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Wetland plant communities of the Tsitsikamma Plateau in relation to fire history, plantation management and physical factors☆

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Abstract

The remnant palustrine wetland plant communities of the highly transformed Tsitsikamma Plateau are almost entirely located as linear features within commercial pine plantations. Being highly flammable fynbos wetlands, these features pose a serious hazard to plantations. Consequently, foresters require management guidelines that will reduce fire hazard to plantations but also maintain the biodiversity of wetlands. Here we report on the floristic community structure of wetlands located in plantations on the Tsitsikamma Plateau, and attempt to explain this structure in terms of geographic location, fire history and plantation management. We identified five palustrine wetland communities whose structure was primarily determined by location along a west–east gradient and fire history. Maintaining wetland plant biodiversity, especially populations of the rare *Leucadendron conicum*, will require a fire return interval in the order of 10 years; fire season is unlikely to have a significant effect. However, implementing this burning regime is likely to pose important challenges to the forestry sector. The forestry industry should internalise these risks and associated costs as a consequence of persisting with an industry not suited to a fire-prone environment.

Keywords: Community analysis; Eastern CFR; Fire management; NMDS; Palustrine wetlands

1. Introduction

From a landscape perspective wetlands are becoming exceedingly rare and wetland losses both internationally and nationally are estimated at over 50%, with agriculture and forestry accounting for most of this loss (Cronk and Fennessy, 2001; Joosten, 2009; Kotze et al., 1995; Maltby, 2009). Afforestation alters species and ecosystem diversity, alters the fire regime, reduces water yield and increases nutrient run-off after fertilisation (Joosten, 2009; Van Wilgen et al., 1994). Throughout South Africa plantation forestry has encroached onto natural ecosystems, and in turn the occurrence of wildfires has threatened the plantation forestry industry (Kraaij et al., 2011; Van Wilgen, 2009). Presently the Tsitsikamma Plateau is extensively afforested with pine plantations which have widely replaced the fire-prone fynbos vegetation (Geldenhuys, 1994; Kraaij et al., 2011) and within these stands occur the wetlands of our study — irreplaceable in the unique perennially moist environment of the Tsitsikamma (Vromans et al., 2010). Although wetlands in South Africa are delineated and protected from afforestation as stipulated by the National Water Act (No. 36 of 1998), the National Wetland Classification System (NWCS) and commonly the Forestry Stewardship Council (FSC) certification (Forestry Industry Environmental Committee, 2002; SANBI, 2009), the wetlands in our study are considered to increase fire risk. These wetlands are linear features oriented north to south within plantations and considered by foresters to behave as fire funnels by channelling wind along these corridors. When mature, post-fire, the Tsitsikamma wetlands support a high biomass which can support high-intensity fires, especially when these coincide with extreme weather conditions such as fierce hot, dry, north–

☆ Nomenclature: Goldblatt and Manning (2000).

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northwest bergwinds (Van Wilgen et al., 2007). Weather conditions, rapid post-fire fuel accumulation rates and principally a non-seasonal natural fire regime in the eastern Cape Floristic Region (CFR), support intense fires across a wide range of vegetation ages (Cary et al., 2009; Geldenhuys, 1994; Kraaij et al., in press-a–b; Southey, 2009; Van Wilgen, 2009; Van Wilgen et al., 2010). In addition, high fuel loads limit access and make fire fighting extremely difficult. This poses a severe risk to the commercial forestry sector and since 1998, four uncontrolled fires have devastated vast areas of plantation in the Tsitsikamma, with resultant financial loss. However, apart from an alien eradication programme, wetland management within plantations in the Tsitsikamma is non-existent and foresters require guidelines for wetland management that will reduce the fire hazard, while maintaining biodiversity and functioning.

Here we focus on the composition and management of the palustrine wetlands (freshwater wetlands dominated by emergent vegetation) on the Tsitsikamma Plateau. Palustrine wetlands are the dominant wetland type on the plateau and are those not directly associated with flowing or permanent water, but rather with soils high in organic matter, which may be saturated for extended periods without the presence of surface water (Kotze et al., 1994; Masundire and Mackay, 2002; Mergili and Privett, 2008). These wetlands fall within the eastern division of the CFR and support fire-prone fynbos vegetation. In South Africa, there are special cases, where the morphological signs of wetness are not readily detectable in the soil profile (Department of Water Affairs and Forestry, 2005). One of these special cases involves the sandy soil profiles of coastal aquifer systems such as the Coastal Aquifer System of the Southern Cape (e.g. Tsitsikamma). Therefore, as elsewhere, the dominant delineator of palustrine wetlands on the Tsitsikamma Plateau is certain plant species that are indicative of soil wetness (Cronk and Fennessy, 2001; DWAF, 2005; Schafer, 2002; Tiner, 1991) and in the CFR these include *Berzelia intermedia* (D. Dietr.) Schltdl., *Carpha glomerata* (Thunb.) Nees, *Cliffortia ferruginea* L.f. and *Wachendorfia thyrisiflora* Burm. (Kirkman, 2007; Mergili and Privett, 2008; Schafer, 2002; Werger et al., 1972). However, there has been very little research specifically on the community structure of Cape wetland vegetation. Here we contribute to filling this gap by undertaking a floristic survey of the palustrine wetlands of the Tsitsikamma Plateau. We also attempt to explain this structure in terms of geographic location, the height of the adjacent plantation and fire history, in order to provide guidelines for managing these wetlands in a plantation forestry context.

