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Biotic interactions, climate and disturbance underlie the distribution of two *Julbernardia* tree species in miombo woodlands of Africa

Emmanuel N. Chidumayo

Makeni Savanna Research Project, P.O. Box 50323, Lusaka, Zambia

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Abstract: Occurrence data for *Julbernardia globiflora* and *J. paniculata* at 617 sites in the miombo woodland region of central, eastern and southern Africa and forest inventory data for 512 woodland plots in Zambia were used to determine species distribution and dominance. Distribution of the two *Julbernardia* species overlaps in the central region of the miombo woodland range while the eastern and western range regions are exclusively for only one of the two species. In the region of co-occurrence, there is a clear spatial separation in the dominance of the two species. In old-growth woodland a significant proportion of the variation in the dominance of *J. globiflora* was explained by the dominance of *J. paniculata* while mean annual maximum temperature and tree species richness negatively affect the dominance of *J. paniculata*. Old-growth woodland clearing changes the local climatic conditions and alters the way *Julbernardia* species in re-growth stands respond to potential evapo-transpiration (PET). Climate change, especially global warming, may further reinforce the impacts of PET to differentially favour *J. globiflora*. Because of this altered response of *Julbernardia* species in re-growth miombo, preserving old-growth miombo and preventing present human disturbances in designated areas, such as forest reserves and national parks, may be a useful climate adaptation strategy for these species.

Key Words: distribution, dominance, *Julbernardia*, miombo, potential evapo-transpiration, species richness, Zambia

INTRODUCTION

Miombo is a Tanzanian Kinyamwezi name for *Brachystegia boehmii* that was later used by the Germans to describe woodlands dominated by trees of the genera *Brachystegia* and *Julbernardia* (Mansfield *et al.* 1976). Miombo woodland occurs in Angola, Democratic Republic of Congo (DRC), Malawi, Mozambique, Tanzania, Zambia and Zimbabwe (Figure 1). Historically the miombo distribution range extended north of the equator into Ethiopia (Bonnefille 2010) and southwards into South Africa (Pienaar 2015). *Julbernardia* is a tropical African genus with six species of which *Julbernardia globiflora* (Benth.) Troupin and *J. paniculata* (Benth.) Troupin are miombo woodland species with similar traits but the latter is distinguished by its two to four pairs of large leaflets from the former that has four to seven pairs of small leaflets.

Miombo woodland is regarded as a vegetation type that has been maintained by man through a long history of cutting, cultivation and frequent dry-season fires over the last 55 000 y (Lawton 1978). The latter part of the 20th century witnessed the intensification of these land-use activities as a result of increasing human and livestock populations and this trend has continued into the 21st century. How *Brachystegia* and *Julbernardia* species are responding to these land-use changes remains debatable. Fanshawe (1971) observed that miombo woodland regenerates unchanged after clearing but a recent account has revealed a decline in the frequency of *Brachystegia* and *Julbernardia* species in areas of high forest use (Jew *et al.* 2016).

A number of *Brachystegia* and *Julbernardia* species have overlapping distribution ranges but little is known about factors that permit this co-existence. Some studies have indicated that co-existence at larger spatial scales is due to topographic heterogeneity (Cole 1963, Werger & Coetzee 1978) or spatial separation in the use of soil resources due to different rooting depths (Savory 1962). *Julbernardia globiflora* and *J. paniculata* have been reported to replace each other along a precipitation gradient with the latter replacing *J. globiflora* in the more sub-humid zone (Grundy 1995, Rees 1974). Vinya (2010) has recently shown that wide-ranging *Brachystegia* and *Julbernardia* species are less vulnerable to xylem cavitation and therefore

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Email: echidumayo@gmail.com or chidumayoe@yahoo.com

