Factors influencing the adaptation and distribution of *Colophospermum mopane* in southern Africa's mopane savannas – A review

Authors:
Rudzani A. Makhado[1]
Isaac Mapaure[2]
Martin J. Potgieter[1]
Wilmien J. Luus-Powell[1]
Amani T. Saidi[3]

Affiliations:
[1]Department of Biodiversity, University of Limpopo, South Africa

[2]Research and Publications Office, University of Namibia, Namibia

[3]South African Environmental Observation Network, National Research Foundation, South Africa

Correspondence to:
Rudzani Makhado

Email:
makhado2002@yahoo.com

Postal address:
Private Bag X1106, Sovenga, South Africa

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Note:
This article was republished with the correct R^2 values reflecting in Figure 3.

Colophospermum mopane is the dominant tree or shrub within mopane woodland in the subtropical areas of southern Africa's savanna ecosystems. This article provided a review on the adaptation capabilities of mopane against fire, browsing activity and environmental stresses. It further reviewed and tested the extent to which rainfall, temperature, altitude and soil types had an effect on the distribution of mopane in southern Africa. Mopane is adapted to survive moisture stresses, low nutrient environments and even disturbances caused by fire and browsing by large herbivores through its physical, physiological and chemical responses. Adaptation of mopane to various stresses enables it to dominate the low-lying areas of southern Africa's savannas. The distribution of mopane is best associated with low to moderate rainfall (R^2 = 0.38), high temperature (R^2 = 0.42), low altitudes (R^2 = 0.44) and a variety of soil types. An increase in the annual rainfall (> 800 mm) and altitude (> 800 m.a.s.l.), coupled with a reduction in the minimum temperature and acidic soil, limits the distribution of mopane. Mopane in South Africa occurs under similar environmental conditions to those in Zimbabwe and Zambia, but quite different from those in Angola, Namibia, Mozambique, Malawi and Botswana where mopane occurs.

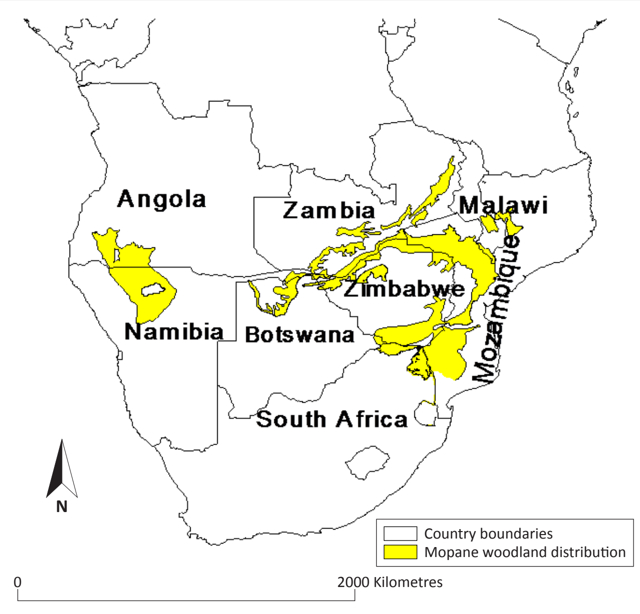
Introduction

Colophospermum mopane (Kirk ex Benth.) Kirk ex J.Léonard, commonly known as mopane, is the dominant tree or shrub within mopane woodland in the subtropical areas of southern Africa's savanna ecosystems, between latitudes 9° S and 25° S (Henning 1976; Mapaure 1994; Sebego 1999; Werger & Coetzee 1978; White 1983). Estimates show that mopane woodland accounts for about 30% – 35% of the 1.5 million km^2 of savannas in southern Africa (Mapaure 1994; White 1983), which represents more than a quarter of land area in the region. Mopane is distributed in the hot, dry, valley bottoms and adjacent plains of southern Angola and northern Namibia, across Botswana and Zimbabwe to central and southern Mozambique, and from the Luangwa valley in Zambia and central Malawi to northern South Africa (Mapaure 1994; Porter 1968; Siebert 2012; Timberlake, Chidumayo & Sawadogo 2010; Werger & Coetzee 1978; White 1983) (Figure 1). The total area covered by mopane woodland in the whole of southern Africa is 555 000 km^2 (Mapaure 1994) (Table 1).

Previous studies have demonstrated that rainfall, altitude and soil types influence the distribution of mopane in southern Africa (e.g. Burke 2006; Cole 1986; Mapaure 1994; Voorthuizen 1976; Werger & Coetzee 1978). Mopane occurs in areas receiving low to moderate annual rainfall ranging from 400 mm to 800 mm (Madams 1990; Thompson 1960; Werger & Coetzee 1978). These are normally areas at altitudes ranging from 200 m.a.s.l. to 600 m.a.s.l. (White 1983), with variable soils, but usually fine-grained, having textures ranging from sandy through loamy to clayey. The species is also known to occupy both shallow and deep soils, containing significant amounts of exchangeable sodium (Madams 1990; Thompson 1960; Werger & Coetzee 1978).

