Chapter 6

Vachellia (*Acacia*) *karroo* Communities in South Africa: An Overview

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Additional information is available at the end of the chapter

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Abstract

Vachellia karroo is a useful and widespread tree in Africa. It belongs to the family Fabaceae, which is the third largest woody plant family in southern Africa. This is an ecologically and economically important species as almost all of its parts, including bark, pods, seeds, leaves and thorns, are extremely useful to both humans and animals. Various commercial products are also obtained from the tree, and gum is one of the most important products. *V. karroo* in South Africa has an extensive distribution range that includes several biomes. It is very adaptable and has wide habitat tolerance, growing under many differing conditions of soil, climate, and altitude. Although it is often associated with heavy, clayey soils on the banks of rivers and streams, it also grows in bushveld, dry thornveld, grassland and woodland. *V. karroo* is easy to grow and as a result can become an aggressive invader of valuable farming land and grazing areas, a phenomenon usually referred to as bush encroachment. An analysis of historic data comprising 1553 relevés and 2006 species, compiled from all areas of South Africa where *V. karroo* is known to occur was conducted, and TWINSPAN classification produced five main vegetation types.

Keywords: *Acacia*, biome, bush encroachment, ecological significance, economic value, geographical range, soil enrichment, sweet thorn, *Vachellia*

1. Introduction

Vachellia karroo is a highly useful tree that is widespread throughout Africa [1], and it is the most widely distributed tree in South Africa [2]. It belongs to the family Fabaceae (Legume family), which is one of the largest woody plant families in southern Africa. Species of the *Vachellia* genus vary in their distribution range; there are species that are very widely distributed and occupy a diverse range of habitats, while others have a very restricted distribution [3]. The species are a prominent feature in the Savanna biome (bushveld) in South Africa but can also form local dominant stands in other biomes such as the Grassland and Nama-Karoo biomes. Those with a broad distribution range, like *V. karroo*, occur in several biomes [1].

The *Vachellia* species are pod-bearing woody plants that range from shrubs to large trees. They can be sprawling or climbing, and this character differs with habitat [4]. This genus in Africa is readily recognised by its thorns, which are typically paired and straight. These thorns are modified stipules, which become hard and spiny [1, 5] and are important for identification of the trees [6]. *Vachellia* trees can further be distinguished by their characteristic growth form, by bark, and also by pods. This is however a taxonomically difficult genus containing a number of closely related species whose recognition and identification are not always simple [3, 5].

1.1. *Vachellia* split from the *Acacia* genus

Until 2005, *V. karroo* was known as *Acacia karroo*, but according to recent taxonomic research and molecular evidence, the *Acacia* genus was shown to be polyphyletic [7]. It could not be maintained as a single entity, and a proposal was put forward for it to be divided into five genera [8–10]. According to the new proposed classification, ratified at the International Botanical Congress in Vienna in July 2005, *Acacia* genus was split into five monophyletic genera, with all the African *Acacia* now falling under *Vachellia* and *Senegalia* as follows:

(i) *Acacia*, preserved for more than 960 largely Australian species, which all belonged to the former sub-genus *Phyllodineae*.

(ii) *Vachellia*, former sub-genus *Acacia*, approximately 161 pantropical species (Africa, Asia and Latin America).

(iii) *Senegalia*, former sub-genus *Aculeiferum*, with 203 pantropical species (Africa, Asia and Latin America).

(iv) *Acaciella*, former sub-genus *Aculeiferum* section *Filicinae*, contains 15 species from the Americas.

(v) A yet unnamed genus with 13 species from the Americas.

There were objections toward preserving the name *Acacia* for the Australian and other related species [11], but the decision taken in Vienna in 2005 was finalised at the next International Botanical Congress held in Melbourne in 2011. Before the split, there was a total of 40 *Acacia* species, subspecies and varieties represented in South Africa [1]. The split has now resulted in 23 species, subspecies and varieties of *Vachellia* and 17 of *Senegalia* (**Table 1**). The key diagnostic character distinguishing *Vachellia* from *Senegalia* is the presence of stipular spines in *Vachellia*, while *Senegalia* may have prickles but always lack stipular spines [12].