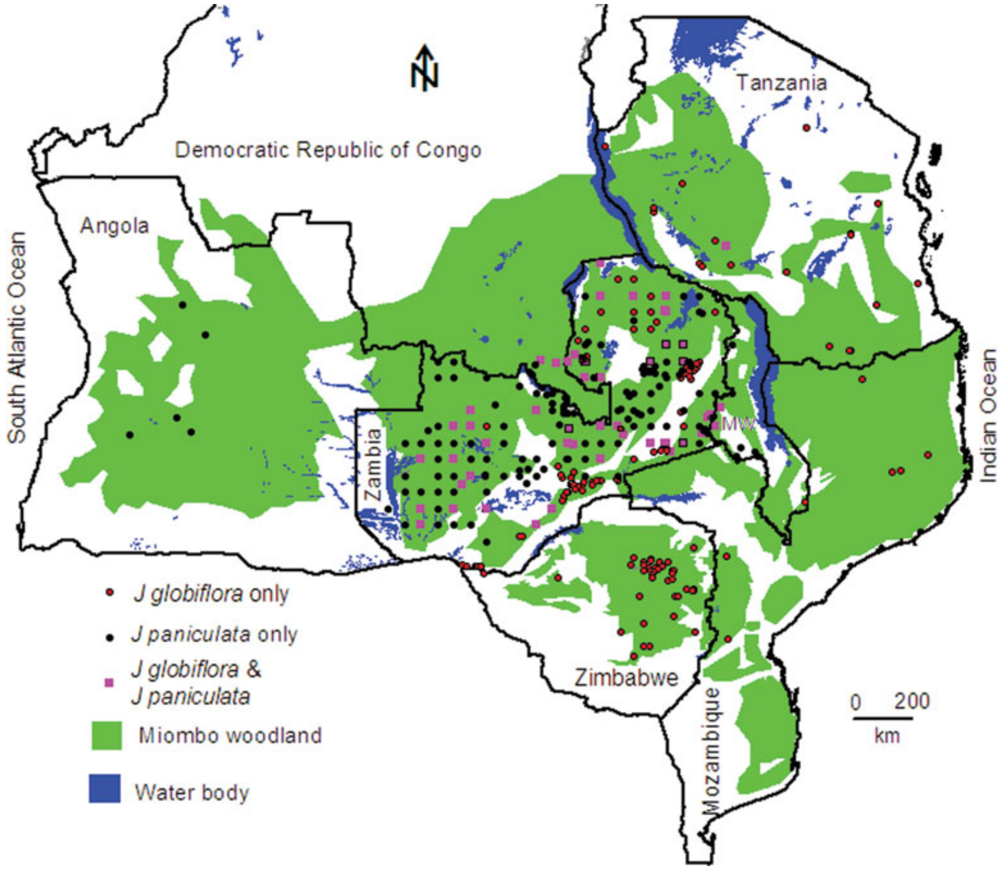

Figure 1. Extent of miombo woodlands in central, eastern and southern Africa (based on White 1983) and location of sites where *Julbernardia* species have been recorded. MW is Malawi.

can survive better under warmer and drier conditions than species that are restricted to more mesic conditions. In southern Africa a relationship between woody plant species richness and potential evapo-transpiration (PET) has been demonstrated (O'Brien 1993). The present study tested the hypothesis that the distribution and abundance of *Julbernardia* species in miombo woodlands is largely influenced by environmental factors. It is hoped that the research findings will contribute to the knowledge of the biogeography of *Julbernardia* species in miombo woodlands of central, eastern and southern Africa.

MATERIALS AND METHODS

Study area

The study area covers the whole miombo region in seven countries (Angola, DRC, Malawi, Mozambique, Tanzania, Zambia and Zimbabwe) that lie between latitudes 2° and 25°S and longitudes 10° and 40°E. The distribution of miombo woodlands is largely restricted to the central African plateau that consists of gentle undulating landscapes (Cole 1986). Mean annual precipitation ranges from 600 mm to over 1600 mm which is distributed from November to April. Over much of the miombo ecoregion the trend in precipitation during 1951–2010 was not significant and little or no change is expected by mid-21st century for both the RCP2.6 and RCP8.5 projections relative to the 1986–2005 period but reduced rainfall at the beginning of the wet season is projected (Niang *et al*. 2014). Mean annual temperature ranges from 19°C to 25°C and projected future median increases in temperature range from under 3.5°C to over 5.0°C by the end of the 21st century with the highest increases in the south and south-west of the miombo region (Niang *et al*. 2014). Mean annual PET ranges from under 3.0 mm d^{-1} in the north to over 4.0 mm d^{-1} in the south-east. The dominant soils in the high-rainfall zones are Ferralsols while in the low-rainfall zones these are Cambisols (Frost 1996).

Field inventories

This study is based on forest inventories involving a total of 65 and 447 plots in re-growth (RG) and old-growth (OG) stands, respectively, conducted in Zambia (8–18°S, 22–34°E, Figure 1) between 1980 and 2015.

The plot sizes ranged from 0.02 ha to 2.0 ha and the details of these inventories have been described by Chidumayo (1987, 2016). Except for the 2005–2008 and 2015 inventories, all the OG plots were preferentially located in stands with little or no present human disturbances and all the plots were sampled only once. The 2005–2008 inventory was conducted by the Forestry Department (Zambia Forestry Department & Food and Agriculture Organization of the United Nations 2009) and aimed primarily at assessing forest resources in Zambia and used a systematic sampling design in which inventory plots were located at the intersections of half degree latitude and longitude (about 59 km apart) throughout the country. The 2015 survey was based on a 235-km transect in south-west Zambia with the objective of assessing habitat and floristic diversity on the Zambezi valley terraces and used a preferential sampling design to locate sample plots in all the habitats along the transect. Re-growth sample plots included sites where woodland was cleared for charcoal production (Chidumayo 1991), tsetse-fly control (Chidumayo 2013) and shifting cultivation (Chidumayo & Mbata 2002). The coordinates (latitude and longitude) of each sample plot were determined using a hand-held Global Positioning System (GPS) instrument and recorded. All trees in a plot were identified either by scientific or local name and trees with diameter at 1.3 m above ground (dbh) of ≥3.0 cm were measured and recorded. Trees identified by local names were later given their corresponding scientific names using a checklist of local names of woody plants of Zambia (Fanshawe 1965).