Other factors influencing the distribution of mopane include minimum temperature and dry season day length (Stevens *et al*. 2014). Mopane is commonly distributed in high temperature areas (Table 2) and minimum temperature of < 5 °C limits its distribution (Burke 2006; Cole 1986; Henning 1976; Stevens *et al.* 2014; Timberlake, Nobanda & Mapaure 1993; Werger & Coetzee 1978; White 1983; Whitecross, Archibald & Witkowski 2012), especially in its southern range (Stevens *et al*. 2014). However, although mopane is predominantly in frost free areas, the species is capable of withstanding light frost (Thompson 1960) and tall mopane trees of > 4 m in height can survive minimal frost damage (Whitecross *et al.* 2012).

Mopane is considered an important plant species to people, and wild and domestic animals in its distribution in southern Africa. Rural dwellers use it for firewood (Liengme 1983), construction of traditional structures (Makhado *et al*. 2009) and, to a lesser extent, for medicinal purposes (Madzibane & Potgieter 1999; Mashabane, Wessels & Potgieter 2001). In some parts of the region, there has been increasing use of mopane in urban areas for firewood as the cost of electricity keeps increasing. Mopane also hosts mopane worms, larvae of the moth *Imbrasia belina*, which are consumed for their nutritional value (Dreyer & Wehmeyer 1982; Voorthuizen 1976) and traded to generate income (Styles 1996). Dry mopane leaves, twigs and pods provide a valuable source of browse for wild animals such as elephants (Ben-Shahar & MacDonald 2002) and greater kudu (Hooimeijer *et al*. 2005), especially during the dry season and drought periods (Bonsma 1942; Macala, Sebolai & Majinda 1992; Mosimanyana & Kiflewahid 1988; Timberlake 1995), when the tannins have leached out. In addition, the secretion of *Arytaina mopane* nymphs, commonly known as lerp, increases the palatability of mopane leaves (Ross 1977; Van Wyk 1972), because the lerps have high sucrose content (Styles 1993). The lerps are highly sought after by baboons, monkeys, birds (Herremans-Tonnoeyr & Herremans 1995) and even humans, especially in the northern part of South Africa (Pettey 1925) and Botswana (Sekhwela 1989), because of their sweetness; they contain about 53% water-soluble sugars (Sekhwela 1989).



Source: This map is an extract from Mucina and Rutherford's (2006) data on the vegetation of South Africa, Lesotho and Swaziland (VegMap) and White's (1983) data on vegetation of Africa. For more information, please consult the reference list of the article: Makhado, R.A., Mapaure, I., Potgieter, M.J., Luus-Powell, W.J. & Saidi, A.T., 2014, 'Factors influencing the adaptation and distribution of *Colophospermum mopane* in southern Africa's mopane savannas – A review', *Bothalia* 44(1), Art. #152, 9 pages. http://dx.doi.org/10.4102/abc.v44i1.152

FIGURE 1: The distribution of mopane-dominated woodlands in southern Africa.

Considering the extensive distribution of mopane in the low-lying areas of southern Africa and its importance to human livelihoods, domestic and wild animals throughout its distribution range, it becomes a research challenge when factors influencing its distribution are not easily detectable (Siebert 2012) or not even well understood (Stevens *et al.* 2014). Various sources have contributed to the understanding of mopane distribution (e.g. Cole 1986; Du Plessis 2001; Henning 1976; Madams 1990; Mapaure 1994; Thompson 1960; Timberlake 1995; Timberlake *et al.* 1993; Werger & Coetzee 1978; White 1983), but there is still a gap in identifying the underlying factors influencing mopane distribution in southern Africa (Siebert 2012; Stevens *et al.* 2014). This is creating a subsequent gap in our ability to

TABLE 1: Area covered by mopane-dominated woodland in southern Africa.

Country	Area (km²)	Proportion of country area (%)	Proportion of total mopane area (%)
Angola	112 500	9	20
Zimbabwe	101 500	26	18
Mozambique	98 000	13	18
Botswana	85 000	15	15
Namibia	77 000	9	14
Zambia	43 500	6	8
South Africa	23 000	2	4
Malawi	10 000	9	2
Total	**550 500**	**89**	**100**

Source: These data are taken from Mapaure, I., 1994, 'The distribution of *Colophospermum mopane* (Leguminosae-Caesalpinioideae) in Africa', *Kirkia* 15, 1–5

TABLE 2: Environmental factors associated with the distribution of mopane in southern Africa.

Country	Mean annual rainfall (mm)	Mean daily temperature (°C)	Altitudinal range (m.a.s.l.)	Soil types	References
Angola	100–600	16–25	100–1200	g, s, a	1, 2, 7, 9
Zimbabwe	450–700	16–30	300–950	c, so, l, g, ss, fe	1, 6, 7, 9
Mozambique	400–700	20–29	100–500	c, ls, s, bs, a	1, 2, 6, 9
Botswana	400–600	13–30	800–900	s, si, cl, c, b, h	1, 2, 6, 9
Namibia	50–600	12–31	150–1000	l, f	2, 6, 7, 8, 9, 11
Zambia	600–1000	14–30	400–1000	a, fv, sl, g, l, ss, fe, h	1, 2, 5, 6, 7, 9
South Africa	250–650	15–31	200–800	a, g, b, c, s, l	1, 3, 4, 6, 9, 10
Malawi	700–800	19–28	450–500	sc, m	1, 2, 9
Minimum	50–550	12–25	100–500	-	-
Maximum	700–1000	20–31	800–1200	-	-
Average	369–700	16–29	313–856	-	-