Vachellia		*Senegalia*	
Old name	**New name**	**Old name**	**New name**
Acacia borleae	*Vachellia borleae*	*Acacia ataxacantha*	*Senegalia ataxacantha*
Acacia davyi	*Vachellia davyi*	*Acacia brevispica* subsp. *dregeana*	*Senegalia brevispica* subsp. *dregeana*
Acacia erioloba	*Vachellia erioloba*	*Acacia burkei*	*Senegalia burkei*
Acacia exuvialis	*Vachellia exuvialis*	*Acacia caffra*	*Senegalia caffra*
Acacia gerrardii var. *gerrardii*	*Vachellia gerrardii* var. *gerrardii*	*Acacia erubescens*	*Senegalia erubescens*
Acacia grandicornuta	*Vachellia grandicornuta*	*Acacia fleckii = A. cinerea*	*Senegalia cinerea*
Acacia haematoxylon	*Vachellia haematoxylon*	*Acacia galpinii*	*Senegalia galpinii*
Acacia hebeclada subsp. *hebeclada*	*Vachellia hebeclada* subsp. *hebeclada*	*Acacia goetzei* subsp. *microphylla*	*Senegalia goetzei* subsp. *microphylla*
Acacia karroo	*Vachellia karroo*	*Acacia hereroensis*	*Senegalia hereroensis*
Acacia luederitzii var. *luederitzii*	*Vachellia luederitzii* var. *luederitzii*	*Acacia kraussiana*	*Senegalia kraussiana*
Acacia luederitzii var. *retinens*	*Vachellia luederitzii* var. *retinens*	*Acacia mellifera* subsp. *detinens*	*Senegalia mellifera* subsp. *detinens*
Acacia nebrownii	*Vachellia nebrownii*	*Acacia nigrescens*	*Senegalia nigrescens*
Acacia nilotica subsp. *kraussiana*	*Vachellia nilotica* subsp. *kraussiana*	*Acacia polyacantha* subsp. *campylacantha*	*Senegalia polyacantha* subsp. *campylacantha*
Acacia permixta	*Vachellia permixta*	*Acacia schweinfurthii* var. *schweinfurthii*	*Senegalia schweinfurthii* var. *schweinfurthii*
Acacia rehmanniana	*Vachellia rehmanniana*	*Acacia senegal* var. *leiorhachis*	*Senegalia senegal* var. *leiorhachis*
Acacia robusta subsp. *clavigera*	*Vachellia robusta* subsp. *clavigera*	*Acacia senegal var. rostrata*	*Senegalia senegal* var. *rostrata*
Acacia robusta subsp. *robusta*	*Vachellia robusta* subsp. *robusta*	*Acacia welwitschii* subsp. *delagoensis*	*Senegalia welwitschii* subsp. *delagoensis*
Acacia sieberiana var. woodii	*Vachellia sieberiana* var. *woodii*		
Acacia stuhlmannii	*Vachellia stuhlmannii*		
Acacia swazica	*Vachellia swazica*		
Acacia tenuispina	*Vachellia tenuispina*		
Acacia tortilis subsp. *heteracantha*	*Vachellia tortilis* subsp. *heteracantha*		
Acacia xanthophloea	*Vachellia xanthophloea*		

Table 1. South African *Vachellias (Acacias*) and their new name combinations [1, 12, 13].

1.2. Morphological variation of *V. karroo*

The species displays considerable variation in its appearance, size and other characters [3, 14]. This variation in *V. karroo* is seemingly regional with plants from different geographical areas appearing distinctly different with regard to one or more features [1, 13, 15]. The "typical" form of *V. karroo* grows in the Karoo, Free State, KwaZulu-Natal, and some northern parts of the country [1]. It is a small to medium-sized tree commonly growing to 5–12 m in height but may become a very large tree of up to 22 m on river banks or in other favourable conditions [1, 2]. The tree is usually single-stemmed though sometimes multi-stemmed, branching high above the ground to give a rounded crown (**Figure 1**).

