion of low30 (>82 ± 25%) at >600 mm. Group proportions did not differ between the <250 mm and 250–600 mm, or between 600 and 1000 mm and >1000 mm MAP domains, respectively. However, when defined on their uppermost trait limit, the proportion of medium-sized grasses (up360) were statistically higher in the >1000 mm MAP domain. In the

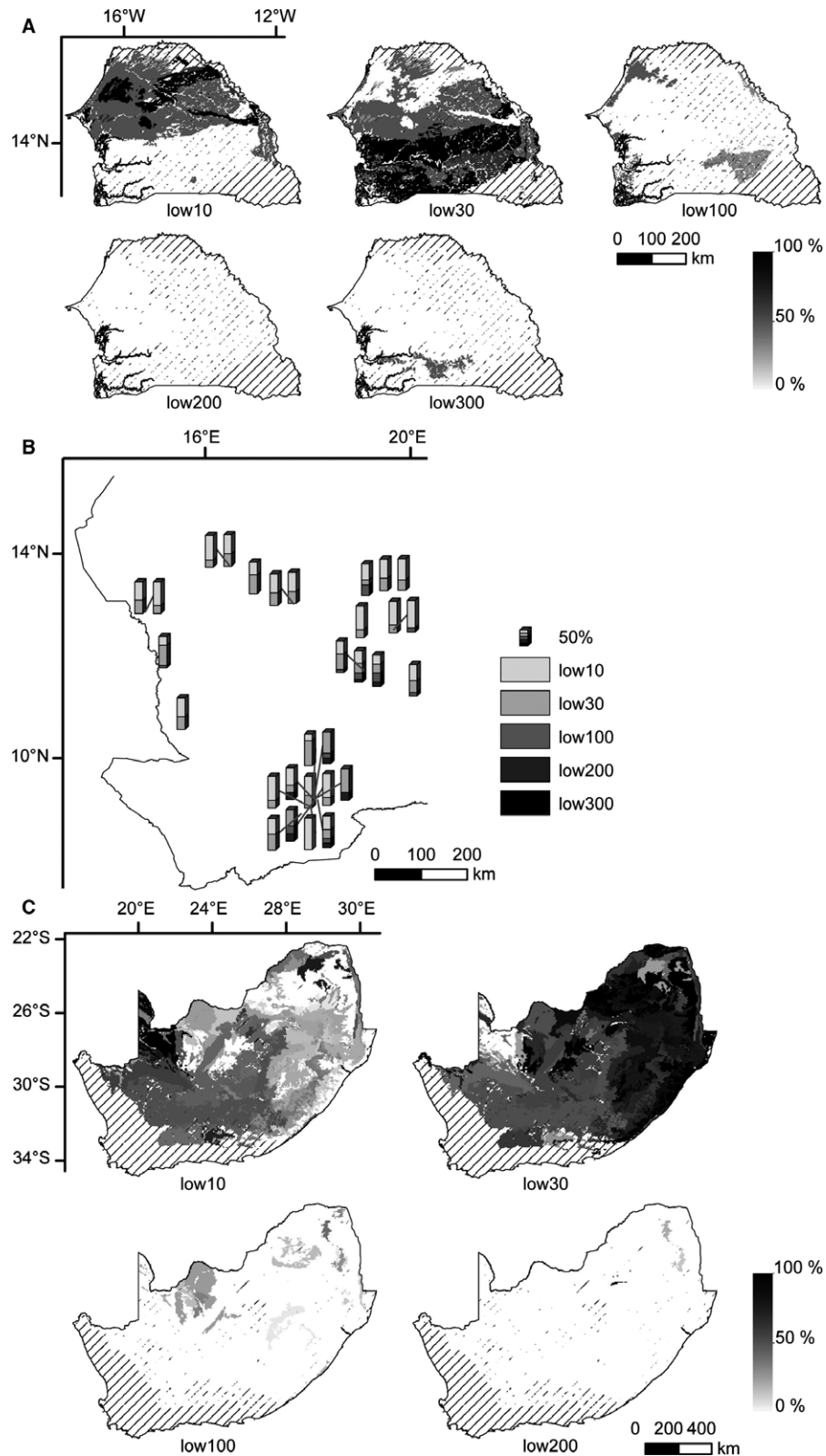


FIGURE 2. Spatial abundance of the grass groups defined by their lowermost limit of physiognomic traits (expressed as percentage of grass species of a given group) in (A) Senegal, (B) Chad, and (C) South Africa. Hatched areas, representative of edaphic or particular conditions, were not taken into account in this study.

