Classification and mapping of the composition and structure of dry woodland and savanna in the eastern Okavango Delta

Authors:
Michelle J. Tedder[1]
Kevin P. Kirkman[1]
Craig D. Morris[1]
Winston S.W. Trollope[2]
Mpaphi C. Bonyongo[3]

Affiliations:
[1]School of Life Sciences, University of KwaZulu-Natal, South Africa

[2]Working on Fire International, Nelspruit, South Africa

[3]Okavango Research Institute, University of Botswana, Botswana

Correspondence to:
Michelle Tedder

Email:
michelle.j.tedder@gmail.com

Postal address:
Private Bag X01, Pietermaritzburg 3209, South Africa

Dates:
Received: 15 July 2012
Accepted: 11 June 2013
Published: 31 July 2013

How to cite this article:
Tedder, M.J., Kirkman, K.P., Morris, C.D., Trollope, W.S.W. & Bonyongo, M.C., 2013, 'Classification and mapping of the composition and structure of dry woodland and savanna in the eastern Okavango Delta', *Koedoe* 55(1), Art. #1100, 8 pages. http://dx.doi.org/10.4102/koedoe.v55i1.1100

The dry woodland and savanna regions of the Okavango Delta form a transition zone between the Okavango Swamps and the Kalahari Desert and have been largely overlooked in terms of vegetation classification and mapping. This study focused on the species composition and height structure of this vegetation, with the aim of identifying vegetation classes and providing a vegetation map accompanied by quantitative data. Two hundred and fifty-six plots (50 m × 50 m) were sampled and species cover abundance, total cover and structural composition were recorded. The plots were classified using agglomerative, hierarchical cluster analysis using group means and Bray-Curtis similarity and groups described using indicator species analysis. In total, 23 woody species and 28 grass species were recorded. *Acacia erioloba* and *Colophospermum mopane* were the most common woody species, whilst *Urochloa mossambicensis*, *Panicum maximum*, *Dactyloctenium gigantium* and *Eragrostis lehmanniana* were the most widespread grasses. Eleven vegetation types were identified, with the most widespread being Short mixed mopane woodland, Tall mopane woodland and Tall mixed mopane woodland, covering 288.73 km^2 (28%), 209.14 km^2 (20%) and 173.30 km^2 (17%) of the area, respectively. Despite their extensive area, these three vegetation types were the least species-rich, whilst Palm thornveld, Short mixed broadleaf woodland and Open mixed *Acacia* woodland were the most taxonomically variable. By contrast, Closed mixed *Acacia* woodland and Closed *Acacia*–*Combretum* woodland had the most limited distribution, accounting for less than 1% of the mapped area each.

Conservation implications: The dry woodland and savanna vegetation of the Okavango Delta comprises a much wider suite of plant communities than the *Acacia*-dominated and *Mopane*-dominated classifications often used. This classification provided a more detailed understanding of this vegetation and essential background information for monitoring, management and research.

Introduction

De Cáceres and Wiser (2011:387) state that, 'Vegetation classification is a useful tool for basic and applied research as well as for environmental management.' The major goal when conducting such an exercise is to simplify a complex continuous pattern of change in vegetation composition and structure across the landscape in order to understand how species are distributed and why, as well as to predict how species, communities and landscapes will respond to environmental changes (Symstad 2002). As a result of the varied applications of vegetation classification, the properties utilised in their construction are equally varied (De Cáceres & Wiser 2011; Symstad 2002). The more commonly used properties, listed by Symstad (2002) are: structure, taxonomy, resource use, response to change and role in ecosystem function. Vegetation classification becomes an even more powerful research and management tool when combined with some form of mapping indicating the distribution and spatial coverage of the groupings produced.

Current vegetation mapping practices are strongly influenced by the availability of remote-sensing tools (Bredenkamp *et al.* 1998). Over reliance on these remote sensing tools may, however, result in map inaccuracies because poor resolution of the available predictor variable maps and low levels of correlation between predictor variables and vegetation units may affect map accuracy (Van Etten 1998). But remote sensing can be an extremely powerful tool if used in conjunction with appropriate ground truthing (Bredenkamp *et al*. 1998). One of the more efficient methods for the construction of multipurpose vegetation maps is a floristic-based classification, supported by multivariate analysis and structural data (Dias, Elias & Nunes 2004). This allows the classification to be used to investigate both long-term change indicated by the floristic composition and short-term change indicated by the structural composition (Lux & Bemmerlein-Lux 1998). Vegetation maps and descriptions can also be used for a range of purposes such as: landscape planning, development and implementation of management plans, forestry, conservation, monitoring and many varied forms of research (Bredenkamp *et al*. 1998; Dias *et al*. 2004).

Although a vegetation map covering the whole of Ngamiland (110 000 km²), the north-western region of Botswana, was produced in 2002 (Jellema, Ringrose & Matheson 2002), it has limited applicability to research within the Okavango Delta as the Delta itself only comprises 26% of the mapped area (Ramberg *et al.* 2006). Several other maps focused on the peripheral dryland regions of the Okavango Delta (McCarthy, Gumbricht & McCarthy 2005; Ringrose, Van Der Post & Matheson 2003; Rűbbel & Child 1976; Tinley 1966), referring to woody cover at a finer scale than the broad division of *Acacia*-dominated woodland and tall and short *C. mopane*-dominated woodlands (Ellery & Ellery 1997).

The objectives of this study were to, firstly, taxonomically and structurally classify the vegetation of the dry woodland and savanna regions in the eastern Okavango Delta. Secondly, they aimed to provide a broad description of those vegetation types in terms of their, (1) woody species composition, (2) mean canopy cover, (3) indicator woody species, (4) diversity, (5) height structure of the woody species layer (based on the relative cover of pre-defined tree height classes) and (6) composition of the most prominent grasses. Thirdly, was to produce a vegetation map that provides background data for the ongoing research in the Eastern Okavango Delta.