Data analysis

The following structural variables were calculated for each plot: number of *Brachystegia*, *Julbernardia* and total tree species, stem density, basal area and dominance of each species. The Importance Value (IV) index was used to determine the dominance of each species in each sample plot because it has been applied in vegetation classification in the miombo ecoregion (Banda *et al*. 2008, Ribeiro *et al*. 2008). The species Importance Value (IV) was calculated using PC-ORD software version 4 (McCune & Mefford 1999). The IV was calculated using the following formula:

$$IV_i = (RF_i + RD_i + RB_i)/3$$

Where IV_i is Importance Value of species i, F is number of sample plots containing a particular species, D is number of stems of a particular species and B is basal area of a particular species. RF_i is relative frequency $(100(F_i/\Sigma F_i))$, RD_i is relative density $(100(D_i/\Sigma D_i))$ and RB_i is relative dominance $(100(B_i/\Sigma B_i))$ of species i in a plot (McCune & Mefford 1999).

Table 1. Predictor variables used in the best subset regression analysis to determine their significance in explaining variation in Importance Value (IV) of *Julbernardia* species in Zambia.

Physical factors	Mean annual minimum temperature (°C) Mean annual maximum temperature (°C) Annual rainfall (mm) Potential evapo-transpiration (PET, mm d^{-1}) Latitude Longitude Plot size (ha)
Biotic factors	Species per plot *Brachystegia* species per plot *Julbernardia* species per plot *Brachystegia* species IV *Julbernardia globiflora* IV or *J. paniculata* IV

To model the spatial dominance of *Julbernardia* species in Zambia, the IVs of the two species in sample plots were arcsine-transformed and treated as Z-values in a matrix in which plot coordinates were entered as X-values on the longitude scale and Y-values on the latitude scale. The IV values were then subjected to spatial modelling procedures to generate a dominance map at the country level. The modelling was done in SYSTAT 7.0 using the scatter-plot technique (Anonymous 1997). The scatter-plot technique in SYSTAT 7.0 first computes its own square grid of interpolated or directly estimated IV-values from the matrix using the method of Lodwick & Whittle (1970) combined with linear interpolation.

In order to determine factors (explanatory or predictor variables) that might explain variation in IV (hereafter also referred to as dominance) of each *Julbernardia* species in sample plots, data were subjected to best subset regression analysis in STATISTIX 9.0 (Analytical Software 1985–2008). Twelve predictor variables were used in the analysis (Table 1) and arcsine-transformed IV values were subjected to regression analyses that were done in two phases. Firstly, the best-subset regression analysis was carried out to select predictor variables that explained the largest variation in the species IV. When two independent variables are highly correlated the analytical procedure used automatically drops one of the predictor variables to avoid problems of collinearity (Analytical Software 1985–2008). Best-subset regression analysis simultaneously compares models with single variables and all their possible combinations. The model with the lowest Akaike's Information Criterion (AIC) for small samples (AIC_c) was selected as the best model (Burnham & Anderson 2002). Secondly, the predictor variable(s) in the selected best model was/were used to develop predictive additive models using ordinary linear regression analysis.

Differences in IV between OG and RG plots for each species were tested by the Wilcoxon Rank Sum Test (*U*) at $P = 0.05$ using a two-tailed test for normal approximation.

Table 2. Sites in the miombo woodland countries at which *Julbernardia* species have been recorded but for which no individual tree measurement data were available.

Country	Sites	Sources
Angola	5	Ceriaco *et al.* (2014), Dean (2001), Piedade (2013)
Democratic Republic of Congo	4	Malaisse *et al.* (1975, 1999), Raynes (2007)
Malawi	9	Abbot & Lowore (1999), Hursh (1960), Jachmann & Bell (1985), Kamangadazi *et al.* (2016), Kamwendo & Chikuni (2001), Kuyah *et al.* (2014), Missanjo *et al.* (2014), Timberlake *et al.* (unpubl. data)
Mozambique	7	Müller *et al.* (unpubl. data), Ribeiro *et al.* (2008, 2013), Ryan *et al.* (2011)
Tanzania	17	Backéus *et al.* (2006), Banda *et al.* (2006), Boaler & Sciwale (1966), Jew *et al.* (2016), McNicol *et al.* (2015), Munishi *et al.* (2010), Obiri *et al.* (2010), Shelukindo *et al.* (2014), Shirima *et al.* (2015), Singo (2007)
Zambia	21	Chibinga & Nambeye (2016), Chomba *et al.* (2013), Eriksen (2007), Handavu *et al.* (2011), Hansen *et al.* (2002), Mansfield *et al.* (1976), Oyama (1996), Rees (1974), Shea *et al.* (1996), Smith (1998), Stromgaard (1985)
Zimbabwe	43	Chapano *et al.* (2013), Chinuwo *et al.* (2010), Grundy *et al.*(1993), Mapanda *et al.* (2013), Mapaure (2013), Muboko *et al.* (2013), Muposhi *et al.* (2014), Strang (1974), Wuta *et al.* (2013), Zimudzi *et al.* (2013), Zingore *et al.* (2005)
Total	106	