Sources: 1, Mapaure (1994); 2, Werger and Coetzee (1978); 3, Acocks (1953); 4, Mucina and Rutherford (2006); 5, Porter (1968); 6, Henning (1976); 7, Madams (1990); 8, Erkkilä and Siiskonen (1992); 9, Du Plessis (2001); 10, Rutherford *et al.* (2006); 11, Okitsu (2005).
For more information, please consult the reference list of the article: Makhado, R.A., Mapaure, I., Potgieter, M.J., Luus-Powell, W.J. & Saidi, A.T., 2014, 'Factors influencing the adaptation and distribution of *Colophospermum mopane* in southern Africa's mopane savannas – A review', *Bothalia* 44(1), Art. #152, 9 pages. http://dx.doi.org/10.4102/abc.v44i1.152
Soil types symbols: a, alluvial; b, basaltic; bs, brown soils; c, clayey; cl, clay loamy; f, ferruginous; fe, ferrallitic; fv, fluvisol-vertisol; g, granitic; h, halomorphic; l, lithosols; ls, loamy sand; m, mopanosols; s, sandy; sc, sandy clays; sl, sandy-loamy; si, silt; so, sodic; ss, sandstone.

effectively manage mopane and the wild animals it supports. Current climatic changes provide further complexities for predicting the distribution of mopane. As a result, there is a need to adequately review existing information in an integrated manner. This will allow a better understanding of the factors influencing the distribution of mopane in southern African. This review is also critically important because it gives insight into the potential future distribution scenarios of mopane. An extensive review of a mixture of literature (i.e. journal articles, books, conference proceedings and reports), specifically dealing with adaptation of mopane and factors influencing its distribution in southern Africa was carried out. The aim of this article is therefore to provide a review of the mechanisms that enable mopane to survive disturbances caused by fire, browsing activity by large herbivores and environmental stresses in the savanna ecosystem. The article further tested the effect of environmental factors on the distribution of mopane in the southern Africa's savanna ecosystem.

Adaptation of mopane to fire and browsing activity

Mopane is widely distributed in the southern Africa's savanna (Mapaure 1994), an ecosystem which supports frequent fires (Andreae *et al*. 1994; Kennedy 2000; Scholes 1995) and large herbivores (Sankaran & Anderson 2009). Fire negatively affects the morphology of mopane (Gandiwa & Kativu 2009; Mlambo & Mapaure 2006), destroys the aerial components of mopane shrubs (Henning 1976) and causes a reduction in mopane height and stem circumference (Kennedy & Potgieter 2003).

In addition, mopane is highly browsed by large herbivores such as elephants (Ben-Shahar 1993; Ben-Shahar & MacDonald 2002; Smallie & O'Connor 2000), mainly owing to its high nutritional value (Ben-Shahar & MacDonald 2002; Bonsma 1942; Macala *et al.* 1992; Mosimanyana & Kiflewahid 1988). Elephants' preference for mopane makes it susceptible to elephant-induced damage (Lewis 1991). Elephants' feeding behaviour can transform mopane woodlands to coppiced shrubby stands. Furthermore, elephants also inhibit height recruitment of mopane by repeatedly breaking the branches, ring-barking, heavy browsing and toppling the tree (Lewis 1991; Smallie & O'Connor 2000). As a result, fire and browsing activity has a notable effect on mopane structure, which also has implications on the growth and distribution of mopane in southern Africa's savannas.

Despite the disturbances caused by fires and browsing activity by large herbivores, mopane is capable of surviving through its coppicing ability and production of chemicals for defence. Various authors have shown that mopane coppices rapidly (Luoga, Witkowski & Balkwill 2004; Mlambo & Mapaure 2006; Mushove 1992; Mushove & Makoni 1993; Tietema 1989) after it has been disturbed by fire and browsing animals. In addition, mopane wood contains crystals of calcium oxalate, which contribute to high wood density (Prior & Cutler 1992) and also enhance resistance of the wood to fire (Centro Informatico Cientifico de Andalucia [CICA] 1996). These crystals effect the burning properties of the wood through producing considerable amounts of carbon dioxide, which retards the fire flame (CICA 1996). During the growing season, mopane also produces a high concentration of secondary metabolites, such as tannins and phenols, in order to deter herbivores from browsing it (Kohi *et al*. 2010; Wessels, Van der Waal & De Boer 2007), regardless of its high nutritional value. Therefore, the ability of mopane to coppice after disturbances and produce chemical defence enables it to survive disturbances caused by fire and browsing animals.