Research method and design

Setting

The study was conducted in the southern Okavango Delta, Botswana, in the controlled hunting areas NG33 and NG34 and a portion of Moremi Game Reserve (NG28) (Figure 1). These three sections of the study area cover an area of 60.55 km², 851.68 km² and 579.59 km², respectively. These dry woodland regions in the south-eastern Okavango Delta function as a transition zone between the Okavango swamps and the Kalahari Desert, resulting in a region of high species richness and endemism (Mazizi Resources Pty Ltd 2009). The selected area is predominantly dry woodland and savanna and provides good representations of both *Acacia*-dominated savanna and mopane-dominated woodland. The area experiences a dry winter season from April to September, with minimum temperatures dropping to 15 °C, and a warm summer from October to March, with maximum temperatures rising to 40 °C (Mazizi Resources Pty Ltd 2009). The mean annual rainfall is 560 mm, with the majority falling between November and March (Mazizi Resources Pty Ltd 2009). The area provides habitats for a wide range of mammal, reptile and bird species, many of which are rare and protected (Mazizi Resources Pty Ltd 2009).

Sampling procedure

The composition and structure of the dryland woody-dominated vegetation in NG33 and NG34 was sampled between February and May 2009 using 256 plots, each 50 m × 50 m in size. This plot size is considered to be suitable

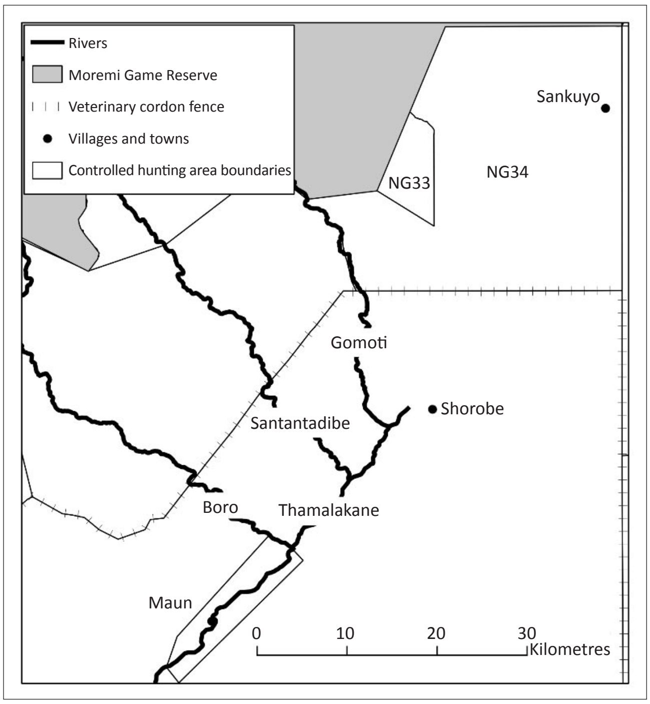


FIGURE 1: Location of the study area (NG33, NG34 and Moremi Game Reserve) in the Okavango Delta, north-western Botswana.

for mapping vegetation on a landscape scale as it minimises standard error over sampling cost (Xiao *et al.* 2004). Sample sites were systematically located along existing tracks, with the minimum distance between any two sites being 1 km, to cover the study area as extensively as possible and to facilitate access.

At each sample plot, all woody species were recorded and each species was allocated an absolute cover abundance value (Goodall 1980). This was achieved by estimating the percentage of the whole site cover occupied by each species separately. In addition, the total woody cover was visually estimated and GPS coordinates were recorded for each plot. The structural composition of the woody layer was sampled by visually estimating the absolute cover of each of the following height classes, < 0.50 m, 0.50 m – 0.99 m, 1.00 m – 1.99 m, 2.00 m – 2.99 m and > 3.00 m. Absolute cover (aerial) of each grass species in the understory was also estimated and later relativised so that total plot cover equalled 100% to describe the grass species composition. Identification was performed to species level and nomenclature was according to Coates-Palgrave (2002), Roodt (1998) and Van Oudtshoorn (1999) and names were confirmed as current by the South African National Biodiversity Institute (accessed through the SIBIS portal, http://sibis.sanbi.org on 05 April 2013).

Data analysis

The woody species absolute cover data were subjected to an agglomerative, hierarchical cluster analysis via the software program PRIMER (Clarke & Gorley 2006), using the group mean clustering method and Bray-Curtis similarity to create groups. A similarity profile test (SIMPROF), also conducted in PRIMER (Clarke & Gorley 2006), was used to identify sub-groups for which species composition was not statistically distinguishable ($p \geq 0.05$, n = 10 000 permutations) and thus could be retained as a single branch of the dendrogram.

The woody layer within each vegetation type was described in terms of species composition, based on mean cover abundance of each species in that vegetation group, and indicator species. In addition, mean woody canopy cover and species richness were calculated for each vegetation type. Vegetation classes with a mean woody canopy cover of greater than 50% were considered to have a closed canopy and those with a mean woody canopy cover of less than 50% were described as open canopy. Indicator species for each vegetation type were identified using indicator species analysis, conducted in PC-ORD (McCune & Mefford 1997) using 9999 permutations in a Monte Carlo test for indicator values (McCune & Mefford 1997).

Diversity within the vegetation types was described using mean Hill's diversity indices and mean Pielou's evenness co-efficient (Begon, Townsend & Harper 2005) using the following formulae:

$$\text{Hill's N1} = e^{H'} \quad \text{[Eqn 1]}$$

where $H' = -\Sigma p_i.\ln(p_i)$ and p_i = the proportion of species i in the sample.

$$\text{Hill's N2} = 1/\lambda \quad \text{[Eqn 2]}$$

where $\lambda = \Sigma n_i(n_i - 1)/N(N\text{-}1)$, n_i = number of individuals of species i in the sample and N = total number of individuals in the sample.

$$\text{Pielou's evenness co-efficient} = H'/\ln S \quad \text{[Eqn 3]}$$

where S = total number of species in the sample.

Hill's diversity numbers N1 and N2 describe the diversity of abundant and very abundant species respectively, whilst Pielou's evenness co-efficient ranges from 0 to 1 with low values indicating dominance by a few species (Begon *et al*. 2005).