Other data

The geographic coordinates of other sites at which *J. globiflora* and *J. paniculata* have been recorded in countries with miombo woodland but for which no individual tree dbh data were available were obtained from literature. If the coordinates (latitude and longitude) were not given, these were derived from maps using a digitizing tool and for large areas, such as protected areas, centre coordinates of the areas were used to describe the sites. A total of 106 such sites were obtained from literature sources (Table 2).

Climate data for each quarter-degree square for Zambia were obtained from the Climatic Research Unit at the University of East Anglia, UK that were interpolated from real climate-station records. These data included mean annual minimum and maximum temperatures, rainfall and potential evapo-transpiration (PET) for the period 1951–2010. These climate data were assigned to sample plots on the basis of the grid in which plots were located. These data were used to assist in determining the distribution of the two *Julbernardia* species. The relationship between PET and woodland clearing was only analysed with the Zambian data for which the climate and tree dbh data were available.

RESULTS

Distribution of *Julbernardia* species

Julbernardia species are widely distributed in the miombo woodlands of central, eastern and southern Africa although *J. paniculata* tends to occur more in the west while *J. globiflora* occurs more in the east of the miombo woodland range with areas of co-occurrence concentrated in Zambia and western Malawi (Figure 1). The only record of the species co-occurrence in Tanzania was at Kabungu (Figure 1) but *J. paniculata* was only represented by plants in the pre-sapling stage (suffrutices). The most southern site of occurrence for *J. paniculata* was at latitude 17°S in Zambia and 14.4°S in Malawi while the most eastern site was at 34.2°E in Malawi. Excluding the Tanzanian record cited above, the most northern site for *J. paniculata* was at 8.4°S in Zambia. The most western site for *J. globiflora* was at 24°E in Zambia while the most northern and southern sites were at 4.4°S and 20.5°S in Tanzania and Zimbabwe, respectively, although a website source (zambiaflora.com/speciesdata/species.php?/speciesid=126770) gives a site at 22°S and 35.32°E along the coastal zone of Mozambique (not shown in Figure 1). *Julbernardia globiflora* is the only member of the genus in miombo woodland in Mozambique, Zimbabwe and possibly Tanzania and appears to be absent in Angola where *J. paniculata* is the only member of the genus in miombo woodland. Out of the 447 enumerated OG sample plots in Zambia, *J. globiflora* and *J. paniculata* occurred in 2.46% and 36.2% of the plots, respectively, indicating that *J. paniculata* is more widespread in Zambia than *J. globiflora*.

Factors influencing *Julbernardia* species dominance

Each species was assumed to be dominant at a sample plot if it had an IV > 10% because miombo woodland is a mixed species community with IV of individual *Brachystegia* and *Julbernardia* species rarely exceeding 40% and using this arbitrary cut-off point the modelled spatial variation in the dominance of the two species indicates that only one of these species is dominant in any particular area in Zambia