Adaptation of mopane to environmental stresses

It is well documented that mopane has the ability to survive low to moderate rainfall (Henning 1976; Timberlake 1995), water stresses (Choinski & Tuohy 1991; Mantlana 2002) and high temperatures (Dye & Walker 1980; Henning 1976), but *how* the species is able to survive such 'harsh' environmental conditions in southern Africa has not been adequately reviewed. It is the physical characteristics (e.g. Henning 1976; Madams 1990) and physiological mechanisms (e.g. Choinski & Tuohy 1991; Dye & Walker 1980; Henning 1976; Johnson *et al.* 1996; Mantlana 2002), which enable mopane to tolerate water stress and high temperature conditions. It is the response of mopane roots and leaves to changes in the surrounding environment that enables it to survive these 'harsh' environmental conditions and dominate most low-lying parts of southern Africa's savanna. The physical and physiological abilities of mopane are therefore discussed in this article in order to better explain the mechanisms that enable the species to survive in hot, dry, low-lying areas of southern Africa.

Root-related adaptations

Mopane is essentially a shallow-rooted species (Henning 1976; Smit & Rethman 1998) and has high root biomass (Smit & Rethman 1998). It is considered a shallow-rooted species because its roots are mainly found at a depth of 20 cm – 120 cm (Mantlana 2002; Smit & Rethman 1998; Thompson 1960), but can also reach 2 m in deep soils (Mantlana 2002; Sebego 1999; Timberlake & Calvert 1993). Mantlana (2002) indicated that the total root density for short and tall mopane was highest in the first 20 cm of the soil profile and then declined with increase in soil depth. The combination of a shallow rooting system and high root biomass places mopane in a competitive advantage in areas where conditions lead to the development of a zone of maximum water retention and nitrogen near the surface (Dye & Walker 1980; Henning 1976; Mlambo, Nyathi & Mapaure 2005; Smit & Rethman 1998). The high, fine root densities of mopane, especially at a depth of 20 cm – 120 cm (Mantlana 2002; Smit & Rethman 1998; Thompson 1960), are important as they facilitate quick water and nutrient acquisition and transport (Madams 1990; Mantlana 2002).

Another advantage is that the B horizon under mopane sodic soils is relatively impermeable (Dye & Walker 1980), which provides more moisture retention to the A and O Horizons where most of mopane roots are found. The relatively impermeable B horizon further restricts moisture from filtrating down to the C horizon. As indicated by Dye and Walker (1980), these characteristics enable shallow-rooted species such as mopane to have a competitive advantage for moisture uptake over deep-rooted species. It is believed that the shallow rooting system of mopane, complemented by its high root biomass, enables it to quickly absorb and store the available moisture and nutrients near the soil surface, enabling it to survive the 'harsh' environmental conditions of southern Africa's savanna.

The roots play a further critical role in the survival of mopane. Mopane coppices easily (Mushove 1992; Mushove & Makoni 1993; Tietema 1989; Tietema, Kgathi & Merkesdal 1988), mainly because its roots have the ability to produce root suckers, which enables the shoots to grow faster than newly established seedlings (Luoga *et al.* 2004). As indicated by Mantlana (2002), the ability of mopane roots to coppice confers a degree of resilience to natural and anthropogenic disturbance, which is critical in ensuring its survival.

Cell sap-related adaptations

Stressed mopane shows a marked increase in relative nitrogen content, which suggests that the resistance of mopane to severe soil moisture stress is partly caused by the build-up of soluble nitrogenous compounds within the cell sap. In addition, the uptake of magnesium also plays a direct role in the maintenance of water use efficiency of mopane by catalysing the metabolic production of organic solutes, thereby increasing the osmotic pressure of the cell sap and thus enhancing the ability of mopane to withstand moisture stresses (Henning 1976).

Leaf-related adaptations

Mopane is physiologically adapted to dry (moisture-stressed) environmental conditions (e.g. Choinski & Tuohy 1991; Dye & Walker 1980; Prior 1991). It is adapted through restricting transpiration, a mechanism that enables the species to maintain high water potential (Henning 1976). This is largely through folding the leaves, stomatal responses and osmotic adjustment, which are considered critical mechanisms in enabling mopane to survive water-stressed and high temperature conditions of southern Africa.

Leaf responses

The mopane leaf has two triangular leaflets shaped like wings of a butterfly. The leaves are leathery and resinous (Henning 1976). The leathery membrane on the leaf acts as a buffer layer to avoid direct heat from the sun and also reduces the rate of water loss through evapotranspiration. Mopane also has a tendency to fold its leaflets together, especially during the heat of the day (Madams 1990; Timberlake 1995). When the leaflets are folded together, especially when the leaf temperature exceeds 30 °C, it reduces direct heat from the sun. This means that the few exposed stomata will close, which also assists in reducing the loss of water through evapotranspiration. When the stomata are closed, the rate of photosynthesis is reduced, confirming the findings by Prior (1991), who indicated that photosynthesis by mopane leaves is lower during the heat of the day than during the night or cool days when the temperature is relatively low. In addition, mopane is a deciduous species and sheds its leaves during the dry season, mainly from August to October. The ability of mopane to lose its leaves enables it to conserve water that could have been lost during evapotranspiration.