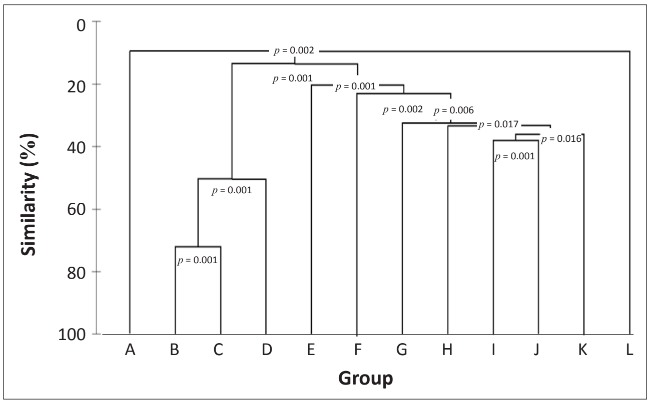
Differences in height structure between the vegetation types were examined using an analysis of similarity (ANOSIM) in PRIMER based on Bray-Curtis similarity and tested with 9999 permutations (Clarke & Gorley 2006). The p-values were controlled for false discovery rate using the Benjamani and Hochberg procedure (Verhoeven, Simonsen & McIntyre 2005). A similarity percentages routine (SIMPER), also conducted in PRIMER (Clarke & Gorley 2006) was then used to determine the contribution of each height class to the difference in Bray-Curtis similarity between vegetation types. Vegetation was considered to be tall if more than 35% of the woody layer fell into the height class > 3 m, whilst it was considered to be short if less than 30% of the woody component fell into this height class. The vegetation types were named according to their dominant species, height structure and level of woody cover.

To provide a complete overview of the vegetation types, the mean abundance for each grass species occurring in each vegetation type was calculated. The vegetation types were then mapped using *ArcMap* 10 (Esri 2010) by overlaying the categorised sample sites on aerial photographs obtained from the Okavango Research Institute.

Results

Twenty-three woody species belonging to 16 genera and 28 grass species belonging to 19 genera were identified in the study area. The cluster analysis and SIMPROF test produced 18 groups, which were significantly different from one another ($p < 0.05$). These groups were examined and those with a mean similarity of greater than 70% and comparable woody cover and species richness were combined. This resulted in 12 final groups, of which one (with two sites) was subsequently excluded from the woody classification because it had less than 5% woody cover (Group A) (Figure 2). The vegetation types were then named according to the dominant species, and then further differentiated according to their dominant height classes (tall or short) and percentage canopy cover (open or closed). If there were numerous co-dominant species present, then the term mixed was used. The 11 vegetation types derived from this classification are as follows (Figure 2):

- Group B: Tall mopane woodland.
- Group C: Tall mixed mopane woodland.
- Group D: Short mixed mopane woodland.
- Group E: Short mixed broadleaf woodland.
- Group F: Open mixed *Acacia* veld.
- Group G: Closed *Acacia*–*Combretum* woodland.
- Group H: Closed mixed *Acacia* veld.
- Group I: Closed *Acacia erioloba* savanna.
- Group J: Tall mixed broadleaf woodland.
- Group K: Open *Acacia erioloba* savanna.
- Group L: Palm thornveld.



p-Values are from similarity profile tests for differences in species canopy cover composition between braches within each node of the dendrogram. Branches not significantly different ($p < 0.05$) in composition were concatenated.
A, Grassland with less than 5% woody cover; B, Tall mopane woodland; C, Tall mixed mopane woodland; D, Short mixed mopane woodland; E, Short mixed broadleaf woodland; F, Open mixed *Acacia* veld; G, Closed *Acacia*–*Combretum* woodland; H, Closed mixed *Acacia* veld; I, Closed *Acacia erioloba* savanna; J, Tall mixed broadleaf woodland; K, Open *Acacia erioloba* savanna; L, Palm thornveld.

FIGURE 2: Dendrogram of an agglomerative cluster analysis (based on Bray-Curtis similarity measure) of canopy cover composition of woody species in the eastern Okavango Delta, Botswana.

TABLE 1: Mean estimated relative cover (%) of woody species for the vegetation types of NG33 and NG34 in the eastern Okavango Delta.

Woody species	Tall mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia–Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld
Acacia erioloba	1	**7**	**6**	**9**	**7**	**13**	**17**	**3**	**17**	**12†**	**3**
Acacia hebeclada	0	1	2	2	**16†**	**4**	1†	2	0	1	2
Acacia luederitzii	0	1	1	2	**7†**	0	0	1	1	0	0
Acacia nigrescens	0	0	0	1	0	0	**34†**	1	0	0	2
Boscia albitrunca	0	2	**3**	2	0	0	**5†**	0	0	1	0
Boscia mossambicensis	0	0	0	0	1	1	1	0	1	0	0
Colophospermum mopane	**86†**	**59†**	**34†**	**6**	**4**	**4**	**5**	2	2	2	1
Combretum imberbe	0	1	1	0	1	**25†**	0	**3**	**7**	1	2
Croton megalobotrys	0	0	0	0	2	2	0	0	**21†**	1	**4**
Dichrostachys cinerea	0	0	1	**8†**	1	0	0	0	0	1	0
Diospyros lycioides	0	0	0	0	0	0	0	0	1	0	**3**
Grewia flava	1	0	1	0	0	0	0	0	0	0	0
Grewia flavescens	1	0	1	0	0	0	0	1	1	1	0
Grewia retinervis	1	0	0	0	0	0	0	0	0	0	0
Gymnosporia senegalensis	0	0	0	0	0	2	0	0	2	0	0
Hyphaene petersiana	0	0	0	0	0	1	1	0	1	1	**7**
Kigelia africana	0	0	0	0	0	0	0	0	1	0	0
Philenoptera violacea	0	0	0	0	0	0	0	0	1	0	0
Philenoptera nelsii	1	1	**6**	**15†**	2	0	2	2	**6**	2	2
Searsia tenuinervis	0	0	0	0	0	**14**	0	0	2	0	0
Terminalia sericea	0	1	**3**	**19†**	0	0	1	0	0	2	0
Ximenia americana	0	0	0	0	0	0	0	0	1	0	0
Ziziphus mucronata	0	1	1	1	0	1	**5**	2	**3**	1	**8**

Bold indicates species with a mean relative canopy cover of 3% or greater.
†, indicator species.