1.1. Study area

The study area was located on the Tsitsikamma Plateau in the eastern part of the CFR, roughly 30 km east of Plettenberg Bay and 30 km west of Humansdorp. The plateau comprises an approximately 7 km wide coastal platform bounded in the south by steep cliffs abutting the Indian Ocean and in the north by the Tsitsikamma Mountains, an arm of the Cape Folded Belt (Grey et al., 1987; Rebelo et al., 2006). Altitude ranges between 150 and 260 m. Most of the plateau is underlain by the Peninsula Formation quarzitic sandstones of the Table Mountain Group (Geldenhuys, 1994; Strydom and Schafer, 1997). Soils are infertile, poorly drained, duplex forms (sand overlying clay at 0.5–1.0 m depth) — the largest coherent area of such soils in South Africa (Louw, 1991; Strydom and Schafer, 1997).

The mean annual temperature at Storms River Bos – a station in the centre of the Tsitsikamma Plateau – is 15.4 °C (Grey et al., 1987); temperatures exceed 35 °C in summer and drop below 5 °C in winter. Rainfall data for this study were obtained from the Lottering and Witelsbos weather stations. Rainfall is fairly constant throughout the year and mean annual rainfall (1970–2008) for the Lottering and Witelsbos Plantation was 1019.8 mm and 1093.7 mm respectively. The study period coincided with a severe drought in the area, and the annual rainfall for 2009 at Lottering was 563 mm and at Witelsbos was 711 mm; the lowest ever recorded.

The predominant vegetation is Tsitsikamma Sandstone Fynbos, a tall (up to 5 m) proteoid shrubland (*Protea mundii* Klotzsch, *Protea neriifolia* R.Br., *Protea coronata* Lam., *Leucadendron eucalyptifolium* H. Buek ex Meisn.) with a dense understorey of ericoid shrubs and restioids (Rebelo et al., 2006). Patches of Southern Afrotemperate Forest occupy fire-protected bergwind shadows associated with heavier soils of the Gydo Formation (Geldenhuys, 1994). About 90% of the fynbos on the plateau has been transformed by plantation forestry and dairy pastures (Hugo, pers. obs.).

2. Methods

2.1. Data collection

As study regions we identified two plantations managed by the forestry company Mountain to Ocean (MTO): the Lottering Plantation, as the main study area owing to its varied fire history, and the Kromriver Plantation, 50 km east of Lottering. All wetlands generally had a north to south orientation running parallel to one another from the mountains towards the ocean.

We sampled 21 sites (in 17 wetlands) at the Lottering Plantation and three sites (in three wetlands) at the Kromriver Plantation between July 2009 and January 2010. We attempted as far as possible to sample a wide range of fire histories, hereafter referred to as fire treatments. At Lottering, we distinguished between seven different fire treatments based on number of fires in the past 25 years (this was the period for which we could get accurate records) and post-fire vegetation age: (i) no burn (one treatment) — sites that had not burnt in more than 25 years; (ii) one burn (four treatments) — sites which had burnt once in the last 25 years but in different periods and therefore represent different post-fire vegetation ages (August 1998, August 1999, July 2000 or October/November 2005); (iii) two burns (two treatments) — sites which had burnt twice in the last 25 years, the first in different periods (August 1998 and August 1999) and the second in the same period (October/November 2005), and thus had four year old vegetation at the time of sampling. The three sites at Kromriver all experienced a single burn in the last 25 years (October/November 2005) and had four year old vegetation. From these data, we derived two fire-related variables: post-fire vegetation age and number of fires in the past 25 years. Since all fires were in the late winter and spring months (Jul–Nov), we were unable to investigate fire-season effects.

We surveyed each site in a location representative of the wetland (Higgins et al., 1997) using a cross-sectional transect from the western edge to the lowest point. All transects were located at least 50 m from any road or other obstruction. Along each transect, we surveyed three 2×2 m plots (edge, intermediate and lowest point) but three sites were too narrow to sample three plots and we sampled one plot at one site and two plots at the other two sites (total number of plots=68).

Within each plot, we estimated the cover-abundance of each species using the Braun-Blanquet scale (Werger, 1974). We allocated a B-B value of 1 to species with a cover of less than 5% as well as species that were observed only outside the plot, within 1–2 m of its periphery. We also noted the maximum height of each species, its reproductive state (i.e. flowering, fruiting), and its post-fire reproductive mode (i.e. resprouter, reseeder). We also noted the percentage of bare ground and, as an indication of senescence, the cover of dead plant material. Nomenclature followed Goldblatt and Manning (2000).

In order to assess the effects of plantation management on wetland composition and structure, we recorded wetland width (i.e. delineation of wetland corridor; Schafer, 2002), proximity to plantation (i.e. distance in m between plot and edge of plantation), and height of plantation pines (i.e. whether adjacent pine stands were high (>3 m) or low (<3 m)).