TABLE 1. Proportion of grass groups defined according to their lowermost limit of physiognomic traits (column) per mean annual precipitation (MAP) domain (line) for Senegal, Chad, and South Africa. Values are expressed in percentage of grass species: mean and (standard deviation; with (–) if only one occurrence). Different letters indicate significant differences from the Kruskal–Wallis test in group proportion among MAP domains for a given region ($P < 0.05$). No letter means no significant difference.

MAP domain	low10	low30	low100	low200
Senegal				
<250 mm	70 (32) ^a	23 (32) ^b	7 (18) ^{ab}	0 (0)
250–600 mm	55 (35) ^a	41 (36) ^b	4 (14) ^b	0 (0)
600–1000 mm	5 (16) ^b	82 (25) ^a	10 (20) ^a	0 (0)
>1000 mm	2 (10) ^b	83 (35) ^a	14 (33) ^{ab}	1 (6)
Chad				
250–600 mm	52 (19) ^a	43 (20)	4 (10) ^b	0 (–)
600–1000 mm	46 (29) ^b	37 (18)	10 (12) ^a	10 (–)
South Africa				
<250 mm	48 (16) ^a	50 (16) ^d	1 (5) ^{bc}	0 (0)
250–600 mm	35 (17) ^b	64 (16) ^c	1 (5) ^c	0 (0)
600–1000 mm	16 (15) ^c	81 (17) ^a	2 (8) ^b	0 (5)
>1000 mm	15 (19) ^c	74 (27) ^b	6 (13) ^a	0 (2)

Chadian area, the proportion of the short-grass group low10 differed between the <600 and >600 mm MAP domains, with the highest proportion of low10 ($52 \pm 19\%$) at <600 mm, alike in Senegal. In South Africa, the medium-sized-grass group low30 distinguished four MAP domains (<250 mm, 250–600 mm, 600–1000 mm, and >1000 mm), its proportion increasing from $50 \pm 16\%$ at <250 mm to $81 \pm 17\%$ in the 600–1000 mm MAP domain. The proportion of the short-grass group low10, increasing from wet to dry areas, distinguished the three MAP domains <250 mm, 250–600 mm, and >600 mm.

PHYSIOGNOMIC GROUP PROPORTIONS DISTINCTIVE OF BIOMES.—In Senegal, the steppe biome was distinguished by the highest proportion of the short-grass group low10 ($60 \pm 36\%$) and the lowest proportion of the medium-sized-grass group m30 ($34 \pm 38\%$; Table 2). Conversely, the forest and savanna biomes were characterized by the highest proportion of the medium-sized-grass group low30 ($>69 \pm 38\%$). In Chad, the low10 group proportion was close to that found in Senegal, but was not statistically different among biomes. This may be explained by the small representation of steppe sites (2) relative to savanna sites (25) in the Chad dataset. In South Africa, the nama-karoo biome was distinguished from the other biomes by having the highest proportion of the short-grass group low10 ($48 \pm 7\%$). The savanna biome was distinguished by a significantly high proportion of the medium-sized-grass group low30 ($81 \pm 23\%$) and low proportion of low10 ($15 \pm 21\%$). The grassland biome was distinguished from the other biomes by significantly intermediate

TABLE 2. Proportion of grass groups defined according to their lowermost limit of physiognomic traits (column) per biome (line) for Senegal, Chad, and South Africa. Values are expressed in percentage of grass species: mean and (standard deviation; with (–) if only one occurrence). Different letters indicate significant differences from the Kruskal–Wallis test in group proportion among biomes for a given region ($P < 0.05$). No letter means no significant difference.