Tall mopane woodland (Group B)

Tall mopane woodland almost solely comprised the indicator species *C. mopane* ($p < 0.001$) (Table 1) and was the densest of all 11 woody vegetation types, with a mean woody cover of 92.0% (± 0.9%) (Table 2). The majority of this cover was taller than 3 m (Table 4). Tall mopane woodland covered an area of 209 km^2 (Table 2), occurring mainly in the northern and eastern regions of NG34 and continuing north into Moremi Game Reserve (Figure 3). It had a low mean species richness (1.90 ± 0.14) (Table 2), with a small proportion of the woody cover comprising *Acacia*, *Combretum* and *Grewia* species growing in the understory (Table 1). The grass layer was fairly diverse, comprising 18 species, but was dominated by *U. mossambicensis* (25.0%) and *Eragrostis rigidior* (19.0%) (Table 3).

Tall mixed mopane woodland (Group C)

Tall mixed mopane woodland was dominated by the indicator species *C. mopane* ($p < 0.001$) (Table 1), with some *A. erioloba* occurring in more open patches. Tall mixed mopane woodland had a mean woody cover, predominantly taller than 3 m (Table 4), of 75.0% (± 3.4%) (Table 2) and a mean species richness of 3.30 (± 0.32) (Table 2). Other species contributing to the understory cover were *Acacia hebeclada*, *Acacia luederitzii*, *Boscia albitrunca*, *Combretum* species and *Terminalia sericea* (Table 1). The grass layer comprised 14 species with *U. mossambicensis* (21.0%) and *P. maximum* (19.0%) dominating (Table 3). Tall mixed mopane woodland, covering 173 km^2, occurred mainly in the central and eastern regions of NG34 along the edges of the Tall mopane woodland (Figure 3) (Table 2).

Short mixed mopane woodland (Group D)

Short mixed mopane woodland had the lowest cover of the three mopane-dominated vegetation types, with a mean woody cover of 66.0% (± 3.1%) (Table 2). This cover was spread evenly between the three tallest height classes (Table 4). *Colophospermum mopane* comprised approximately one-third of the woody cover, with the remainder a mix of *Acacia* species, *B. albitrunca*, *Grewia* species, *Philenoptera nelsii* and *T. sericea* (Table 1), resulting in a mean species richness of 5.20 (± 0.32) (Table 2). The grass layer predominantly comprised *E. lehmanniana* (17.0%), *D. gigantium* (16.0%), *P. maximum* (14.0%), *Pogonarthria squarrosa* (13.0%) and *U. mossambicensis* (12.0%), with occasional occurrences of eight other species (Table 3). Short mixed mopane woodland, the most widespread vegetation type covering 288 km^2, occurred in large patches in NG34 south of the boundary of NG33 and east of the Gomoti River and as small patches on the boundaries of Tall mopane woodland and Tall mixed mopane woodland in the central and northern sections of NG34 (Figure 3).

Short mixed broadleaf woodland (Group E)

Short mixed broadleaf woodland covered an area of 43 km^2 and was characterised by the indicator species *P. nelsii*

TABLE 2: Number of sites, Hill's diversity indices, mean (± standard error) species richness, maximum species richness and mean (± standard error) woody cover (%) for the vegetation types of NG33 and NG34 in the eastern Okavango Delta.

Vegetation types	Area (km²)	Hill's N1	Hill's N2	Pielou's evenness	Mean species richness	Maximum species richness	Mean woody cover
Tall mopane woodland	209.16	1.3	1.1	0.1	1.90 ± 0.14	4.0	92.0 ± 0.9
Tall mixed mopane woodland	173.30	2.0	0.4	0.2	3.30 ± 0.32	5.0	75.0 ± 3.4
Short mixed mopane woodland	288.73	3.0	3.2	0.2	5.20 ± 0.32	11.0	66.0 ± 3.1
Short mixed broadleaf woodland	43.39	3.9	3.5	0.3	5.00 ± 0.30	8.0	66.0 ± 3.2
Open mixed *Acacia* veld	14.01	3.9	3.5	0.2	5.20 ± 0.57	8.0	41.0 ± 4.9
Closed *Acacia–Combretum* woodland	1.00	4.0	3.3	0.3	5.70 ± 0.33	6.0	67.0 ± 14.5
Closed mixed *Acacia* veld	7.64	4.9	4.0	0.2	7.00 ± 1.00	8.0	73.0 ± 22.5
Closed *Acacia erioloba* savanna	73.71	2.9	2.4	0.2	4.20 ± 0.24	8.0	50.0 ± 1.8
Tall mixed broadleaf woodland	30.67	4.9	4.6	0.3	5.90 ± 0.64	10.0	66.0 ± 4.5
Open *Acacia erioloba* savanna	122.93	3.2	3.0	0.2	4.40 ± 1.98	8.0	23.0 ± 12.7
Palm thornveld	60.41	3.5	3.3	0.3	4.40 ± 0.34	7.0	36.0 ± 4.3

(p = 0.034), *T. sericea* (p = 0.003) and *Dichrostachys cinerea* (p = 0.030) (Table 1). Short mixed broadleaf woodland had a mean woody cover of 66.0% (± 3.2%) (Table 2), which was generally shorter than 3 m in height (Table 4) and contained small proportions of *Acacia* species, *B. albitrunca* and *C. mopane* (Table 1), resulting in a mean species richness of 5.0 (± 0.3) (Table 2). *Eragrostis lehmanniana* (18.0%), *Stipagrostis hirtigluma* (15.0%) and *P. maximum* (14.0%) dominated the grass layer, with limited cover of 11 other species (Table 3). Short mixed broadleaf woodland occurred mainly between the southern tip of NG33 and the southern buffalo fence, with some patches occurring east of the boundary of NG33 and along the cutline between NG33 and Moremi Game Reserve (Figure 3).