The typical *V. karroo* has a rough, longitudinally fissured bark which is dark on the trunk (**Figure 2A**) and main branches but rusty red in younger branches (**Figure 2B**). The foliage is generally dense and comprises dark green compound leaves (**Figure 2C**). Inflorescences are balls of small sweetly scented yellow flowers (**Figure 2D**), while the pods are flat, mostly sickle shaped with minor constrictions between seeds and dehiscent (**Figure 2E**). The thorns are long, paired, straight, and shining white (**Figure 2F**) and indicate an adaptation of *V. karroo* to its environment because of their protective function [2]. They are larger and abundant on the lower branches that are within reach of animals (and also on young trees) (**Figure 3**) but fewer on the higher parts of larger (and old) trees [2, 4].

Figure 1. A *Vachellia karroo* tree near Bloemfontein, South Africa (photo: M. Dingaan).

Figure 2. *Vachellia karroo* trunk (A), branches (B), leaves (C), flowers (D), pods (E) and thorns (F) (photos: M. Dingaan).

Due to the extreme variation in *V. karroo* form, many of the variations have been described as different species in the past, resulting in numerous synonyms. The differences in form have thus been considered by some botanists to be distinct enough to warrant division of the species into sub-species or at least varieties or even to again regard some forms as different species altogether. Ross [13] concluded that it would be preferable to regard *V. karroo*

Figure 3. A young *Vachellia karroo* tree, splendidly armoured with long white thorns (photo: M. Dingaan).

Morphological variation [1, 13]	**Current taxonomic status [5, 16]**
1. White-barked trees or shrubs with short spines, found in Eastern Cape, KwaZulu-Natal, Mpumalanga and neighbouring countries (Swaziland, Zimbabwe and Mozambique)	*V. natalitia*
2. Small slender shrubs found near the Kei River mouth, Eastern Cape	*V. dyeri*
3. Fire resistant shrubs in the Nongoma District, KwaZulu-Natal	Formerly *A. inconflagrabilis*, still a synonym
4. Slender sparsely branched trees in the Hluhluwe and Umfolozi Game Reserves, KwaZulu-Natal	*V. theronii* (or *V. montana*)
5. Large trees with greyish-white bark along the Tugela River mouth (KwaZulu-Natal), and northwards into Mozambique	*V. kosiensis*
6. Sparse indumentum on young shoots, leaves peduncles and pods on the Highveld from Pretoria eastwards (for example Sekhukhuneland, Limpopo)	*V. robbertsei*
7. Small shrubby form on the Springbok flats north of Pretoria	Still *V. karroo*, closely resembles *V. tenuispina*

Table 2. The *Vachellia karroo* complex.

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as a variable polymorphic species rather than to divide the species into a number of infra-specific taxa. Regardless, the *V. karroo* complex has recently been split, with some authors recognising the following as distinct species (**Table 2**): *V. natalitia*, *V. dyeri*, *V. kosiensis* [5, 16] and *V. theronii* (previously published incorrectly as *V. montana,* i.e., an invalid name) [17]. Coates Palgrave [5] further recognises *V. robbertsei* as a species that could have evolved from *V. karroo* and *V. gerrardii* genes. The locations where these different forms (previously) recognised within the *V. karroo* complex occur are shown in **Figure 4**.