	low10	low30	low100	low200
Senegal				
Steppe	60 (36) ^a	34 (38) ^b	7 (17) ^b	0 (0)
Savanna	11 (25) ^b	79 (32) ^a	9 (23) ^b	0 (0)
Forest	2 (9) ^b	69 (38) ^a	27 (35) ^a	2 (11)
Chad				
Steppe	48 (20)	49 (15)	3 (5)	0 (0)
Savanna	48 (27)	38 (20)	9 (12)	5 (9)
Forest	58 (12)	42 (12)	0 (0)	0 (0)
South Africa				
Desert	22 (33) ^{cd}	67 (37) ^{ab}	3 (10) ^{abc}	0 (0)
Nama-karoo	48 (7) ^a	52 (7) ^d	0 (0) ^c	0 (0)
Grassland	28 (14) ^b	68 (15) ^c	2 (9) ^b	0 (0)
Savanna	15 (21) ^c	81 (23) ^b	4 (8) ^a	1 (6)
IOCB	7 (17) ^d	92 (17) ^a	1 (4) ^{abc}	0 (0)

proportions of both low10 and low30 ($28 \pm 14\%$ and $68 \pm 15\%$, respectively). The IOCB biome was distinguished from the nama-karoo, grassland, and savanna biomes by the highest proportion of low30 ($92 \pm 17\%$) and the lowest proportion of low10 ($7 \pm 17\%$). These proportions were also found in the desert biome, which made the two biomes undistinguishable. The desert biome could not be discriminated from the other biomes due to high standard deviations associated with the abundances of the physiognomic groups.

DISCUSSION

THE PHYSIOGNOMIC GROUPS RELEVANT TO DISTINGUISH MAP DOMAINS AND BIOMES.—Uppermost and lowermost limit values of culm height, leaf width, and leaf length of grasses dominating the herbaceous biomes in Senegal, Chad, and South Africa were sufficiently variable to discriminate eight physiognomic groups. Among these eight groups, two groups (low10 and low30) were relevant to trace MAP domains previously associated with African vegetation types described through their tree component. The <600 mm and >600 mm MAP domains were indeed clearly characterized from the proportions of the short grasses (low10) varying inversely with the proportions of the medium-sized grasses (low30). This agrees with the spatial distribution of short- and tall-grass groups (based on culm height averages) previously found in Burkina Faso (Schmidt *et al.* 2011), which suggests a rainfall-dependent spatial pattern valid at the West African scale. Although high proportions of short grasses differentiated the

<250 mm MAP domain in South Africa, this was not the case in Senegal. This difference may result from a methodological bias, as the >250 mm MAP domain was underrepresented in the original Senegal dataset (1% of the mapped centroids). The distribution of the short and medium-sized grasses also allowed us to discriminate the steppe from the savanna and forest biomes in Senegal, and the nama-karoo, savanna, and grassland biomes in South Africa. The proportions of the short grasses (low10) were maximal in steppe and nama-karoo (steppe-like) biomes, whereas the proportions of the medium-sized grasses (low30) were higher in savanna and grassland biomes than in steppe. In the desert biome, high standard deviations associated with physiognomic group abundances indicated high variability in composition and physiognomy of the grass layer (Table 2), preventing discrimination of the desert biome.