To assess the effects of physical factors on wetland composition and structure, we recorded wetland location (i.e. along a west to east gradient), plot location (i.e. edge, intermediate or lowest point) and collected soil samples. For the latter, we sampled three 20 cm-deep soil cores at each plot and combined these into one sample. These were analysed by Bemlab for soil pH, organic carbon content and 5-fraction soil texture. Since 2009 marked an extreme drought in the Southern Cape and soil moisture levels may vary considerably – yearly, seasonally, even daily – we did not measure this variable (Tiner, 1991).

2.2. Data analysis

2.2.1. Wetland vegetation communities and flora

In our study, 33 of 71 recorded plant species occurred in less than 5% of the plots and were thus excluded from analyses (McCune and Mefford, 2002). We identified communities using classification and indicator species analyses in PC-ORD 5 (McCune and Mefford, 2006), which offers a wide array of classification methods (Gilliam and Saunders, 2003). We used a hierarchical agglomerative cluster analysis, with Sørensen (Bray–Curtis) distance and a flexible beta (−0.25) linkage, to identify different plant communities, and the multi-response permutation procedure (MRPP) with Sørensen distance in order to determine the optimum number of communities (McCune and Mefford, 2002; Mielke and Berry, 2001). We used a Monte Carlo test ($P<0.05$) with 1000 randomizations to identify statistically significant indicator species (McCune and Mefford, 2002). In this analysis an indicator value above 55% indicates asymmetrical indicator species that ideally occurs in all sites of a single community, while values of less than 55% belong to asymmetrical indicator species (Dufrêne and Legendre, 1997).

2.2.2. Community patterns in relation to fire history, plantation management and physical factors

We used non-metric multidimensional scaling (NMDS) to examine patterns and interrelationships of identified communities; this ordination technique can be used for both ordination and dimensionality assessment and can accommodate both discontinuous and non-normally distributed data (McCune and Mefford, 2002). NMDS uses an iterative search for the best positions of n entities in k dimensions, while minimising the stress; the closer the stress is to 0%, the better the given configuration represents the data (Kruskal, 1964). Species inputs for the NMDS analysis comprised only indicator species; importance values were mid-points of Braun-Blanquet classes expressed as percentage cover values. These values were then relativized by species maxima (by sample units) to shift the focus of the analysis from absolute abundances to relative abundances (McCune and Mefford, 2002). By superimposing abiotic variables onto the floristic ordination, relationships (correlations) between community data and the following categories of variables were examined: number of fires in the past 25 years (i.e. plots burnt nought, once or twice in the last 25 years); post-fire vegetation age (i.e. last fire 4, 9, 10, 11 or more than 25 years ago); plantation management — wetland width, proximity to plantation and plantation height; and physical factors — wetland location, plot location and soil characteristics.

Initial analysis in 6-dimensional space using Sørensen distance, indicated that a 3-dimensional solution would best represent the data. The final NMDS analysis of 100 runs, using three axes with a randomly selected starting configuration, represented the general trend of previous runs. We used the PC-ORD 5 default setting for significance ($r^2=0.2$; McCune and Mefford, 2002).

We used univariate analysis to further examine relationships among identified communities. The one-way ANOVA and Tukey's test (for data where the assumptions of normality and homoscedacity were met) and the Kruskal–Wallis ANOVA and multiple comparisons test of mean ranks (for non-normally distributed data) (STATISTICA 9; StatSoft, 2009) were used to test for difference among communities in vegetation height, wetland width, proximity to plantation, soil pH and percentages of dead vegetation, bare soil, organic carbon, clay, silt and fine, medium or coarse sand.

3. Results

3.1. Wetland vegetation communities and flora

The multivariate analysis identified five plant communities: Elegia, Carpha, Conicum, Scirpus and Verrucosa communities (Table 1). The Elegia community had two significant indicators, namely *Tetraria cuspidata* and *Elegia fistulosa*. The Carpha community also had two significant indicators, namely *C. glomerata* and *Helichrysum cymosum*. With indicator values above 55%, *T. cuspidata* and *C. glomerata* were the only symmetrical indicator species identified by the indicator species analysis. The Conicum community, with *Cliffortia* *graminea* and *Leucadendron conicum* as its two significant indicators, was the most frequently encountered community, encompassing 23 plots. The fynbos wetland indicator, *B. intermedia*, was also frequently recorded in this community. The Scirpus community, which comprised only six plots, had four significant indicator species, namely *Scirpus* sp., *C. ferruginea*, *Calopsis paniculata* and *Cliffortia odorata*. The Verrucosa community had the largest number of significant indicator species, namely *Psoralea verrucosa*, *Erica copiosa*, *Metalasia pungens*, *Senesio purpureus*, *Arctotheca calendula*, *Lobelia anceps*, *B. intermedia*, *Tetraria involucrata* and *L. eucalyptifolium*. Many of these species were restricted to this community which also had the highest mean richness per plot.