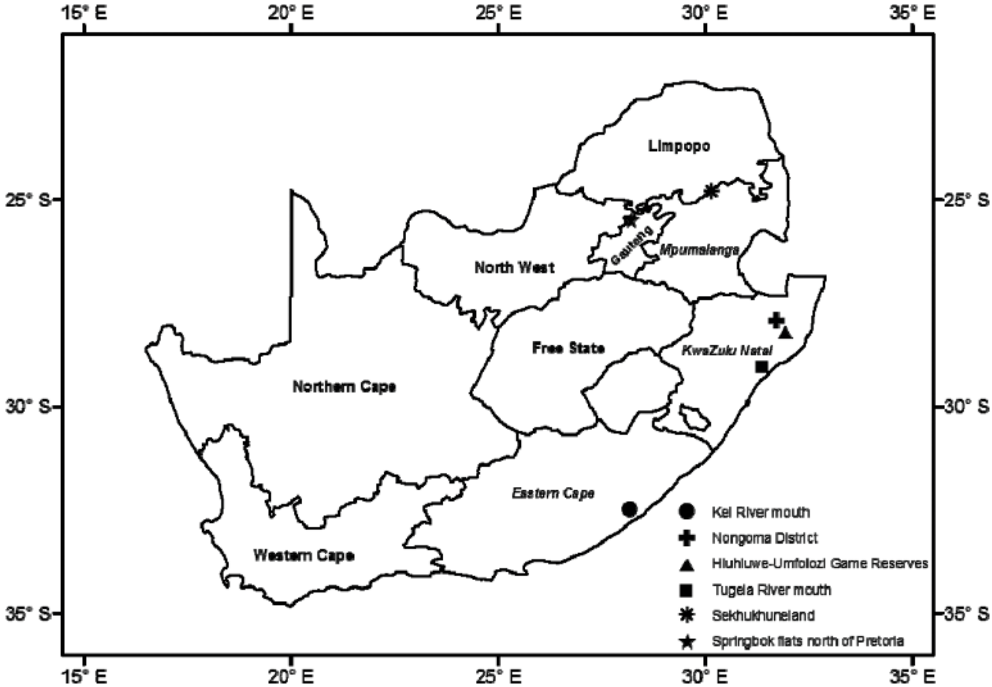

Figure 4. Map indicating occurrences of the various morphological variations (described in **Table 2**) within the *Vachellia karroo* complex. Note: The three provinces labelled in italics indicate occurrence of variation 1.

2. Ecological significance

This is an ecologically and socio-economically important species described by many as a multi-purpose tree and an asset to any farm [18].

2.1. Value as fodder and food supplement

Vachellia karroo attracts many insects and therefore birds, and its flowers also form an important food supplement for animals [1]. The flowers have significant amounts of pollen and are rich in protein and are thus eaten by birds such as Grey Go-Away birds (also known as Grey Louries) and monkeys [5]. In addition, the larvae of several butterfly species feed on the pods and flowers [5, 16]. Its flowers also provide nectar for bees and are important for the production of honey [1]. *V. karroo* trees are important for bee farming as they indirectly result in the production of a pleasantly flavoured honey [6].

Furthermore, parts of *V. karroo* are used as food for humans, as an example, seeds are roasted and used as coffee substitute [19]. *Vachellia* species can produce large amounts of seeds which are known to have been eaten by pastoral people when the need arose, and indirect food sources include the edible cerambycidae wood borer larvae found in the dead wood of *V. robusta* [1].

Despite its thorniness, *V. karroo* is a good fodder tree and forms an important part of the diet of a wide range of herbivore species [2]. It is palatable [20] and consumed by both domestic and wild species [21]. Its foliage is highly favoured by stock and game, so are its seeds and dehiscent pods, which are rich in protein [18]. The pods and seeds also play an important role as feed supplements during the dry season [22] as they are at times collected by farmers to feed their livestock [1]. *V. karroo* has been shown to be an important part of the giraffe diet [23], and it has also been observed that goats select *V. karroo* in preference to grass, but less so, when the amount of available browse available is limited [21]. The foliage, pods, and flowers of *V. karroo* are free of hydrocyanic poisoning, a self-protection mechanism used by many trees [6], relating to the toxic substance known as hydrocyanic acid, prussic acid, or cyanide. Some *Vachellia* species pose the danger of such poisoning to animals. These include *V. erioloba*, whose pods and young leaves contain prussic acid, as well as the wilted leaves of *V. sieberiana* [1].

2.2. Bush encroachment

Vachellias are, on the whole, easy to grow and often become an aggressive invader of valuable farming land and grazing areas, a phenomenon that is usually referred to as bush encroachment (**Figure 5**). Bush encroachment has become a serious ecological and farming problem that has affected many grazing areas in grassland and savanna areas of southern Africa. It is

Figure 5. *Vachellia karroo* encroachment of a grassland community, Free State Province, South Africa (photo: M. Dingaan).

a transition from grassy to increasingly shrubby ecosystems [24], whereby trees and shrubs invade into open grassland or thicken up in already wooded areas [25]. *V. karroo*, in particular, has become a serious invader into the grasslands of the Eastern Cape, the Free State area, and the North-West Province [26, 27].