Stomatal responses

Stomata are randomly distributed on the adaxial (top) and abaxial (bottom) surface on mopane leaves, occupying mainly the minor veins (Potgieter & Wessels 1998). However, mopane has fewer stomata on the exposed adaxial leaf surface compared with most other species (Prior 1991), which implies that the stomata are mainly distributed on the abaxial surface. The few exposed stomata on the adaxial surface of mopane leaves therefore limit the number of openings on the leaf; hence less moisture is lost through the leaves. It has also been shown that mopane stomatal conductance declines almost linearly at light saturation from March to August, at 585 mmol $m^{-2}s^{-1}$ – 172 mmol $m^{-2}s^{-1}$, respectively (Mantlana 2002). The decline in mopane stomatal conductance occurs when the soil moisture is low, especially during dry seasons and drought conditions. This mechanism enables mopane to conserve water during hot, dry conditions. Mantlana (2002) suggested that the reduction in stomatal conductance observed when soil water deficit increased may be explained by the reduction in predawn leaf water potential. However, this article states that leaf temperature needs to be taken into account because it also has an influence on mopane stomatal conductance. Nevertheless, the ability of mopane to close the stomata during high temperature and water-stress periods enables it to reduce the loss of moisture and nutrients, which is critical in ensuring its future survival under the hot, dry conditions of southern Africa.

Osmotic adjustment

The ability of mopane to grow and tolerate water-stressed conditions is also through its osmotic adjustment (Henning 1976; Timberlake 1995). Osmotic adjustment processes lower cell osmotic potential, thereby enabling intercellular water to flow towards the inside of cells. This process is an important mechanism in maintaining cell turgor pressure under reduced soil water potential and thus enables the plant to tolerate drought or water-limiting conditions (Chen & Jianga 2010; Hsiao *et al.* 1976).

As a result of the osmotic adjustment, mopane has the ability to germinate and establish root growth at lower water potentials than otherwise would be possible. The seeds of mopane can germinate and withstand water stress from -0.2 MPa to -0.51 MPa without wilting (Choinski & Tuohy 1991; Henning 1976; Johnson *et al.* 1996). Although the predawn xylem pressure potential analysis for mopane suggests a high water stress in the dry season (February *et al.* 2007), the species is able to survive water-stress conditions because of its ability to use water efficiently (Mantlana 2002), which is probably the result of its osmotic adjustment. By using a combination of physical and physiological adaptations, mainly involving roots and leaves, mopane is able to tolerate hot, dry conditions mainly found in low-lying areas of southern Africa.

All these adaptation mechanisms enable mopane to use the available limited moisture and nutrients efficiently in order to survive semi-arid to arid conditions of southern Africa. This article has further reviewed and tested the effect of environmental factors on the distribution of mopane in southern Africa. The variables used include rainfall, temperature, altitude, and soil types.

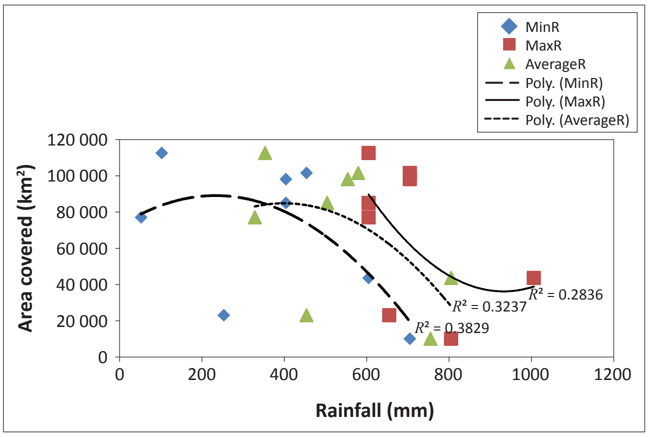
Environmental drivers and factors influencing mopane distribution

Various authors have shown that the distribution of mopane in southern Africa is associated with climatic and edaphic factors (e.g. Madams 1990; Mapaure 1994; O'Connor 1992; Werger & Coetzee 1978). Its distribution is principally influenced by moisture availability expressed through rainfall, temperature, altitude and soil texture (Bennett 1985; Henning 1976; Mapaure 1994; Stevens *et al.* 2014; Timberlake 1995; Werger & Coetzee 1978). It should be noted that rainfall and temperature co-vary with altitude; however, Stevens *et al.* (2014) indicated that there is little evidence of which factors, or combinations thereof, determine the distribution limit of this species. This article therefore reviews and discusses the extent to which rainfall, temperature, altitude and soil types influence the distribution of mopane in southern Africa.

The data used were derived from various sources (Table 1 and Table 2). The areas covered by mopane in southern Africa (Table 1) were plotted against minimum, average and maximum rainfall, temperature and altitude using a polynomial regression analysis (Figures 2–4). The rationale for using polynomial regression was that all functions (linear and non-linear) were showing weak relationships and this was worse when fitting a linear function. However, a polynomial function gave a better fit compared to linear function, which is the reason it was used here.