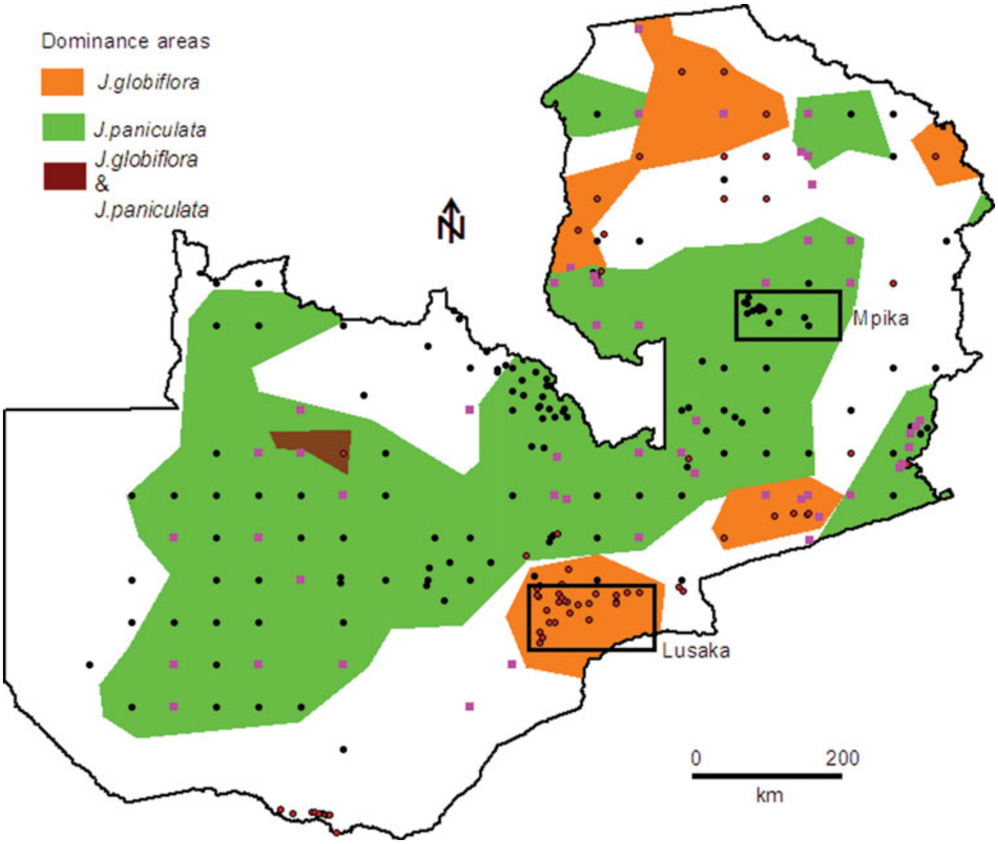

Figure 2. Extent of areas in Zambia in which *Julbernardia globiflora* and *Julbernardia paniculata* are dominant (IV >10%). Boxes represent areas in which IV in old-growth and re-growth miombo were compared for each species in the absence of the other species. Symbols as in Figure 1.

(Figure 2). The exception is a 2500-km^2 area in Kasempa and Mufumbwe districts of north-western Zambia and it is not clear whether this is an artefact of the modelling procedure or is real. The area over which *J. paniculata* is dominant is ~210 000 km^2 compared with 30 000 km^2 over which *J. globiflora* is dominant.

The additive model that included latitude and *J. paniculata* IV explained a significant proportion (30%) of the variation in *J. globiflora* IV in OG woodland while a model that included latitude, mean annual maximum temperature and species richness explained a lower but significant proportion (13%) of the variation in *J. paniculata* IV (Table 3). Latitude had a positive effect on IV for both species. For *J. paniculata* both mean annual maximum temperature and tree species richness had a negative effect on IV while for *J. globiflora* IV decreased with increasing IV of *J. paniculata* indicating the existence of interspecific interaction. Indeed the difference in IV for *J. globiflora* in the presence and absence of *J. paniculata* was significant ($U = 5.72$, $P < 0.0001$) but this was not the case with *J. paniculata* ($U = 0.1$, $P = 0.92$) (Figure 3). The remaining predictor variables in Table 1 had no significant effect on the variation in IV of the two *Julbernardia* species in OG woodland.

Response of *Julbernardia* species to woodland clearing

The response to woodland clearing of *Julbernardia* species was assessed by comparing IV and stem density for each species in OG and RG stands. In both species trees in RG stands had significantly more stems per tree (1.89 ± 0.079 and 1.16 ± 0.016 in *J. globiflora* and *J. paniculata*, respectively) than in OG stands (1.06 ± 0.024 and 1.02 ± 0.007 in *J. globiflora* and *J. paniculata*, respectively) ($U = 7.06$, $P < 0.0001$). However, the range of stems per tree in *J. globiflora* was larger (1–16) than in *J. paniculata* (1–6) in RG stands. Stem density was significantly higher in RG (1753 ± 119 ha^{-1}) than in OG (339 ± 31 ha^{-1}) in *J. paniculata* ($U = 3.8$, $P < 0.0001$). Similarly *J. globiflora* stem density was significantly higher in RG (1712 ± 239 ha^{-1}) than in OG (377 ± 34 ha^{-1}) ($U = 3.1$, $P < 0.0001$).

In general there were no significant differences in dominance between OG and RG miombo for the two species ($U = 0.7$, $P > 0.45$) but comparison between the two woodland stands in two areas in which only one of the two species was dominant (Figure 2) yielded somewhat different results. In the Mpika area of northern Zambia in which *J. paniculata* is predominant, IV was

Table 3. Additive models that explained a significant proportion of variation in Importance Value (IV, arcsine transformed) of *Julbernardia* species in Zambia. AICc is Akaike's Information Criterion for small samples and SE is standard error.