The most detrimental effect of *V. karroo* encroachment (and other woody species) to farming is that it depresses the production of grasses, mainly due to tree-grass competition for soil moisture [28]. Bush encroachment thus drastically reduces the carrying capacity of grazing areas because browse is generally a poor substitute for grass, especially in sheep/cattle areas [29]. For example, in some parts of the Molopo area, grass production was thought to have already decreased by over 80% due to bush encroachment, and this has subsequently affected the economic viability of many farms [30].

2.2.1. Factors promoting bush encroachment

Vachellia species regenerate vegetatively and from seed, but regeneration from seed is most dominant [31]. The encroaching species of *Vachellia* are spread by seed, which in many of these species has impermeable seed coat resulting in a high percentage of dormancy [32]. According to O'Connor [33], the encroachment of woody species requires successful seed dispersal, germination, and seedling establishment. The two most vulnerable phases in the regeneration of *Vachellia* are during seed germination and seedling establishment; these phases are characterised by high mortality rates that influence the populations of *Vachellias* [31]. Seedling establishment can be influenced by competition from established surrounding vegetation, as well as moisture availability and irradiance [33]. Du Toit [26] has shown that *V. karroo* seedlings require high irradiance levels for optimal growth, although they may still survive under certain levels of low irradiance.

According to Trollope [25], the plausible reasons why bush encroachment was not a serious problem before the advent of commercial livestock production could have included the control of bush by fire, mechanical damage brought about by wild browsers and climatic factors. On the other hand, the factors promoting encroachment in the modern era are complex, with the most predominant being the introduction of domestic livestock and subsequent overgrazing and the elimination of veld burning [24, 33, 34]. The successful and prolific nature in which *V. karroo* has been able to encroach onto grasslands is largely due to the fact that the species is an adaptable pioneer with an ability to establish itself without shade, shelter or protection from grass fires. It is fast growing, tolerant of defoliation by herbivory and is resistant to fire and frost [18]. Its seeds do not only have a great tolerance to high temperatures produced during burning but may actually be stimulated to germinate by fire [35].

2.2.2. Combating bush encroachment

Clearing of woody species has been found to greatly increase grass and subsequently animal production [28, 30]. Mechanical, chemical and biological methods are employed in trying to control the spread of bush. Chemicals such as Tordon 225 and tebuthiuron have been successfully used, but the use of Tordon 225 is restricted by certain physiological and environmental conditions [30]. Concerns about tebuthiuron on the other hand pertain to the accumulation and persistence of the chemical in the soil thus posing potential threats to non-target species [36, 37]. Biological methods sometimes employed include the controlled use of herbivores (especially goats) and fire. Du Toit [29] observed in a study in the Eastern Cape that in comparison to continuous/rotational sheep grazing of a *V. karroo* stand, there was a higher mortality of trees and more efficient control of seedling regrowth under continuous goat grazing than rotational grazing. Goat grazing resulted in a marked improvement in the cover, composition and vigour of the grass sward [29].

Fire has also been extensively used in combating bush encroachment in savanna because it is known to maintain a balance of grass to trees and shrubs in the savanna areas [25]. Trollope [25] has observed that fire generally has different roles in controlling bush encroachment in the moist and arid savannas. In the moist savanna regions (>600 mm p.a.), bush encroachment may be controlled with fire alone because there is adequate grass material under grazing conditions to support frequent enough fires to burn down and control the bush. This is unlikely in the arid savanna regions (<600 mm p.a), which constitute the major portion of the South African savannas, because the rainfall is too low and erratic to support frequent enough fires under grazing conditions to prevent the regeneration of bush [25]. In grassland, Du Toit [34] made observations that the application of fire to combat *V. karroo* intrusion in the Eastern Cape sweetveld was not a practical approach. While fire was found to retard *V. karroo* seedling development, it could however not prevent the seedling establishment.

All in all, eradication of *V. karroo* is difficult once the thorn has invaded an area where it was previously absent, since a seed bank which did not previously exist is established. *V. karroo* trees can produce large amounts of seeds annually, and these have a high longevity. As a result, destruction of a stand of *V. karroo* is often times still followed by seedling establishment and considerable regeneration [34].