The short and medium-sized grasses low10 and low30 showed biological and taxonomical characteristics relevant to definition and parameterization of future PFTs. As expected in intertropical low elevation and high temperature habitats (Vogel *et al.* 1978, Livingstone & Clayton 1980, Sage *et al.* 1999), all were dominated by C_4 grasses. The short-grass group (low10) is mainly composed of Chloridoideae species, known to dominate in warm and dry habitats (Gibbs Russell 1988, Liu *et al.* 2012). Although most short grass species are annual in Senegal and Chad (>80% of the grass species), they are quasi-exclusively perennial in South Africa. However, it is worth noting that species can regionally or locally modify their life cycles. For example, the short species *Aristida congesta* is described as annual or short-lived perennial in the Karoo (O'Connor & Roux 1995), whereas it is described as perennial in the global data base (Clayton *et al.* 2006). The medium-sized and tall grasses (low30, low100, and low200) are dominated by Panicoideae species, known to develop wide leaves under conditions of high water availability (Liu *et al.* 2012). No groups could be physiognomically defined for South Africa due to its highly heterogeneous grass cover, which is rich in endemic and disjunctive species (Gibbs-Russell *et al.* 1990, Mucina & Rutherford 2006, Cordova *et al.* 2013). The use of the groups characterized in Senegal allowed us to bypass this issue and highlighted regional tendencies, thus validating the use of the physiognomic groups for parameterization of grass PFTs.

To our knowledge, the only vegetation classification that discriminates Sub-Saharan African herbaceous biomes according to their grass cover is the Yangambi classification (CSA 1956). It assumed a grass height threshold of 80 cm to discriminate steppes from savannas. However, the high degree of culm height variability within a given group (Table S2) suggests that the use of height ranges should be preferred to height thresholds.

THE TALL-GRASS GROUPS LOW100, LOW200, AND LOW300: LOCAL MARKERS OF PARTICULAR CONDITIONS.—These tall-grass groups are present in areas where water does not seem to be a limiting factor. The low100 grasses are abundant along the coast in Senegal where relative humidity is higher than inland and where the range of diurnal temperatures is the narrowest in Senegal (New *et al.*

2002). These grasses are also reported inland in Senegal and South Africa, in areas where dense river networks, associated with closed canopy vegetation (forest or wooded savannas), keep the atmosphere moist. In South Africa, they also occur in overgrazed areas (e.g., *Aristida meridionalis* in Kalahari; Cordova, pers. comms.).

The tall grass species that constitute the group low200 in Senegal and South Africa occur in the wettest areas close to permanent or temporary streams. In Senegal, consistent with the ecological preferences of bamboo species (Inada & Hall 2008), the tallest grass species *O. abyssinica* that constitutes the group low300 occurs only in areas that are wet and have mean annual temperatures cooler than 28°C (New *et al.* 2002). Finally, although tall grasses (low100, low200, and low300) occupy small localities in Senegal and South Africa, they indicate special conditions that may be worth noting for local environmental reconstruction.

DRAWBACKS AND ADVANTAGES OF THE SELECTED METHODOLOGY FOR IDENTIFYING NEW C_4 GRASS PFTs.—Soil properties (e.g., clay or silt content, bulk density, organic carbon content) were not taken into account when characterizing the link between grass physiognomic groups, biomes, and MAP domains. Nevertheless, they are expected to influence the floristic composition and productivity of the herbaceous cover, by altering water and nutrient availability (Knoop & Walker 1985, Weltzin & Coughenour 1990, Nicholson & Farrar 1994, Rietkerk *et al.* 2000, Lehmann *et al.* 2014). This could be assessed using soil data bases such as the Harmonized World Soil Database (FAO, IIASA, ISRIC, ISSCAS, and JRC 2012). Similarly, disturbances such as fire and grazing (in terms of frequency and intensity) affect the species composition and spatial boundaries of herbaceous biomes (Bond *et al.* 2005, Devineau *et al.* 2010). For example, in West Africa increasing fire frequency or intensity induced shifts from forest to savanna (Ratnam *et al.* 2011), and from perennial to annual grass species in the savanna and steppe biomes (Le Houérou 1980). In West and South Africa, the distribution of fire frequencies roughly fits with MAP domains and biomes at the regional scale (Archibald *et al.* 2010, N'Datchoh *et al.* 2015), because fire occurrence is directly related to fuel production (mainly from herbaceous species), which in turn is positively related to annual precipitation (Hély *et al.* 2003, 2007). Thus, the trends observed between the C_4 grass physiognomic groups, MAP domains, and biomes distributions may also fit with fire regime distribution. Comparison of physiognomic group composition in fire- or grazing-protected versus unprotected areas will be necessary to verify this point and to mimic potential natural vegetation simulated by DGVMs.