Woodland/Species	Predictor Variable	Coefficient (±1SE)	*F*-value	Significance level (P)	AICc	*R*-squared
Old-growth						
J. globiflora	Intercept	12.5 ± 4.15	3.02	0.003		
	Latitude	0.61 ± 0.29	2.08	0.040		
	J. paniculata IV	− 0.35 ± 0.06	− 5.96	<0.0001		
	Model		22.6	<0.0001	1539.0	0.30
J. paniculata	Intercept	62.0 ± 19.5	3.18	0.002		
	Latitude	0.91 ± 0.41	2.20	0.03		
	Maximum temperature	− 1.61 ± 0.67	− 2.41	0.02		
	Species richness	− 0.31 ± 0.09	− 3.55	0.0005		
	Model		7.50	0.0001	1639.6	0.13
Re-growth						
J. globiflora	Intercept	− 74.3 ± 13.6	− 5.47	<0.0001		
	Potential evapo-transpiration	27.2 ± 4.70	5.77	<0.0001		
	Model		33.35	<0.0001	177.98	0.42
J. paniculata	Intercept	108 ± 19.0	5.68	<0.0001		
	Potential evapo-transpiration	− 31.3 ± 6.59	− 4.75	<0.0001		
	Model		22.57	<0.0001	210.39	0.33

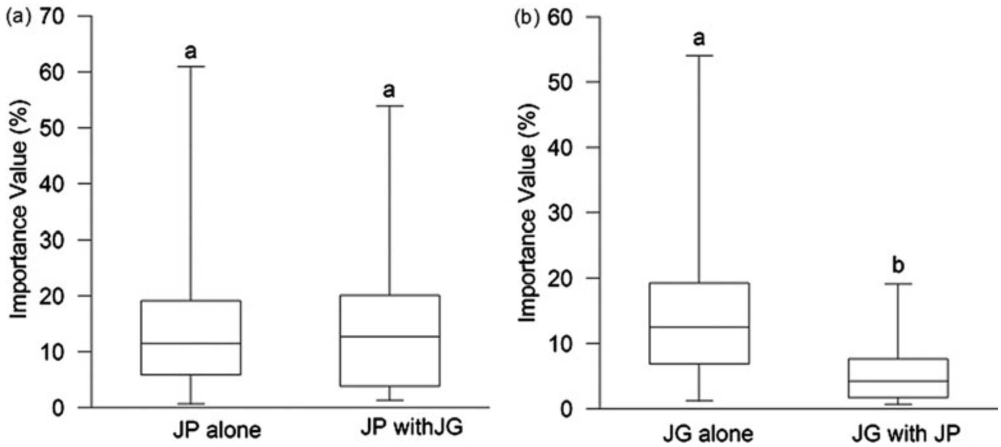

Figure 3. Box and whiskers plots for Importance Value in the presence and absence of one of the *Julbernardia* species: *Julbernardia paniculata* (JP) (a) and *Julbernardia globiflora* (JG) (b). The box hinges represent the first and third quantiles, the centre horizontal lines represent the median and the whiskers indicate the range of values that are within 1.5 of the hinges. Different letters on top of the whiskers indicate significant differences at $P \leq 0.05$.

significantly higher in RG than OG stands ($U = 2.36$, $P = 0.02$) (Figure 4a) largely due to an increase in the relative density from a mean of 11.8% in OG to 37.4% in RG stands. However, for *J. globiflora* the difference in IV in RG and OG stands in the Lusaka area of central Zambia was not significant ($U = 1.03$, $P = 0.31$) (Figure 4b).

In both species, PET explained a significant proportion of the variation in IV in RG stands. The linear model involving PET explained 33% of the variance in IV in *J. paniculata* and 42% in *J. globiflora* but this effect was negative for *J. paniculata* and positive for *J. globiflora* (Table 3). The other variables in Table 1 had no significant effect on IV in the two species in RG stands.

DISCUSSION

Distribution and dominance of *Julbernardia* species in old-growth woodland

Rees (1974) stated that *J. paniculata* replaces *J. globiflora* in the high-rainfall zones of Zambia but this study found no evidence in support of this notion. It is apparent that the replacement of *J. globiflora* by *J. paniculata* in northern miombo woodlands in Zambia is not a product of a single factor. On the basis of this study, these factors include interspecific interactions, climate, species richness and disturbance (woodland clearing). The study provided some evidence that the dominance of *J. globiflora* is negatively affected by the dominance of *J. paniculata*