2.3. Role in soil fertility

The effect of *V. karroo,* and other tree species, on herbaceous species (and grasses) may not always be negative, and there is evidence that trees may actually have a beneficial effect on neighbouring plants. For example, increased herbaceous layer productivity has been reported under tree canopies, due to favourable conditions such as improved soil water status and soil fertility [38, 39]. Likewise, *V. karroo* has various favourable influences on herbaceous production. First, *V. karroo* is a leguminous tree known to form root nodules [40], which are swellings on the root that contain nitrogen-fixing microorganisms (bacteria) known as *Rhizobium. Rhizobium* possesses the enzyme systems (including nitrogenase enzyme complex) that convert atmospheric nitrogen to nitrogen compounds useful to plants [41, 42]. Legumes like *V. karroo* then use the compounds to construct amino acids and protein [41, 43]. This ability of *V. karroo* to fix nitrogen is beneficial to other plants as well, mainly because the nitrogen content in the soil increases, and soil fertility is thus enhanced under these trees. In addition, *V. karroo* is able to use water and nutrients from deep underground because it has a long taproot, and this again leads to grasses and other plants thriving in its shade [6]. The ability of *V. karroo* to use water from deep underground means that it can grow in arid and otherwise inhospitable environments, as long as there is an assured supply of underground water [27]. It hence also acts as an indicator of surface and underground water, especially in arid land [2, 5]. The tree is further considered an indicator of sweet veld, which is highly valued for good grazing and fertile soils [5, 6]. This is due to the beneficial effects such as provision of shade, improved soil fertility, and water availability, which lead to the development of palatable and nutritious grasses under the *V. karroo* trees [18].

Several studies have been conducted on the positive effect of woody plants on grasses. In southern African savannas, *Panicum maximum* is well known to be associated with tree canopies, especially those of several *Vachellia* species. *P. maximum* is one of the most important fodder grass species in many savanna areas, mainly because it is highly palatable to cattle and other grazers, and it also has a high production potential [44]. The grass is strongly associated with tree canopy cover; it is common under trees but seldom occurs in the open [45]. Smit and Swart [46] suggest that such grass-tree associations, which exist in many semi-arid savanna areas, warrant that bush control measures should not simply imply a complete removal of woody plants but rather tree thinning with a view to reducing negative competition effects. This kind of approach can ensure that the important forage contribution by *P. maximum* is maintained.

This association is likely due to enhanced supply of nutrients such as nitrogen and phosphorus under tree canopies and suitable germination conditions for *P. maximum* seeds due to the relative abundance of litter and low temperatures under tree canopies [1]. A study investigating the relation between tree height of *V. karroo* and *V. tortilis* and the associated occurrence of *P. maximum* in the Sourish Mixed Bushveld [27] of Limpopo Province indicated that *P. maximum* mainly occurs under larger trees, but the grass attained pure stands under smaller *V. tortilis* trees of >2.0 m height [44]. In the False Thornveld of the Eastern Cape [27], Stuart-Hill et al. [47] proposed that the net effect of the favourable or unfavourable influences of *V. karroo* on grass production is dependent on tree density. It was observed that in situations where there were a few *V. karroo* trees, grass production was greater than where there were no trees but declined as tree density increased beyond a critical level.

3. Socio-economic significance and uses

V. karroo is of considerable socio-economic value as almost all of its parts, including bark, pods, seeds, leaves and thorns, are extremely useful to both humans and animals.

3.1. Domestic uses

Vachellia karroo is one of the most preferred species for fuelwood [48] because the wood has excellent fuel properties. It burns clean with little smoke and is valued for its sustained high temperature [18] and thus produces high-quality fuelwood for many rural communities which still rely on wood for cooking and heating. The wood is also used as rough construction material for building traditional huts and fences in many rural communities [1, 18]. The thorns are used as sewing needles, pegs or pins, while its branches are used in farms to make fencing kraals for livestock, to protect them from predators [1, 2]. The bark, leaves, gum and other parts are used medicinally in many ways. An infusion of the bark is used to cure diarrhoea and dysentery, while the dried and powdered form of its gum is used for eye treatments [2]. A boiled liquid from the bark is sometimes used to treat cattle which have tulp poisoning caused by *Moraea* (*Homeria*) species, which are bulbous plants poisonous to cattle [6]. Other *Vachellia* species are known to have medicinal properties as well. For example, the bark of *V. erioloba* is used to treat headaches and that of *V. xanthophloea* is used for fevers and eye complaints [1].