Wright *et al.* (2005) highlighted that although average trait values can differ between PFTs, average values must be considered with caution, as trait variability found within a PFT could be larger than the variability among them. Moreover, Ackerly and Cornwell (2007) underlined that high trait variability can be observed both among and within sites. We have, thus chosen to consider the uppermost and lowermost values of three C_4 grass

physiognomic traits, and assumed that their regional variability were higher than their variability at the local scale in West and South Africa. The trends observed between the short and medium-sized physiognomic groups low10 and low30 MAP domains and biomes confirmed this assumption. However, the use of these groups to characterize other tropical herbaceous biomes (e.g., in South America or Australia) may not be straightforward as relationships between tropical herbaceous biomes, precipitation regimes and fire occurrence vary from one continent to another due to environmental and historical differences (Lehmann *et al.* 2014). Nevertheless, the cluster methodology described in the present study should be useful to identify the relevant physiognomic groups from regional data bases.

CONCLUSION

Biome simulation in models is mostly based on tree cover and tree species composition; however, the need to consider the grass component becomes very clear when one wants to analyze herbaceous ecosystems in which the tree signature may be secondary, non-significant, or even absent. This study demonstrates that the C₄ grass diversity characterizing herbaceous biomes in Senegal, Chad, and South Africa can be categorized into five physiognomic groups defined by their lowermost limits of culm height, leaf length, and leaf width. Among these five grass groups, the shortest and medium-sized groups (low10 and low30) clearly reflect rainfall patterns, which in turn enable the delineation of steppes from savanna and forest biomes in Senegal, and of nama-karoo, savanna, and grassland biomes in South Africa. Proportions of these two physiognomic groups additionally delineate the MAP domains <600 and >600 mm in Senegal, Chad, and South Africa, as well as the <250 mm and >1000 mm domains in South Africa. These findings should help either to re-parameterize the only C₄ grass PFT present in most DGVMs using the increasing gradient in culm and leaf sizes observed from the dry to the wet areas in West and South Africa, and to create more C₄ grass PFTs by fitting the distribution of the short and medium-sized physiognomic groups and of the associated herbaceous biomes.

ACKNOWLEDGMENTS

This study was conducted in the course of M. Pasturel's PhD (MESR studentship, CEREGE- AMU-OSU Pytheas). The authors gratefully acknowledge the support of the French ANR-09-PEXT-001 C3A and of CEREGE and ISEM internal funds. We thank B. Chase for sharing the South African reference dataset in the framework of the CeMEB LabEx. We are grateful to C. Ansberque and J. Fleury for GIS support and to P. Poilecot for grass species determination. Data from Chad were originally collected thanks to the Franco-Chadian cooperation (DCSUR Paris and French Embassy in Ndjamen, Chad; FSP, Project-#2005-54), the ANR (ANR-09-BLAN-0238), and the Région Poitou-Charentes. Finally, we thank Mahesh Sankaran and two anonymous reviewers for their valuable comments and sugges-

tions that allowed us to greatly improve the manuscript, and Marc Coudel for proofreading the English.

SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Dominant grass species dataset.*

TABLE S2. *Grass physiognomic traits description per group.*

TABLE S3. *Association of grass physiognomic groups defined on uppermost and lowermost trait values.*

TABLE S4. *Proportion of grass groups defined on their uppermost limit of physiognomic traits per mean annual precipitation (MAP) domain for Senegal, Chad, and South Africa.*

TABLE S5. *Proportion of grass groups defined on their uppermost limit of physiognomic traits per biome for Senegal, Chad, and South Africa.*

FIGURE S1. Perenniality proportion of the grass species in each physiognomic group.

FIGURE S2. Spatial abundance of the grass groups defined on their uppermost limit of physiognomic traits in Senegal, Chad, and South Africa.

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