Open mixed *Acacia* woodland (Group F)

Open mixed *Acacia* woodland was characterised by the presence of widely scattered individuals of the indicator species *A. hebeclada* (p = 0.001) and *A. luederitzii* (p = 0.009) growing with *A. erioloba*. Other species that were present but with low canopy cover include *Boscia mosambicensis*, *C. mopane*, *Combretum imberbe*, *Croton megalobotrys*, *Diospyros lycioides* and *P. nelsii* (Table 1). Open mixed *Acacia* woodland had a mean canopy cover of 41.0% (± 4.9%) (Table 2), the majority of which was taller than 2 m (Table 4) and a mean species richness of 5.20 (± 0.57) (Table 2). The grass layer comprised 14 species with *U. mossambicensis* (24.0%) and *E. lehmanniana* (17.0%) being dominant (Table 3). Open mixed *Acacia* woodland covered an area of 14 km² (Table 2) and occurred mainly along the northern boundary of NG33 and NG34, in small patches in the central and eastern regions of NG34 and east of the Gomoti River in Moremi Game Reserve, north of the NG34 boundary (Figure 3).

Closed *Acacia–Combretum* woodland (Group G)

Closed *Acacia–Combretum* woodland had a mean woody cover of 67.0% (± 14.5%) (Table 2), a mean species richness of 5.70 (± 0.33) (Table 2) and was dominated by *A. erioloba* and the indicator species *C. imberbe* (p = 0.001) (Table 1). *Acacia hebeclada*, *B. mosambicensis*, *C. mopane*, *C. megalobotrys*, *Gymnosporia senegalensis*, *Hyphene petersiana* and *Searsia tenuinervis* contributed a small proportion to the canopy cover (Table 1). The majority of the woody cover was between 1 m and 3 m tall (Table 4). The grass layer comprised 11 species, with *U. mossambicensis* (32.0%) being dominant and *E. lehmanniana* (15.0%) and *P. maximum* (15.0%) being sub-dominant (Table 3). Closed *Acacia–Combretum* woodland covered an area of approximately 1 km² and occurred in small patches in central and western NG34 (Figure 3).

Closed mixed *Acacia* veld (Group H)

Closed mixed *Acacia* veld had a mean canopy cover of 73.0% (± 22.5%) and was characterised by the presence of the indicator species *Acacia nigrescens* (p < 0.001), *A. hebeclada* (p = 0.001) and *B. albitrunca* (p = 0.013) growing with *A. erioloba* (Table 1). The woody cover was mostly between 1 m and 3 m tall and had a mean species richness of 7.0 (± 1.0) (Table 2). The grass layer was dominated by *E. lehmanniana* (25.0%) and *U. mossambicensis* (25.0%), with *D. giganteum* (15.0%) and *P. maximum* (15.0%) being sub-dominant and four other species occurring occasionally (Table 3). Closed mixed *Acacia* woodland occurred in small patches in south-western NG34 close to the Gomoti River (Figure 3), totalling an area of 7 km² (Table 2).

Closed *Acacia erioloba* savanna (Group I)

Closed *A. erioloba* savanna was dominated by tall *A. erioloba* trees (Table 1), the indicator species for this structural vegetation type (p = 0.009), with low cover of *A. hebeclada*, *C. mopane*, *C. imberbe*, *C. megalobotrys*, *P. nelsii* and *Ziziphus mucronata* in the understory (Table 1). Closed *A. erioloba* savanna had a mean woody cover of 50.0% (± 1.8%) (Table 2), with half the woody cover taller than 3 m (Table 4), and a mean species richness of 4.20 (± 0.24) (Table 2). The grass layer comprised 14 species, with *D. giganteum* (17.0%) and *Digitaria eriantha* (17.0%) dominating (Table 3). Closed *A. erioloba* savanna covered an area of 73 km² (Table 2) and occurred in large patches in central NG33, in NG34 south and east of the NG33 boundary and in smaller patches between the *C. mopane*-dominated belts in eastern NG34 (Figure 3).

Tall mixed broadleaf woodland (Group J)

Tall mixed broadleaf woodland is characterised by a combination of tall *A. erioloba* with an understory of

TABLE 3: Mean estimated relative cover (%) of grass species in the vegetation types of NG33 and NG34 in the eastern Okavango Delta.

Grass species	Tall mopane woodland	Tall mixed mopane woodland	Short mixed mopane woodland	Short mixed broadleaf woodland	Open mixed *Acacia* veld	Closed *Acacia–Combretum* woodland	Closed mixed *Acacia* veld	Closed *Acacia erioloba* savanna	Tall mixed broadleaf woodland	Open *Acacia erioloba* savanna	Palm thornveld
Aristida congesta	**10**	**6**	2	2	0	0	**10**	2	1	**3**	1
Aristida diffusa	1	0	0	0	0	0	0	0	0	0	0
Aristida junciformis	0	0	0	0	0	0	0	0	0	1	0
Aristida meridionalis	1	0	**4**	0	0	0	0	0	0	0	1
Cenchrus cilliaris	2	1	0	0	0	0	0	1	0	0	0
Chloris virgata	2	**3**	1	1	**13**	0	**3**	**4**	**3**	**10**	**6**
Cymbopogon caesuis	0	0	0	0	0	0	0	1	0	0	0
Cynodon dactylon	1	0	1	0	**12**	**7**	0	**6**	**3**	**11**	**27**
Dactyloctenium giganteum	**8**	**11**	**16**	**12**	**9**	**8**	**15**	**17**	**19**	**20**	**6**
Digitaria eriantha	**4**	**8**	**4**	**7**	**12**	**8**	0	**17**	**7**	**9**	**6**
Digitaria species	0	0	0	**5**	0	0	0	0	0	1	0
Echinochloa colona	1	0	0	0	1	0	0	0	1	0	0
Eragrostis lehmanniana	**19**	**13**	**17**	**18**	**17**	**15**	**25**	**13**	**13**	**8**	**10**
Eragrostis rigidior	0	0	0	0	0	0	0	1	0	2	**15**
Eragrostis superba	1	1	0	0	0	0	0	0	0	0	0
Heteropogon contortus	0	1	0	0	0	0	0	0	0	0	0
Melinis repens	0	0	2	2	0	2	**5**	0	1	**3**	1
Panicum maximum	**7**	**19**	**14**	**14**	**4**	**15**	**15**	**13**	**22**	**6**	**6**
Pogonarthria squarrosa	**9**	**4**	**13**	**12**	1	2	0	**5**	**5**	2	**4**
Schmidtia kalihariensis	0	0	**4**	**4**	0	**7**	0	0	2	1	**5**
Setaria verticillata	0	0	0	0	1	0	0	0	0	0	0
Sporobolus festivus	1	**3**	0	1	2	0	0	1	1	2	**3**
Sporobolus fimbriatus	1	0	0	0	1	2	0	0	1	0	0
Sporobolus ioclados	0	0	0	1	1	0	0	0	0	0	0
Stipagrostis hirtigluma	**5**	**5**	**10**	**15**	0	**3**	**3**	2	2	**4**	2
Tragus berteronianus	1	0	0	0	0	0	0	0	0	0	0
Urochloa mosambicensis	**25**	**21**	**12**	**6**	**24**	**32**	**25**	**14**	**19**	**17**	**6**
Urochloa species	0	**3**	0	0	2	0	0	0	0	0	0