3.2. Community patterns in relation to fire history, plantation management and physical factors

The greatest reduction in stress for the ordination was achieved with a 3-dimensional solution that had a stress value of 13.38% and final instability of $<10^{-5}$. The stress, therefore, represented a fair

Table 1
The five wetland communities of the Tsitsikamma Plateau with their respective indicator species. Significant indicator species as determined by the Monte Carlo test are in bold. V — species occurrence in 80–100% of plots; IV — species occurrence in 60–79% of plots; III — species occurrence in 40–59% of plots; II — species occurrence in 20–39% of plots; I — species occurrence in 10–19% of plots; '+' — species occurrence in 1–9% of plots. The mean percentage cover is given in brackets. n = number of plots per community.

Species	**Family**	**Indicator value (%)**	**Community**				
			Elegia (n = 19)	Carpha (n = 10)	Conicum (n = 23)	Scirpus (n = 6)	Verrucosa (n = 10)
Tetraria cuspidata (Rottb.) C.B. Clarke	Cyperaceae	$\mathbf{65}^{**}$	V (39)	V (7)	I (2)		
Elegia fistulosa Kunth	Restionaceae	$\mathbf{43}^{**}$	V (26)	III (<1)	IV (5)		V (5)
Laurembergia repens (L.) P.J. Bergius var. *brachypoda* (Welw. ex Hiern) Oberm.	Haloragaceae	12	II (3)	II (4)	I (<1)	I (<1)	I (4)
Ehrharta erecta Lam.	Poaceae	10	I (4)	I (<1)			I (<1)
Carpha glomerata (Thunb.) Nees	Cyperaceae	$\mathbf{65}^{**}$	II (2)	V (62)	III (5)	II (9)	
Helichrysum cymosum (L.) D. Don	Asteraceae	$\mathbf{40}^{**}$	III (3)	V (11)	III (2)	I (<1)	IV (4)
Conyza scabrida DC.	Asteraceae	10	I (<1)	II (<1)			I (<1)
Halleria lucida L.	Stilbaceae	9		II (4)	II (<1)	I (<1)	II (<1)
Helichrysum petiolare Hilliard & B.L. Burtt	Asteraceae	8	I (<1)	II (2)	+		I (4)
Cliffortia graminea L.f.	Rosaceae	$\mathbf{48}^{**}$	IV (22)	IV (9)	V (61)	II (5)	II (5)
Leucadendron conicum (Lam.) I. Williams	Proteaceae	$\mathbf{30}^{*}$	II (<1)		III (7)	II (2)	I (<1)
Phylica axillaris Lam.	Rhamnaceae	11	+		I (3)	I (<1)	
Myrica serrata Lam.	Myricaceae	10	I (<1)	II (2)	II (1)		I (<1)
Psoralea sp.	Fabaceae	8	I (<1)	I (<1)	II (<1)	I (<1)	
Grubbia rosmarinifolia P.J. Bergius	Grubbiaceae	7			I (3)		I (2)
Blechnum tabulare (Thunb.) Kuhn	Blechnaceae	5		I (<1)	I (<1)		I (<1)
Scirpus sp.	Cyperaceae	$\mathbf{52}^{**}$	I (1)	I (<1)	+	IV (23)	I (<1)
Cliffortia ferruginea L.f.	Rosaceae	$\mathbf{49}^{**}$	III (14)	II (<1)	I (<1)	V (50)	IV (30)
Calopsis paniculata (Rottb.) Desv.	Restionaceae	$\mathbf{42}^{**}$		I (<1)	I (<1)	III (11)	
Cliffortia odorata L.f.	Rosaceae	$\mathbf{24}^{*}$	I (2)			II (3)	
Erica fuscescens (Klotzsch) E.G.H. Oliv.	Ericaceae	27	I (<1)	I (<1)	III (2)	III (17)	II (2)
Platycaulos compressus (Rottb.) H.P. Linder	Restionaceae	22	III (6)	IV (11)	IV (28)	IV (31)	II (<1)
Clutia alaternoides L.	Euphorbiaceae	15	I (2)		I (<1)	II (3)	II (1)
Gleichenia polyodioides (L.) Sm.	Gleicheniaceae	11	I (<1)		II (4)	II (2)	II (1)
Erica sparsa Lodd.	Ericaceae	6	+		+	I (<1)	
Psoralea verrucosa Willd.	Fabaceae	$\mathbf{50}^{**}$					III (2)
Erica copiosa J.C. Wendl.	Ericaceae	$\mathbf{40}^{**}$					III (2)
Metalasia pungens D. Don	Asteraceae	$\mathbf{38}^{**}$			+		III (4)
Lobelia anceps L.f.	Campanulaceae	$\mathbf{36}^{**}$			+		III (<1)
Berzelia intermedia (D.Dietr.) Schltdl.	Bruniaceae	$\mathbf{34}^{*}$	II (3)		IV (13)	II (2)	V (18)
Tetraria involucrata (Rottb.) C.B. Clarke	Cyperaceae	$\mathbf{28}^{**}$	+				II (3)
Senecio purpureus L.	Asteraceae	$\mathbf{26}^{*}$			+		II (<1)
Leucadendron eucalyptifolium H.Buek ex Meisn.	Proteaceae	$\mathbf{24}^{*}$	I (<1)			I (<1)	III (1)
Arctotheca calendula (L.) Levyns	Asteraceae	$\mathbf{22}^{*}$	I (<1)				II (<1)
Epischoenus gracilis Levyns	Cyperaceae	21	III (13)	III (6)	+	I (<1)	III (24)
Merxmuellera cincta (Nees) Conert	Poaceae	20	I (1)	II (1)	+		III (7)
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	18	III (<1)	III (<1)	III (2)	II (<1)	III (7)
Pentaschistis malouinensis (Steud.) Clayton	Poaceae	15	I (<1)				II (1)
Total no. of species in community[a]			38	22	43	24	42
Average no. of species per plot			9	7	9	8	11

$^{*}P<0.05$; $^{**}P<0.01$.