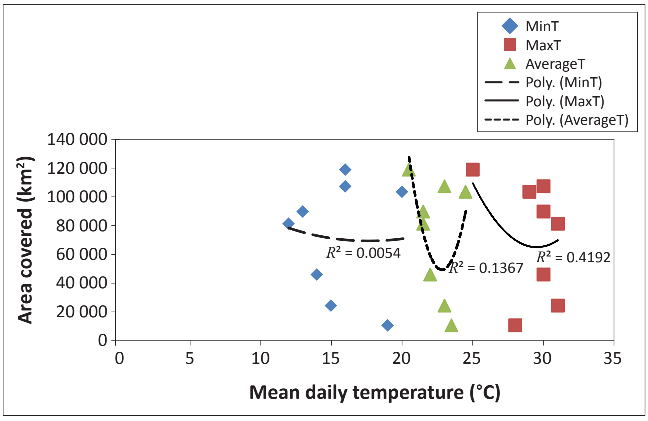
Rainfall

Mopane is distributed along a variable rainfall gradient, ranging from an annual average of 50 mm in Namibia to 1000 mm in Zambia (Table 2). However, areas receiving low to moderate rainfall, especially between 400 mm and 800 mm per annum, better correlate with the distribution of mopane in southern Africa (Madams 1990; Mapaure 1994; Werger & Coetzee 1978). The above finding is closer to the average of 369 mm – 700 mm per annum as estimated in this article (Table 2). It includes all countries within its distribution, with the exclusion of Zambia where rainfall can reach 1000 mm per annum. However, it should be noted that areas receiving 250 mm – 450 mm of rainfall per annum are considered as the most favourable environmental niche for the growth and distribution of mopane (Siebert 2012; Thompson 1960).



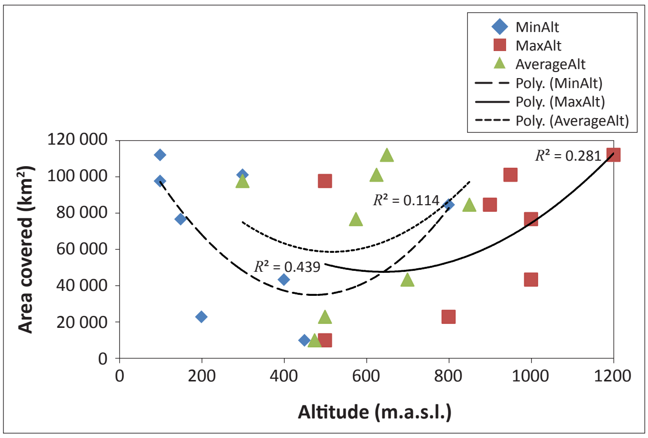
Source: Authors' own creation
Note: The dotted and solid lines represent the fitted polynomial regression curve at 95% confidence interval.
R, rainfall; min; minimum; max, maximum; poly, polynomial regression.

FIGURE 2: Effect of rainfall on the distribution of mopane in southern Africa.



Source: Authors' own creation
Note: The dotted and solid lines represent the fitted polynomial regression curve at 95% confidence interval.
T, temperature; min; minimum; max, maximum; poly, polynomial regression.

FIGURE 3: Effect of temperature on the distribution of mopane in southern Africa.



Source: Authors' own creation
Note: The dotted and solid lines represent the fitted polynomial regression curve at 95% confidence interval.
Alt, altitude; min; minimum; max, maximum; poly, polynomial regression.

FIGURE 4: Effect of altitude on the distribution of mopane in southern Africa.

The review showed that low rainfall positively correlates with the distribution of mopane in southern Africa, but the relationship becomes weak when the annual rainfall exceeds 600 mm per annum (Figure 2). This corroborates well with the findings by Porter (1968) and Henning (1976), who both indicated that an increase in rainfall to > 800 mm per annum becomes the limiting factor to mopane distribution. As also indicated by Thompson (1960), the limitation of mopane from higher rainfall zones is probably the result of competition with other species, which are more suited to those wetter conditions, low temperature, acidic soil conditions and high frequency of disturbances such as fires.

However, our analysis indicated that the relationship between rainfall and mopane distribution was higher at minimum or low annual rainfall ($R^2 = 0.38$), slightly declined at average rainfall ($R^2 = 0.32$) and then significantly declined at maximum or higher rainfall ($R^2 = 0.28$). Although this relationship is positive, it clearly gives a less than 40% confidence (Figure 2), which concurs with Stevens *et al*. (2014) that rainfall alone cannot be considered as the major factor determining the distribution of mopane. It is further indicated that the probability of mopane presence drops to < 50% when precipitation exceeds 380 mm in the wettest quarter (Stevens *et al.* 2014), which confirms that the species favours low rainfall areas (Figure 2). The possibilities of rainfall decline as a result of climate change means that it will further favour the distribution of mopane in areas such as Zambia, which is currently considered a high rainfall area.

Temperature

Mopane is distributed in hot and dry environments, where temperatures can exceed 35 °C (Dye & Walker 1980; Mucina & Rutherford 2006; Porter 1968). Low winter temperature and frost are important limiting factors for mopane distribution, especially along its southernmost boundary (Cole 1986; Henning 1976; Siebert 2012; Stevens *et al.* 2014; Werger & Coetzee 1978; White 1983). The mean daily temperature regime within its distribution in southern Africa ranges from 12 °C to 31°C (Table 2), averaging between 16 °C and 29 °C, as also found by Du Plessis (2001). However, its distribution is limited in areas where the average minimum winter temperature is below 5 °C (Cole 1986; Henning 1976; Rutherford *et al.* 2006; Stevens *et al.* 2014; Voorthuizen 1976; Werger & Coetzee 1978; White 1983), which confirms that the species is adapted to high temperature areas.