Bold indicates species with a mean relative cover of 3% or greater.

C. megalobotrys, the indicator species for this vegetation type ($p < 0.001$) (Table 1). A small proportion of the woody cover also comprised *C. mopane*, *C. imberbe*, *G. senegalensis*, *P. nelsii*, *S. tenuinervis* and *Z. mucronata* (Table 1), resulting in a mean species richness of 5.90 (± 0.64) (Table 2). The mean woody cover in Tall mixed broadleaf woodland was 66.0% (± 4.5%) (Table 2), with 70.0% of this being taller than 2 m (Table 4). The grass layer comprised 15 species, but was dominated by *P. maximum* (22.0%), *D. giganteum* (19.0%) and *U. mossambicensis* (19.0%) (Table 3). The 30 km^2 of Tall mixed broadleaf woodland (Table 2) occurred in scattered patches in NG34, mainly east of the NG33 boundary and in central and western NG33 along the Moremi Game Reserve boundary (Figure 3).

Open *Acacia erioloba* savanna (Group K)

Open *A. erioloba* savanna was characterised by an open canopy (23.0% ± 12.7%) (Table 2), with a scattered distribution of tall *A. erioloba* (Table 1) as an indicator species ($p = 0.009$). Other species present included *C. mopane*, *P. nelsii*, *T. sericea*, *A. hebeclada*, *B. albitrunca*, *C. imberbe*, *H. petersiana* and *Z. mucronata* (Table 1), resulting in a mean species richness of 4.40 (± 1.98) (Table 2). The woody cover was predominantly taller than 1 m, with a fairly even spread between the three tallest height classes (Table 4). The grass was dominated by *D. giganteum* (20.0%) and *U. mossambicensis* (17.0%), with 14 other species occurring occasionally (Table 3). Open *A. erioloba* savanna occurred in two main patches: in NG34 south of the boundary of NG33 and Moremi Game Reserve and in central NG34 between the *C. mopane*-dominated belt to the north and the closed *A. erioloba* savanna to the south (Figure 3), totalling an area of 122 km^2 (Table 2).

Palm thornveld (Group L)

Palm thornveld had an open canopy (36.0% ± 4.3%) (Table 2) and was characterised by a sparse cover of *Z. mucronata* and the indicator species *H. petersiana* ($p = 0.017$), with some occurrences of *A. erioloba*, *A. hebeclada*, *A. nigrescens*, *C. megalobotrys*, *D. lycioides*, *P. nelsii* and *C. imberbe* (Table 1), resulting in a mean species richness of 4.40 (± 0.34) (Table 2). The majority of the woody cover was between 2 m and 3 m tall. The grass layer comprised 15 species, with *Cynodon dactylon* (27.0%) dominating (Table 3). The 60 km^2 area (Table 2) of Palm thornveld was limited to the old floodplain regions south of NG33 and east of the Gomoti River (Figure 3).

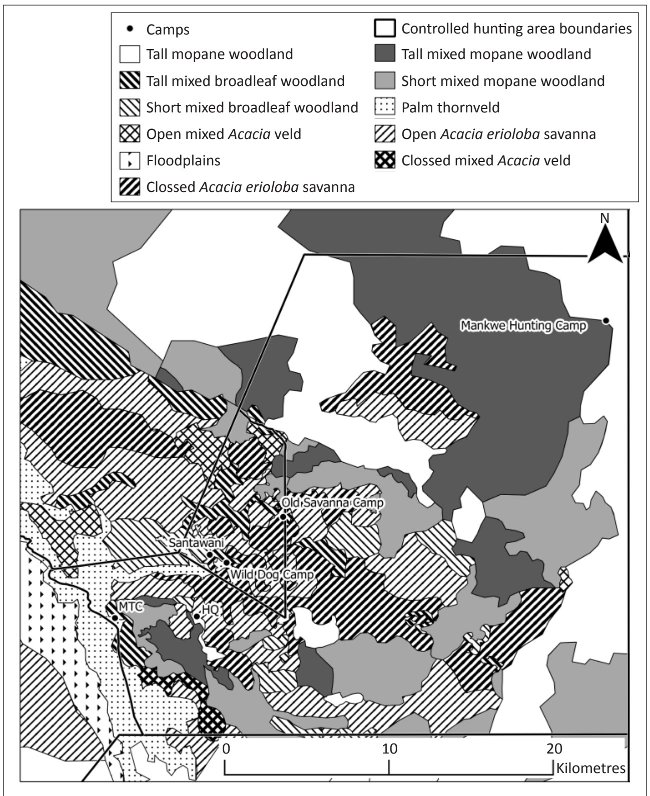
Discussion

Overall, the structure of the woody vegetation in the eastern Okavango Delta was short (< 3 m) according the broad-scale classification guidelines stated by Edwards (1983). The two most widespread woody species occurring in varying densities in every vegetation type were *A. erioloba* and *C. mopane*, whilst the most widespread grass species were *U. mossambicensis*, *P. maximum*, *D. gigantium* and *E. lehmanniana*.