[a] This includes all species recorded per community (i.e. including those occurring in less than 5% of the plots).

goodness of fit (Kruskal, 1964). The three axes accounted for 86% of the variation; axis 1, axis 2 and axis 3 were loaded with 20%, 39% and 27% of variation respectively (Table 2; Figs. 1 and 2). Although a 3-dimensional solution best represented the data, only axes 2 and 3 showed significant relationships with the measured variables. Axis 2 carried the highest load and was significantly negatively related to plantation height (r^2 = 0.23; Table 2) and positively to wetland location (r^2 = 0.22). Axis 2 separated plots associated with the Carpha and Conicum communities from plots associated with the Scirpus and Verrucosa communities (Figs. 1 and 2). Axis 3 was positively related to the number of fires in the past 25 years (r^2 = 0.19; Table 2) and it separated plots associated with the Elegia and Carpha communities from plots associated with the other three communities (Fig. 1). Though not very strong, wetland location and medium sand content were negatively related to axis 3 (r^2 = 0.14 and r^2 = 0.15 respectively; Table 2). Axis 1 was not strongly related to any of the measured variables, although it accounted for 20% of the variation.

Regarding the number of fires, plots which had burnt twice in the past 25 years were generally associated with either the Elegia or Carpha communities, where the majority of the vegetation was four years old (Table 3). Most plots that sustained one burn, at least nine years ago, were either grouped into the Elegia, Conicum or Scirpus community. Plots that had not burnt in the last 25 years were mainly classified into the Conicum or Scirpus communities. All plots from the Verrucosa community sustained one fire in the last 25 years, generally four years ago.

Plots from the Elegia community were more evenly distributed in the study area, while plots from the Carpha community were generally located at the western side of the study area; plots from the Conicum community occurred mainly in the central west; plots from the Scirpus community were mainly in the central east, while plots from the Verrucosa community were located in the east at Kromriver (Table 3).

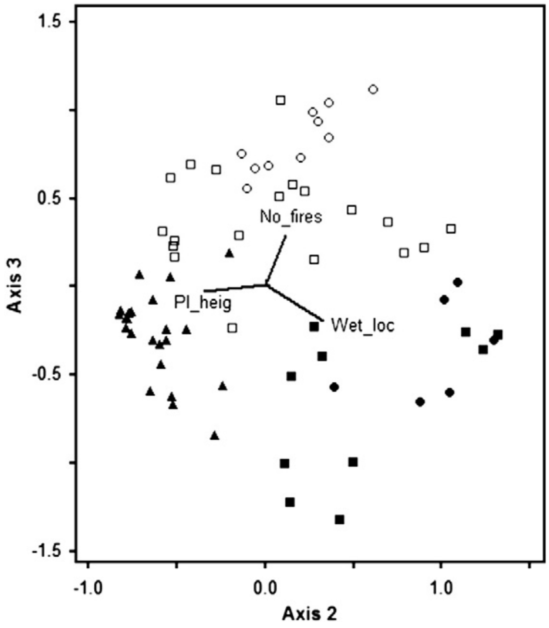

Fig. 1. Two-dimensional (axes 2 and 3) representation of the NMDS ordination of the wetland communities (□ = Elegia; ○ = Carpha; ▲ = Conicum; ● = Scirpus; ■ = Verrucosa) on the Tsitsikamma Plateau. Graphs indicate significant correlations of wetland location (Wet_loc) and plantation height (Pl_heig) with axis 2 and of number of fires in the past 25 years (No_fires) with axis 3. Stress = 13.38%. Final instability < 10^{-5}.

Table 2
Regression coefficients (r^2) of ordination axes with fire history, plantation management and physical factors as determined by the NMDS ordination. Significant coefficients as determined by the default setting of PC-ORD **(≥0.2)**. '(−)' indicates the direction along the axis. The proportion of variance represented by the three axes was 0.20, 0.39 and 0.27 respectively.

Variables	Axis 1 r^2	Axis 2 r^2	Axis 3 r^2
Fire history			
No. of fires in past 25 years	(−) 0.00	0.08	0.19
Post-fire vegetation age	0.01	(−) 0.06	(−) 0.02
Plantation management			
Wetland width (m)	0	0.01	(−) 0.12
Proximity to plantation (m)	0.01	0.01	(−) 0.03
Plantation height	(−) 0.00	**(−) 0.23**	(−) 0.02
Physical factors			
Wetland location	(−) 0.00	**0.22**	(−) 0.14
Plot location	0.07	0.02	0.01
Surface water (%)	0.08	0.07	(−) 0.04
Soil pH	0.12	0.09	0.01
Organic carbon (%)	0.05	(−) 0.01	(−) 0.00
Clay (%)	(−) 0.03	0.07	(−) 0.07
Silt (%)	(−) 0.00	(−) 0.00	(−) 0.10
Fine sand (%)	(−) 0.05	(−) 0.07	0.06
Medium sand (%)	0.04	0.03	(−) 0.15
Coarse sand (%)	0.09	0.06	(−) 0.04

There was a significant difference in vegetation height among the communities and the Conicum community was significantly taller than the others, barring the Scirpus community (Table 4). The Conicum community also had significantly more senescent vegetation than the Elegia community, while the other communities were intermediate.