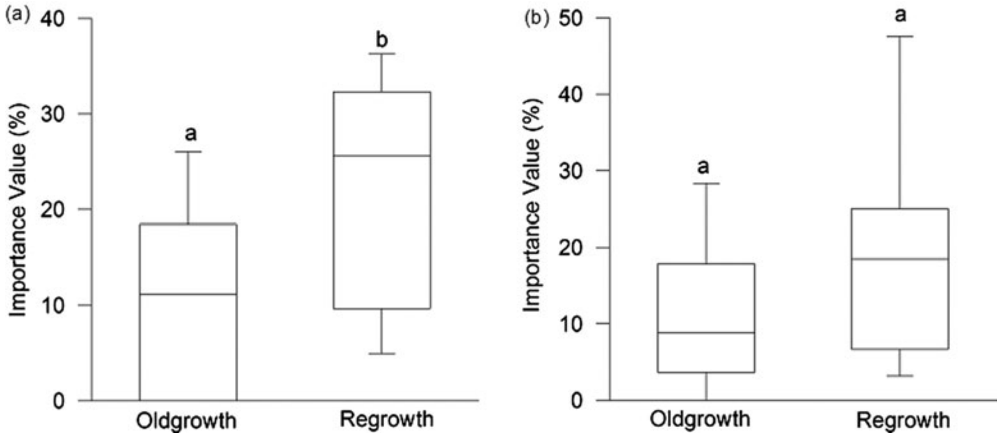

Figure 4. Box and whiskers plots for Importance Values in old-growth and re-growth stands for *Julbernardia paniculata* in Mpika area (a) and for *Julbernardia globiflora* in Lusaka area (b) (see Figure 2 for location of these areas). Different letters on top of the whiskers indicate significant differences at $P \leq 0.05$.

which suggests that the latter is replacing the former as a result of conditions becoming more favourable to it. This replacement of one species by another probably contributes to the spatial separation in the dominance of the two species in Zambia (Figure 2). Three other factors (mean annual maximum temperature, species richness and woodland clearing) appear to affect the dominance of *J. paniculata* more than they affect *J. globiflora*. Both mean annual maximum temperature and tree species richness have a negative effect on *J. paniculata* dominance. It is apparent therefore that high mean annual maximum temperatures may favour the persistence and dominance of *J. globiflora* at the expense of *J. paniculata* and this observation supports the hypothesis that the distribution and abundance of *Julbernardia* species is influenced by environmental factors.

The observation that increasing tree species richness negatively influenced *J. paniculata* is more intriguing but may be related to energy-water regimes as expounded by Baldocchi (2005) and O'Brien (2006). Perhaps this negative effect of tree species richness on *J. paniculata* is more a result of higher functional diversity that is often associated with high levels of biodiversity which puts this species at a disadvantage in landscapes with high species diversity (Baldocchi 2005). Another possible explanation is that *J. paniculata* under low species diversity tends to develop into almost monospecific stands (Trapnell 1996). If indeed miombo woodland has been subjected to successive cycles of clearing in the distant past (Lawton 1978), it is possible that *J. paniculata* in tree species-poor sites increases its dominance with each clearing cycle (Figure 4a) and that what appears to be old-growth woodland now may actually be mature secondary woodland that has developed on previously cleared sites. This would explain the observed high dominance of *J. paniculata* on species-poor, but seemingly old-growth, woodland sites.

Recent work has also shown that *J. paniculata* is more vulnerable to water-stress-induced xylem cavitation (Vinya 2010) which may contribute to this species' lack of competitive advantage in the hotter and drier areas of the miombo woodland distribution range. This may also partially explain the observed current distribution pattern of the *Julbernardia* species in the miombo woodlands. For example, the limit in the north-eastern distribution range of *J. paniculata* is marked by the rift valley lakes of Tanganyika and Malawi and its downstream Shire valley while the Zambezi valley marks the south-eastern boundary of this species distribution range (Figure 1). Climatic changes that were driven by high temperatures, strong trade winds and higher evaporative stress in south-western Tanzania and northern Malawi and the adjoining areas of Zambia that were experienced about 12 300 to 11 800 y ago during the Younger Dryas had a great impact on vegetation dynamics in this region (Ivory *et al.* 2012). It is probable that during this period the distribution range of *J. paniculata* receded westwards into DRC, Malawi and Zambia. The *J. paniculata* suffrutices observed by Boaler & Sciwale (1966) almost 50 y ago may have represented a relict and disappearing population of the species in western Tanzania. Thus the energy-water regimes in these boundary areas probably act as barriers to the distribution of *J. paniculata* but not *J. globiflora*. Werger & Coetzee (1978) noted that *J. globiflora* is dominant on drier and warmer escarpments along the Sabi, Shire and Zambezi valleys and the dominance of this species along the Luangwa escarpment in Zambia was also reported by Smith (1998). The *J. paniculata* boundary in western Zambia and southern Angola may be linked to past climate changes in the Barotse floodplain and the northern Kalahari basin. The Angolan-Zambia Barotse plains experienced dry climates from 35 000–30 000 y ago and moderate wetness from 28 000–18 000 y ago and wetter conditions from 18 000–14 000 y ago before the subhumid conditions appeared 13 000 y ago (Thomas & Shaw 2002). During the drier phases the region experienced the development of aeolian dunes and the return of mesic conditions may have allowed *J. paniculata* to expand its range southwards in Angola and perhaps westwards in Zambia.