The review revealed that the distribution of mopane is best associated with an average daily maximum temperature of 30 °C ($R^2 = 0.42$) (Figure 3), but that relationship declines when the mean daily maximum temperature drops (Figure 3). Although the relationship between mean daily temperature and mopane distribution is positive, it clearly gives a less than 43.0% confidence (Figure 3). Stevens *et al*. (2014) also found that minimum temperature in the coldest month was the strongest determinant for mopane distribution, accounting for 42.2% of the modelled distribution. However, these results do not give a degree of confidence of at least > 50.0% to better explain an important factor associated with the distribution of mopane. This therefore means that temperature alone cannot be considered as the most important factor determining the distribution of mopane in southern Africa. However, it is important to take into account that the probability of mopane presence drops below 50.0% at minimum temperatures less than 5 °C in the coldest month of July. Therefore, minimum temperature is predicted to limit the distribution of mopane from entering the cold interior of the southernmost boundary of southern Africa (Stevens *et al.* 2014). The limitation of mopane at low temperature zones is because of occasional events of frost (Stevens *et al.* 2014; Whitecross *et al.* 2012), which mainly destroys trees and shrubs less than 4 m in height (Whitecross *et al.* 2012). However, an increase in temperature will further facilitate the distribution of mopane in areas currently considered as cold, especially in areas west and slightly south of its current distribution range (Stevens *et al.* 2014).

Altitude

Sebego (1999) indicated that topographic location could be one of the important factors determining the distribution of mopane. Siebert (2012) found that the occurrence of mopane is associated with low-lying, flat and undulating areas. The distribution of mopane is normally along the flood plains and valley bottoms of large rivers such as the Cunene, Chobe, Limpopo, Luangwa, Okavango, Shire and Zambezi (Cole 1986; Mapaure 1994; Werger & Coetzee 1978). However, this article confirms that mopane can be found at variable altitudes ranging from 100 m.a.s.l. to 1200 m.a.s.l. (Table 2), but attaining optimal distribution and growth at altitudes ranging from 313 m.a.s.l. to 856 m.a.s.l. on average (Table 2), which is closer to the 200 m.a.s.l. – 600 m.a.s.l. and 400 m.a.s.l. – 700 m.a.s.l. average as indicated by White (1983) and Mapaure (1994), respectively. Porter (1968) further indicated that mopane rarely occurs at altitudes > 900 m.a.s.l., but this article has shown that it can be occasionally found at > 900 m.a.s.l. in countries such as Angola, Namibia and Zambia (Table 2). These are normally areas where unfavourable soil conditions prevent the growth of other species (Henning 1976), thus favouring the distribution of mopane.

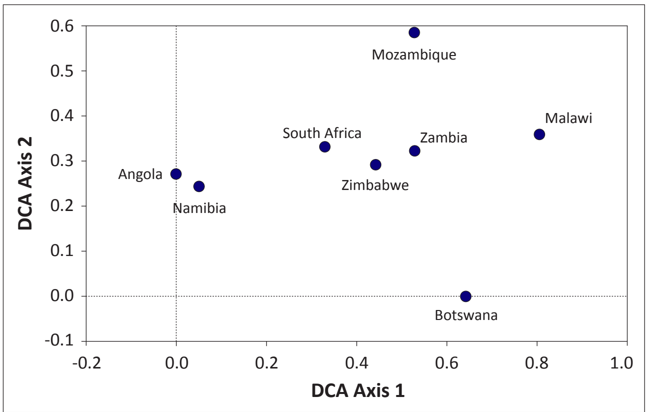
The relationship between altitude and mopane distribution is positive; although, that relationship gives a < 45% confidence (Figure 4). This also means that altitude alone cannot be considered as the important factor determining the distribution of mopane in southern Africa. However, the distribution of mopane correlates well at low altitude ($R^2 = 0.44$), but that relationship declines at higher altitudes ($R^2 = 0.28$) (Figure 4). This finding corroborates the findings from various authors who also indicated that the distribution of mopane is associated with low-lying, flat and undulating areas (e.g. Werger & Coetzee 1978; Cole 1986; Mapaure 1994; Siebert 2012). This implies, as also indicated by Henning (1976), that limited distribution of mopane at higher altitudes might be the result of combined influences of increased precipitation, lower temperatures, acidic soils and disturbances such as fires.

Soil type

According to Madams (1990), soil type also correlates well with the distribution of mopane. Mopane is capable of surviving on a variety of soil types (Henning 1976; Madams 1990). It grows in arid areas on relatively fertile, fine-grained soil, sandy-loamy soil to clayey soil (Henning 1976; Madams 1990; Timberlake 1995; Werger & Coetzee 1978) (Table 2). Mopane is most frequently associated with shallow soils (Henning 1976) and normally found in alluvium and colluvium soils (Timberlake 1995). It is sometimes found in deep soil (Mapaure 1994; Werger & Coetzee 1978), but the calcrete layer near the surface hinders mopane root penetration into the deep soil.