Although none of the axes of the NMDS ordination related well to soil characteristics, they differed significantly among

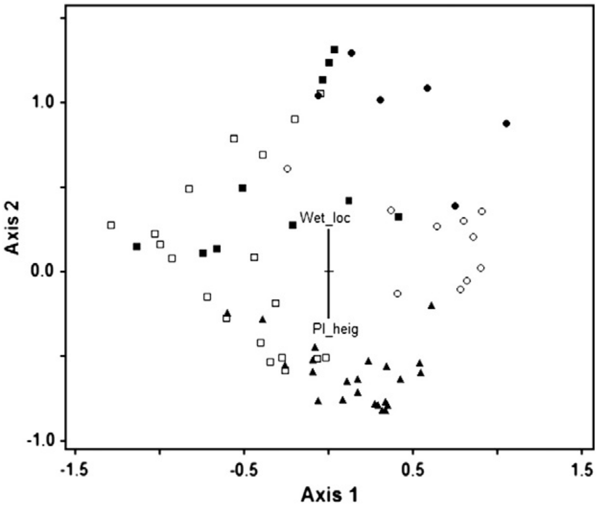

Fig. 2. Two-dimensional (axes 1 and 2) representation of the NMDS ordination of the wetland communities on the Tsitsikamma Plateau. Symbols are same as that for Fig. 1. Stress = 13.38%. Final instability < 10^{-5}.

Table 3
Comparison of wetland communities of the Tsitsikamma Plateau with regards to number of fires in the past 25 years, post-fire vegetation age, plantation height, wetland location and plot location. n=number of plots per community.

Variables	Community				
	Elegia (n=19)	Carpha (n=10)	Conicum (n=23)	Scirpus (n=6)	Verrucosa (n=6)
No. of fires in past 25 years					
No burn	1 (5%)	1 (10%)	5 (22%)	2 (33%)	0
1 burn	10 (53%)	4 (40%)	17 (74%)	3 (50%)	10 (100%)
2 burn	8 (42%)	5 (50%)	1 (4%)	1 (17%)	0
Post-fire vegetation age					
>25 years	1 (5%)	1 (10%)	5 (22%)	2 (33%)	0
>9 years	8 (42%)	2 (20%)	12 (52%)	3 (50%)	1 (10%)
>4 years	10 (53%)	7 (70%)	6 (26%)	1 (17%)	9 (90%)
Plantation height					
Within high stands (>3 m)	11 (58%)	5 (50%)	21 (91%)	5 (83%)	2 (20%)
Within low stands (<3 m)	8 (42%)	5 (50%)	2 (9%)	1 (17%)	8 (80%)
Wetland location					
West	8 (42%)	6 (60%)	8 (35%)	0	1 (10%)
Central west (Lottering)	4 (21%)	1 (10%)	11 (48%)	2 (33%)	0
Central east (Boskor)	7 (37%)	3 (30%)	3 (13%)	4 (67%)	1 (10%)
East (Kromriver)	0	0	1 (4%)	0	8 (80%)
Plot location					
Edge	7 (37%)	2 (20%)	9 (39%)	2 (33%)	4 (40%)
Intermediate	8 (42%)	4 (40%)	8 (35%)	1 (17%)	2 (20%)
Lowest point	4 (21%)	4 (40%)	6 (26%)	3 (50%)	4 (40%)

communities (Tables 2 and 4). Regarding organic carbon, the Scirpus community had significantly more than the Elegia and Verrucosa communities. The clay content of the soil appeared to differ along a west to east gradient and the western Carpha community occurred on soils with significantly lower clay content than the eastern Verrucosa community. Soil texture also appeared to grade from west to east and, for example, medium sand content of the soil was significantly lower in the Carpha community than the Verrucosa community. This explains the NMDS ordination result of a weak negative relationship of medium sand with axis 3.

4. Discussion

4.1. Wetland vegetation communities and flora

We identified five palustrine wetland communities on the Tsitsikamma Plateau, mostly dominated by species endemic to the CFR. *Laurembergia repens*, *C. glomerata*, *C. paniculata* and the unidentified *Scirpus* sp. are obligate wetland species that designate permanently wet soils, while *B. intermedia*, *Cliffortia* spp., *E. fistulosa*, *Epischoenus gracilis*, *H. cymosum*, *L. conicum*,

Table 4
Variation among wetland communities of the Tsitsikamma Plateau mean (±standard deviation) vegetation height, wetland width, proximity to plantation, percentage of dead vegetation, bare soil and soil characteristics. Significant differences were determined by the one-way ANOVA or the non-parametric Kruskal–Wallis ANOVA.