TABLE 4: Mean (± standard error) relative cover (%) of height classes and mean within group similarity calculated using analysis of similarities of the vegetation types in NG33 and NG34.

Vegetation types	HT1 (< 0.5 m)	HT2 (0.50 m – 0.99 m)	HT3 (1.00 m – 1.99 m)	HT4 (2.00 m – 2.99 m)	HT5 (> 3 m)	Within group similarity (%)
Tall mopane woodland	9.0 ± 0.7	13.0 ± 1.0	20.0 ± 1.6	23.0 ± 1.4	34.0 ± 2.7	72
Tall mixed mopane woodland	8.0 ± 1.5	11.0 ± 1.1	21.0 ± 2.2	23.0 ± 2.2	37.0 ± 3.7	74
Short mixed mopane woodland	10.0 ± 1.3	13.0 ± 1.4	24.0 ± 1.8	26.0 ± 1.5	28.0 ± 2.5	71
Short mixed broadleaf woodland	5.0 ± 1.0	9.0 ± 0.9	27.0 ± 2.5	34.0 ± 2.6	25.0 ± 2.6	74
Open mixed *Acacia* veld	4.0 ± 1.3	6.0 ± 1.1	17.0 ± 2.9	33.0 ± 6.5	39.0 ± 8.6	65
Closed *Acacia–Combretum* woodland	3.0 ± 1.7	7.0 ± 1.7	27.0 ± 6.7	35.0 ± 2.9	28.0 ± 4.4	†
Closed mixed *Acacia* veld	10.0 ± 0.0	13.0 ± 2.5	28.0 ± 12.5	33.0 ± 12.5	15.0 ± 0.0	†
Closed *Acacia erioloba* savanna	3.0 ± 0.4	6.0 ± 0.5	17.0 ± 1.5	24.0 ± 1.5	49.0 ± 2.6	71
Tall mixed broadleaf woodland	5.0 ± 1.8	7.0 ± 0.7	19.0 ± 3.4	25.0 ± 3.0	45.0 ± 5.5	71
Open *Acacia erioloba* savanna	4.0 ± 1.7	8.0 ± 1.0	26.0 ± 2.5	26.0 ± 4.0	37.0 ± 6.0	59
Palm thornveld	3.0 ± 1.1	9.0 ± 1.8	28.0 ± 3.5	36.0 ± 4.0	23.0 ± 4.1	64

†, indicates groups that were excluded from the analysis due to a limited number of sample plots.



Closed *Acacia–Combretum* woodland is not shown as the distribution is too limited to be visible at this scale.

FIGURE 3: Distribution of vegetation types in NG33 and 34 in the eastern Okavango Delta, Botswana.

The three *C. mopane*-dominated vegetation types accounted for approximately half the woody cover in NG33 and NG34. The structural differences observed between the tall and short *C. mopane* vegetation may be caused by several factors. Nutrient poor, sandy soils (Roodt 1998) and the associated decrease in available moisture can result in stunted *C. mopane* trees (February *et al.* 2007), whilst disturbance factors such as fire, wood harvesting and extensive utilisation by elephants result in multi-stemmed coppice growth (Lombard 2003; Van Voorthuizen 1976) and may cause the development of Short mixed mopane woodland in areas where soil conditions allow for tall mopane woodland. By contrast, tall stands of *C. mopane* trees tend to occur on nutrient-rich alluvial soils (Roodt 1998) and, although slow-growing initially, they can reach heights of up to 30 m (Venter & Venter 2002).

There is great variation in the number of woody vegetation classes previously described by the four vegetation studies conducted in the dryland regions of the Okavango Delta between 1966 and 2005. Tinley (1966) describes eight vegetation classes predominantly based on species composition but including structure in some descriptions, whilst Rübbel and Child (1976) described five, distinguished mainly by flooding frequency and dominant woody species. Ringrose *et al.* (2003) described twelve ecological units in total, of which seven are woody dominated, whilst McCarthy *et al.* (2005) described only four. Both Ringrose *et al.* (2003) and McCarthy *et al.* (2005) base their descriptions on plant species composition. Of these four studies, the one which is most closely correlated to the eleven vegetation types described here is the oldest classification, conducted by Tinley (1966) in Moremi Game Reserve. Seven of the eight vegetation types described by Tinley (1966) can be matched to groups produced by this classification, whilst the same can be said for only five of the seven groups described by Ringrose *et al.* (2003), who mapped vegetation in the Xudum region of the south-western Okavango Delta. Ringrose *et al.* (2003) do, however, provide a slightly more detailed description of the species composition within the *C. mopane*-dominated vegetation types, describing three distinct groups, whilst Tinley (1966) describes only two forms of *C. mopane* woodland focusing on structural composition. The absence of any broadleaf-dominated communities in the ecoregions described by Ringrose *et al.* (2003) and the limited description given by Tinley (1966) emphasises the level of variation observed in the dry woodland and savanna vegetation in different regions of the Okavango Delta and also the importance of using detailed field-based vegetation studies in conjunction with remote-sensing techniques.

Conclusion

This study highlights the broad suite of vegetation communities present in the dry woodland and savanna vegetation of the eastern Okavango Delta. The vegetation classification and map produced by this study not only provides valuable geo-referenced field data to augment the Delta-wide maps produced in 2002 (Ramberg *et al*. 2006), but also important background data for both the habitat-based monitoring projects to be conducted in NG33 and NG34 and the carnivore and herbivore research being conducted in the area.

Acknowledgements

We would like to thank Mr R.G. Fuhr for his generous financial support for the duration of this project and the staff and fellow researchers of Dubatana Camp and the Okavango Research Institute for their assistance and support in the field.

Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

All field work was conducted by M.J.T. (University of KwaZulu-Natal) as part of a PhD project. K.P.K. (University of KwaZulu-Natal) was the main supervisor and C.D.M. (University of KwaZulu-Natal), W.S.W.T. (Working on Fire International) and M.C.B. (University of Botswana) were co-supervisors. M.J.T., K.P.K. and W.S.W.T. were responsible for project design. M.C.B. assisted in acquiring the necessary permits and permissions for fieldwork. M.J.T. and C.D.M. conducted data analysis and M.J.T. wrote the manuscript which was commented on and edited by all four co-authors.

References

Begon, M., Townsend, C. & Harper, J., 2005, *Ecology: From individuals to ecosystems*, Blackwell Scientific Publications, Oxford.

Bredenkamp, G., Chytery, M., Fischer, H., Neuhauslova, Z. & Van der Maarel, E., 1998, 'Vegetation mapping: Theory, methods and case studies: Introduction', *Applied Vegetation Science* 1, 161–164. http://dx.doi.org/10.1111/j.1654-109X.1998.tb00397.x

Clarke, K. & Gorley, R., 2006, *PRIMER*, PRIMER-E Ltd, Ivybridge.

Coates-Palgrave, M., 2002, *Keith Coates-Palgrave Trees of southern Africa*, 3rd edn., Struik Publishers, Cape Town.

De Cáceres, M. & Wiser, S., 2011, 'Towards consistency in vegetation classification', *Journal of Vegetation Science* 23, 387–393. http://dx.doi.org/10.1111/j.1654-1103.2011.01354.x

Dias, E., Elias, R. & Nunes, V., 2004, 'Vegetation mapping and nature conservation: A case study in Terceira Island (Azores)', *Biodiversity and Conservation* 13, 1519–1539. http://dx.doi.org/10.1023/B:BIOC.0000021326.50170.66

Edwards, D., 1983, 'A broad-scale structural classification of vegetation for practical purposes', *Bothalia* 14, 705–712.

Ellery, K. & Ellery, F., 1997, 'Plants of the Okavango Delta', Tsaro Publishers, Durban. PMid:15093481

Esri, 2010, *ArcMap* version 10, Esri, Redlands.

February, E., Higgins, S., Newton, R. & West, A, 2007, 'Tree distribution on a steep environmental gradient in an arid savanna', *Journal of Biogeography* 34, 270–278. http://dx.doi.org/10.1111/j.1365-2699.2006.01583.x

Goodall, D.W., 1980, 'Numerical methods of classification', *Classification of plant communities* 5(1), 247–286.

Jellema, A., Ringrose, S. & Matheson, W., 2002, 'Northern Botswana vegetation mapping project', Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun.

Lombard, P., 2003, 'The long-term effects of fire frequency and season on the *Colophospermum mopane* shrubveld of the Kruger National Park', Magister Technologiae thesis, Faculty of the Built Environment, Port Elizabeth Technikon.

Lux, A. & Bemmerlein-Lux, F., 1998, 'Two vegetation maps of the same island: Floristic units versus structural units', *Applied Vegetation Science* 1, 201–210. http://dx.doi.org/10.2307/1478949

Mazizi Resources Pty Ltd, 2009, 'Management Plan for NG33 and NG34', Mazizi Resources Pty Ltd, Maun.

McCarthy, J., Gumbricht, T. & McCarthy, T., 2005, 'Ecoregion classification in the Okavango Delta, Botswana from multitemporal remote sensing', *International Journal of Remote Sensing* 26, 4339–4357. http://dx.doi.org/10.1080/01431160500113583

McCune, B. & Mefford, M., 1997, *PC-ORD multivariate analysis of ecological data* version 6, MJM Software Design, Gleneden Beach.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J. *et al.*, 2006, 'Species diversity of the Okavango Delta, Botswana', *Aquatic Sciences* 68, 310–337. http://dx.doi.org/10.1007/s00027-006-0857-y

Ringrose, S., Van Der Post, C. & Matheson, W., 2003, 'Mapping ecological conditions in the Okavango delta, Botswana using fine and coarse resolution systems including simulated SPOT vegetation imagery', *International Journal of Remote Sensing* 24, 1029–1052. http://dx.doi.org/10.1080/01431160210155046

Roodt, V., 1998, *The Shell field guide series: Part I – Trees and shrubs of the Okavango Delta: Medicinal uses and Nutritional value*, Shell Oil Botswana (Pty) Ltd, Gaberone.

Rűbbel, H. & Child, G., 1976, 'Notes on the ecology of the Moremi Wildlife Reserve', Department of Wildlife, National Parks and Tourism, Botswana.

Symstad, A., 2002, 'An overview of ecological plant classification systems', in R. Ambasht & N. Ambasht (eds.), *Modern trends in terrestrial ecology*, pp. 13–50, Kluwer Academic, New York. http://dx.doi.org/10.1007/978-1-4615-0223-4_2

Tinley, K.L., 1966, 'An ecological reconnaissance of the Moremi Wildlife Reserve, Northern Okavango Swamps, Botswana', The Okavango Wildlife Society, Johannesburg.

Van Etten, E., 1998, 'Mapping vegetation in an arid, mountainous region of Western Australia', *Applied Vegetation Science* 1, 189–200. http://dx.doi.org/10.2307/1478948

Van Oudtshoorn, F., 1999, *Guide to grasses of southern Africa*, Briza, Pretoria.

Van Voorthuizen, E., 1976, 'The mopane tree', *Botswana Notes and Records* 8, 223–230.

Venter, F. & Venter, J., 2002, *Making the most of indigenous trees*, 2nd edn., Briza Publications, Pretoria.

Verhoeven, K.J.F., Simonsen, K.L. & McIntyre, L.M., 2005, 'Implementing false discovery rate control: Increasing your power', *Oikos* 108, 643–647. http://dx.doi.org/10.1111/j.0030-1299.2005.13727.x

Xiao, X., Gertner, G., Wang, G. & Anderson, A.B., 2004, 'Optimal sampling scheme for estimation landscape mapping of vegetation cover', *Landscape Ecology* 20, 375–387. http://dx.doi.org/10.1007/s10980-004-3161-z