The soils in areas where mopane occurs tend to have high exchangeable sodium content (Dye & Walker 1980; Werger & Coetzee 1978), which inevitably results in reduced permeability and increased susceptibility to soil erosion (Scholes 1997). Mopane mainly survives on alkaline soils (Werger & Coetzee 1978) and is less common on acidic soils (Henning 1976). White (1983) further indicated that mopane does not occur on true saline soils in which water-soluble salts exceed 0.2% – 0.3%. As a result, mopane is thus considered as an indicator species of alkaline soil (Werger & Coetzee 1978).

Soil having low nitrogen (< 0.2% at 0 cm – 10 cm), phosphorus (< 1.5 ppm), low moisture (15.0%) and exchangeable magnesium favours the growth and performance of mopane, but an increase in soil sodium and potassium levels results in a decline in the growth yield, which is probably because of increased soil osmotic suction, whilst increasing magnesium seems to improve soil moisture uptake (Henning 1976). Therefore, mopane exhibits a shrub structure on shallow sodium-rich soils or clay soils derived from basalt (Mapaure 1994; Mlambo 2006). These are areas with limited soil depth and are normally occupied by 'bonsai' shrubby mopane which grow up to 1.5 m in height. The 'cathedral' mopane grow quite tall on deep nutrient-rich alluvial soils (Mapaure 1994; Timberlake 1995): up to 6 m in height on heavy impervious soils and up to 25 m in areas having sandy-loamy and alkaline soils (Werger & Coetzee 1978). It is also important to note that the distribution of mopane is limited in the acrisolic soils, possibly because acrisols derived from acid igneous and metamorphic rocks, limit the growth of mopane, but support the growth of other species such as *Acacia*, *Boscia*, *Grewia*, *Combretum* and *Terminalia* (Madams 1990).



Source: Authors' own creation
DCA, detrended correspondence analysis.

FIGURE 5: Ordination of the drivers of mopane distribution in different countries in southern Africa.

Ordination of mopane distribution

An ordination diagram illustrates the environmental factors included in Table 2 that are suggested to influence the distribution of mopane in different countries in southern Africa (Figure 5). The ordination graph shows that mopane is distributed in variable environmental conditions in different countries, but there are some similarities. For instance, mopane in Namibia occurs under similar environmental conditions to those in Angola, but quite different from those in Mozambique, Malawi and Botswana (Figure 5). In addition, mopane in South Africa occurs under similar environmental conditions to those in Zimbabwe and Zambia, but quite different from those in Angola, Namibia, Mozambique, Malawi and Botswana (Figure 5). However, mopane demonstrates a relatively wide tolerance range for the various environmental factors under which it occurs within its distribution range.

Conclusion

Colophospermum mopane is distributed along variable local climatic, topographical and edaphic factors in the low-lying areas of -southern Africa. It mainly occupies areas receiving low to moderate rainfall, at low lying altitudes, with high temperature and variable soil types. An increase of annual rainfall (> 800 mm), altitude (> 800 m.a.s.l.), acidic soil and a decline in minimum winter temperature (< 5 °C) limits the distribution of mopane. Limited distribution of mopane in areas receiving high rainfall, low temperatures and at higher altitudes is probably a result of the combined effects of freeze events, competitive interactions with other species and disturbances such as fires. An increase in temperature has the potential to drive mopane from its current distribution in high temperature areas to colder zones at its southernmost boundaries, whilst a reduction in annual rainfall could drive mopane from its current distribution in low to moderate rainfall areas to high rainfall zones. However, this article demonstrated that the distribution of mopane in southern Africa is not fundamentally determined by climatic factors, but possibly by edaphic factors (soil type and nutrients), competitive interaction with other species and disturbances such as fires and browsing activity by large herbivores.

It is further concluded that the physical, chemical and physiological responses of mopane enable it to survive various disturbances and 'harsh' environmental conditions in southern Africa's savanna ecosystem. This means that a better understanding of the adaptation mechanisms and distribution of mopane is critical and can be used to explain the distribution and survival of the species in these ‘harsh’ conditions in southern Africa. This understanding can also be used to further identify the ecology of the many mammalian and invertebrate herbivores that are found within the mopane ecosystem. Such information is essential for holistic management of mopane woodland and shrublands in southern Africa.

However, because of the complexity associated with identifying factors which associate best with the distribution of mopane in southern Africa, we recommend that such complexity be addressed through the development of an integrated model. Such a model needs to include climatic factors (e.g. rainfall and temperature), topographical factors (e.g. altitude and slope), edaphic factors (e.g. soil types and soil nutrients) and disturbances (e.g. fires, herbivory and competition). Once developed, such a model can significantly improve the precision of predicting the distribution of not just mopane, but also other vegetation formations and associated wild animals in the savannas.

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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

R.A.M. (University of Limpopo) was responsible for reviewing the literature and writing of the article. I.M. (University of Namibia), M.J.P. (University of Limpopo), W.J.L-P. (University of Limpopo) and A.T.S. (National Research Foundation) were responsible for providing technical input in the article and supervision.

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