Variables	Community					Statistics
	Elegia (n=19)	Carpha (n=10)	Conicum (n=23)	Scirpus (n=6)	Verrucosa (n=10)	
Vegetation height (m)	0.9 ± 0.3^{a}	0.9 ± 0.2^{a}	$1.4 \pm 0.4^{\mathbf{b}}$	1.0 ± 0.4^{ab}	0.7 ± 0.3^{a}	$F=11.2$ ***
Wetland width (m)	38.1 ± 22.6^{ab}	24.9 ± 11.3^{a}	39.1 ± 22.8^{ab}	$68.3 \pm 17.2^{\mathbf{b}}$	47.8 ± 25.4^{ab}	$H=15.0$ **
Distance to plantation (m)	17.4 ± 9.0	13.7 ± 8.4	15.2 ± 10.7	26.7 ± 16.8	17.4 ± 12.4	$F=1.6$
Dead vegetation (%)	16.7 ± 16.6^{a}	28.2 ± 23.7^{ab}	$44.0 \pm 32.6^{\mathbf{b}}$	27.8 ± 31.4^{ab}	35.5 ± 19.9^{ab}	$F=3.1$ *
Bare soil (%)	0.3 ± 1.1^{a}	7.0 ± 9.8^{ab}	0.7 ± 2.3^{ab}	5.0 ± 10.0^{ab}	$8.6 \pm 9.6^{\mathbf{b}}$	$H=20.1$ ***
Soil pH	3.6 ± 0.2	3.8 ± 0.2	3.6 ± 0.2	3.9 ± 0.2	3.7 ± 0.2	$F=2.3$
Organic carbon (%)	5.5 ± 1.5^{a}	5.8 ± 2.5^{ab}	6.4 ± 2.3^{ab}	$8.8 \pm 2.7^{\mathbf{b}}$	4.1 ± 2.5^{a}	$F=4.8$ **
Clay (%)	1.5 ± 0.8^{a}	1.4 ± 0.8^{a}	1.3 ± 0.9^{a}	1.4 ± 1.0^{ab}	$3.2 \pm 1.6^{\mathbf{b}}$	$H=16.8$ **
Silt (%)	6.0 ± 5.1	7.5 ± 5.2	5.1 ± 4.5	3.4 ± 2.6	3.6 ± 2.3	$F=1.4$
Fine sand (%)	82.6 ± 5.6^{a}	80.9 ± 7.6^{ab}	81.2 ± 5.2^{a}	73.6 ± 8.7^{ab}	72.8 ± 11.6^{b}	$F=4.5$ **
Medium sand (%)	7.8 ± 5.6^{a}	7.3 ± 4.1^{a}	9.8 ± 4.2^{ab}	$15.4 \pm 4.1^{\mathbf{bc}}$	$16.6 \pm 9.2^{\mathbf{c}}$	$F=6.2$ ***
Coarse sand (%)	2.1 ± 1.7^{a}	2.9 ± 3.8^{ab}	2.5 ± 2.0^{a}	6.3 ± 5.1^{bc}	3.8 ± 2.8^{ac}	$F=3.1$ *

Means with the same letters do not differ significantly from one another as determined by the appropriate multiple comparisons test.

* $P<0.05$.

** $P<0.01$.

*** $P<0.001$.

Platycaulos compressus and *Psoralea* spp. designate temporarily wet soils (DWAF, 2005; Goldblatt and Manning, 2000; Kotze et al., 1994; Schafer, 2002; Sieben, 2010). However, many species in our communities can tolerate non-wetland conditions, though most are associated with moist fynbos in the Tsitsikamma region and elsewhere (Hugo, pers. obs.).

Generally, the communities were relatively poorly circumscribed floristically. Only the Elegia and Carpha communities had symmetrical indicators. The poorly circumscribed Conicum community – the most widespread – had the highest incidence of *L. conicum*, the only Red Data species (classified as "Near threatened"; Raimondo et al., 2009; SIBIS, 2010) in our wetland flora. However, this species occurred sporadically in three other wetland communities. The Verrucosa community – exclusively associated with the eastern Kromrivier site – had a distinctive composition reflected in the numerous indicator species. The Scirpus community was characterised by a high cover of obligate wetland species and was the only one observed with surface water during the survey — a time of severe drought; it also had the highest level of soil carbon which correlates generally in wetlands with length of inundation (Jokic et al., 2003).

South African wetlands are generally species-poor at the local (alpha) level, even in species-rich biomes such as the fynbos (Mergili and Privett, 2008; Werger et al., 1972) and grassland (Eckhardt et al., 1996). With only 7–11 species per 4 m^2 plot, our communities were no exception. On average, dryland fynbos communities in the eastern part of the CFR support 17 species per 1 m^2 (Cowling et al., 1992). Low diversity of fynbos wetland communities could be a consequence of numerous factors including physiological constraints associated with periodic inundation (Dwire et al., 2006), strong competition arising from relatively high productivity (Bartelheimer et al., 2010; Kotowski et al., 2006) or a regionally small species pool, owing to the minuscule area occupied by wetlands in most Cape landscapes (Silberbauer and King, 1991). Beta diversity was also low in these wetlands, as evidenced by the low number of symmetrical indicator species. Generally, the wetland flora included mostly wide-ranging species: 65% of the species have ranges extending beyond the CFR and of the 35% CFR endemics, only two are endemic to the south-east, namely *Erica fuscescens* and *Erica sparsa* (Goldblatt and Manning, 2000). The high incidence of wide-ranging species in our wetland flora may well have a bearing on their low alpha and beta components of diversity (Cowling et al., 1992).