Potential evapo-transpiration is a measure of energy that relates the incoming solar energy to potential loss of water into the atmosphere via evaporation and plant transpiration that can affect the energy-water relations at landscape level (Daru *et al*. 2016, Fisher *et al*. 2011). The highest projected increase in median annual temperature will occur in south-east Angola within the *J. paniculata* distribution range that also has the lowest current annual rainfall of <1000 mm (McSweeney *et al*. unpubl. data). This will probably result in higher PET values which are not favourable for *J. paniculata* regeneration. A combination of woodland clearing and higher PET therefore poses a more serious threat to the southern distribution range of this species in Angola. Towards the tropical forest in the north of the current miombo woodland range in Angola and DRC *J. paniculata* is replaced by the congeneric species *J. seretii* and *J. brieyi* (Grundy 1995). It is uncertain whether the projected southern range retreat of *J. paniculata* can be compensated for by an expansion of its northern range into the range of forest *Julbernardia* species which are now outside the miombo woodland range. However, these potential range changes are unlikely to affect *J. globiflora* which currently appears to tolerate higher PET levels in low-rainfall zones. The projected climate warming in the miombo woodland distribution range may therefore favour the persistence of *J. globiflora* but not of *J. paniculata*.

Response of *Julbernardia* species to woodland clearing

Woodland clearing is likely to increase surface air temperature due to reduced transfer of heat from the surface to the atmosphere (Hoffmann & Jackson 2000). Malaisse & Kapinga (1986) noted that woodland clearing increased soil evaporation and mean annual temperature which result in xeric soil conditions. This study revealed that miombo woodland clearing altered the responses of the *Julbernardia* species in RG woodland. The most striking change was that the dominance of both species was significantly influenced by PET. This influence was negative for *J. paniculata* and positive for *J. globiflora*. Mean annual temperature and PET have been found to determine the spatial turnover of phytoregions in southern Africa (Daru *et al*. 2016). It has also been observed that sap flow varies with tree species although other variables such as age and height, can affect tree water use (Baldocchi 2005). Most of the energy that drives PET comes from radiational heating of the land surface which in turn depends on the surface albedo (Shukla & Mintz 1982). Woodland clearing changes the land surface structure or roughness that in turn changes the energy-water relations in cleared areas. As noted above, *J. paniculata* is more vulnerable to water stress-induced xylem cavitation (Vinya 2010) and this situation is probably aggravated in RG trees regenerating in post-clearing landscapes. At the limits of its eastern distribution in Malawi the growth rate of *J. paniculata* coppice has been shown to be slow and weak (Abbot & Lowore 1999) although the species is reported to be predominant on post-cultivation sites in central Angola (Werger & Coetzee 1978) and in northern Zambia (Chidumayo & Mbata 2002) which are in its core distribution range. Thus the increase in dominance of *J. paniculata* in RG stands appears to arise more as a result of increased stem frequency due to coppicing and sapling recruitment than higher production rates. The positive influence of PET on dominance of *J. globiflora* is probably due to the fact that this species is more tolerant of changed energy-water regimes in post-clearing landscapes that favour the maintenance of its dominance in RG stands relative to OG stands. If indeed miombo woodland is a product of human-induced disturbances over many thousands of years (Lawton 1978), such disturbances in areas with high PET may have favoured the maintenance of *J. globiflora* dominance in areas with high temperatures and low rainfall. Such a situation may be the reason why the distribution of *J. globiflora* is more extensive in the semi-arid north-east and south of the miombo woodland range where *J. paniculata* is absent. The predominance of *J. globiflora* on post-cultivation areas has also been reported in Tanzania (Mpingo Conservation & Development Initiative unpubl. data) and Zimbabwe (Chinuwo *et al*. 2010) and young seedlings are reported to survive better in open unshaded environments (Grundy 1995). Climate warming, woodland clearing and land use change are therefore likely to interact and favour the persistence and in some cases the predominance of *J. globiflora* in the drier areas of miombo woodland distribution range.

Conclusion

The dominance of *Julbernardia* tree species is affected by different factors in old-growth and re-growth miombo. Clearing of old-growth woodland alters the response of *Julbernardia* species to environmental factors. There are large spatial gaps in the distribution data of *Julbernardia* species in the miombo ecoregion (see Figure 1), especially in Angola, DRC and Mozambique and data on the structure of regrowth miombo is very limited. More inventories are needed to fill these gaps and improve the knowledge base on *Julbernardia* species in miombo woodlands.

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