4.2. Community patterns in relation to fire history, plantation management and physical factors

Although we did not investigate in detail the effects of inundation period on structuring the composition of the wetland communities of the Tsitsikamma Plateau, it is almost certain that species and communities segregate along fine-scale hydrological gradients, as demonstrated in wetland communities across the world, including the CFR (Araya et al., 2011; Dwire et al., 2006; Silvertown et al., 1999). Thus, the Scirpus community appeared to be physically differentiated by longer inundation cycles, as evidenced by the appearance of surface water, despite the prevailing drought conditions. The only factors that emerged as significantly influencing wetland composition in the multivariate analysis were geographic location along the west–east sampling gradient, number of fires in the past 25 years, and, the height of the adjacent plantation. Although 86% of the variation was accounted for by the measured variables, none of them were very strongly related to species composition. This suggests that abrupt transitions in variable states between communities, non-quantified variables, or random factors were strongly influencing community structure of the wetlands. However, the univariate analysis showed that, the wet Scirpus community had significantly higher levels of soil carbon than the Elegia and Verrucosa communities, while clay content and soil texture appeared to follow a west to east gradient. The latter may well account for the geographical gradient effect observed.

Fire regime is a major determinant of fynbos community structure (Cowling, 1987; Kruger, 1977; Van Wilgen et al., 1992, 2010). Owing to complex fire treatments and a relatively short documentation period, it was not possible to accurately predict the impacts of fire regime on the composition of our wetlands. With the exception of the Verrucosa community, where all plots had been subject to one fire in the past 25 years and all had relatively young post-fire ages, the wetland communities had relatively heterogeneous fire treatments and post fire ages. While most component species were re-sprouters, two were obligate re-seeders, and potentially sensitive to short rotation burns (Bond et al., 1984; Kraaij et al., 2012; Sieben, 2010; Van Wilgen et al., 1992). All dense stands of the serotinous proteoid *L. conicum* were associated with vegetation of a post-fire age of nine years and older; correspondingly Kraaij et al. (2012) suggest a minimum fire return interval of nine years for eastern coastal fynbos. The other obligate reseeder *E. fistulosa* persisted under a wide range of fire treatments, suggesting tolerance. However, we cannot deny that a succession of quick rotation fires may have eliminated *L. conicum* from many sites in the Tsitsikamma wetlands. We noted that *L. conicum* showed marked signs of senescence in stands 12 years post fire and longer. Since most of our fires were in the spring months (the others in late winter), we have little to say on the effects of fire season on recruitment of reseeders. However, research in the eastern CFR has shown that fire season has little bearing on recruitment success in serotinous, reseeding proteoids; instead, the most important factor was whether there was good rainfall in the immediate post-fire period, irrespective of season (Heelemann et al., 2008). Given a naturally non-seasonal fire regime in the Tsitsikamma (Kraaij et al., in press-a) and the high moisture conditions of wetlands year-round, fire season should have little bearing on population sizes of reseeding species.

Shading and homogenisation by invasive or plantation trees are known to influence the floristic and faunal structure of wetland communities in South Africa's fynbos and grassland biomes (Holmes et al., 2005; Richardson et al., 2007; Samways and Steytler, 1996; Samways and Taylor, 2004). Our results showed that most plots belonging to the Conicum community were associated with tall, mature pine forests. However, the same was true for the Scirpus community which clustered in the opposite quadrant of the ordination space to the Conicum community.

Furthermore, height of plantation should interact with delineation width of wetlands to produce a shading effect. We could detect no such relationship in our analyses.

What are the implications of our research for managing the palustrine wetlands of the Tsitsikamma Plateau in a commercial forestry setting? The Forestry Industry Environmental Committee (2002) recommends that wetlands are burnt on a basis that mimics the natural fire regime. Our understanding is that MTO foresters consider the wetlands as a fuel hazard for sustaining fires that threaten the adjacent plantations, especially under hot bergwind conditions when the linear wetland features behave as fire corridors. We see no easy solution to this problem. Our study suggests that burning the wetlands on a rotation short enough to keep fuel loads low will most likely eliminate sensitive species such as *L. conicum*. At the other extreme, wetlands could be burnt after pine harvesting (between 25 and 35 years) as recommended by Everson et al. (2004). Although we have no results in support, this option is also likely to be detrimental to wetland biodiversity, as *L. conicum* already started showing signs of senescence in stands 12 years post fire (Hugo, pers. obs.). We therefore suggest that the wetlands should be burnt at least once during the plantation growth cycle based on our analysis of life-history traits. The implementation of such burns will carry a risk and will be expensive to manage (Kraaij et al., 2011) but we suggest that the forestry industry internalise these risks and associated costs as a consequence of persisting with an industry not suited to a fire-prone environment (Van Wilgen et al., 2010).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.sajb.2012.07.009.

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