3.2. Commercial value

In addition to all the domestic uses of *V. karroo*, various commercial products are also obtained from the tree, of which gum is one of the most important (**Figure 6**). In fact, *V. karroo* gets its common name "sweet thorn" from this gum which comes out from wounds in the bark [6]. It is a pleasant tasting gum that is eaten by people and animals and has also been used for confectionary and adhesives [2, 16]. This gum is similar to gum arabic, which is widely used for thickening many convenience foods, pharmaceuticals and cosmetics [1].

The wood of *V. karroo* is hard and tough, making it suitable for making furniture, poles, and fence-posts [2]. It is also used to make wooden carvings (ornaments), which are very popular ornaments in the tourism industry [1]. The bark is used to make strong ropes and mats [2]. This bark and that of several other *Vachellia* species, notably *V. nilotica* (bark and pods)

Figure 6. *Vachellia karroo* tree exuding gum (photo: M. Dingaan).

contains tannin [1], which is widely used in the tanning of leather, giving it a reddish colour [5]. Tannins are plant polyphenolic compounds (secondary metabolites) that act as a defence mechanism in plants against pathogens and herbivores [49–51] and hostile environmental conditions [52, 53]. Most of the commercially extracted tannin in South Africa comes from Black Wattle (*Acacia mearnsii*), an introduced Australian species which can yield 36–44% tannin from the bark [1].

4. Occurrence and distribution of *V. karroo* in South Africa

A TWINSPAN classification of historical data comprising 1553 relevés and 2006 species, compiled from all areas of South Africa where *V. karroo* is known to occur, was conducted and produced five main vegetation types, namely savanna, grassland, riparian thickets, wetland and Nama-Karoo communities. The riparian thickets and Nama-Karoo communities will only be mentioned briefly in this section, because they form the core of the *Acacia* (*Vachellia*) *karroo* Class suggested and described in more detail by Dingaan [54].

4.1. Savanna communities

Savannas are one of the main biomes in the world and are the dominant vegetation in Africa and southern Africa [55], especially in Botswana, Namibia and Zimbabwe [56]. In South Africa, the Savanna forms the largest biome and occupies over one-third (33.49%) the country's area [57]. It is well developed in Northern Cape, North-West, and Limpopo Provinces; it is also found in parts of Mpumalanga, KwaZulu-Natal, and Eastern Cape Provinces and has isolated occurrences in Gauteng and Free State Provinces. The factors delimiting the biome are complex and can be an interplay of altitude, climate, soils, herbivory, and fire [39, 56, 58]. The biome mostly occurs at altitude ranging from sea level to 2000 m; rainfall is seasonal with wet summers and dry winters and varies from 200 to 1000 mm per year (**Figure 7**) frost may occur from 0 to 120 days per year, with frost free days in low-lying areas and longest frost periods in high-altitude areas [56, 58]. Approximately 8.5% of the biome is conserved in South Africa [57], a fairly good proportion compared to the other biomes. There are several conservation areas in the biome, which include the Kruger National Park. Savanna areas have not been adversely impacted by urbanisation, which could have been hindered by the hot, moist climate and diseases such as malaria [56, 57].

The Savanna biome in South Africa is described by Low and Rebelo [56] and Scholes [55] as vegetation characterised by a grassy ground layer 0.5–2 m tall and a distinct upper layer of woody plants 2–10 m tall (**Figure 8**). It may be delineated according to the height and degree of canopy cover of the tree layer as follows: shrubland, woodland, or bushveld depending on whether the upper layer is near the ground, dense or in the intermediate stages, respectively [55, 56]. Savanna vegetation may be broadly divided into fine-leaved savannas found in nutrient-rich and arid environments and broad-leaved savannas in nutrient-poor and moister environments [55, 58]. Broad-leaved species such as *Terminalia sericea*, *Burkea africana*, various *Combretum* species, *Pterocarpus rotundifolius* and several others dominate the higher rainfall

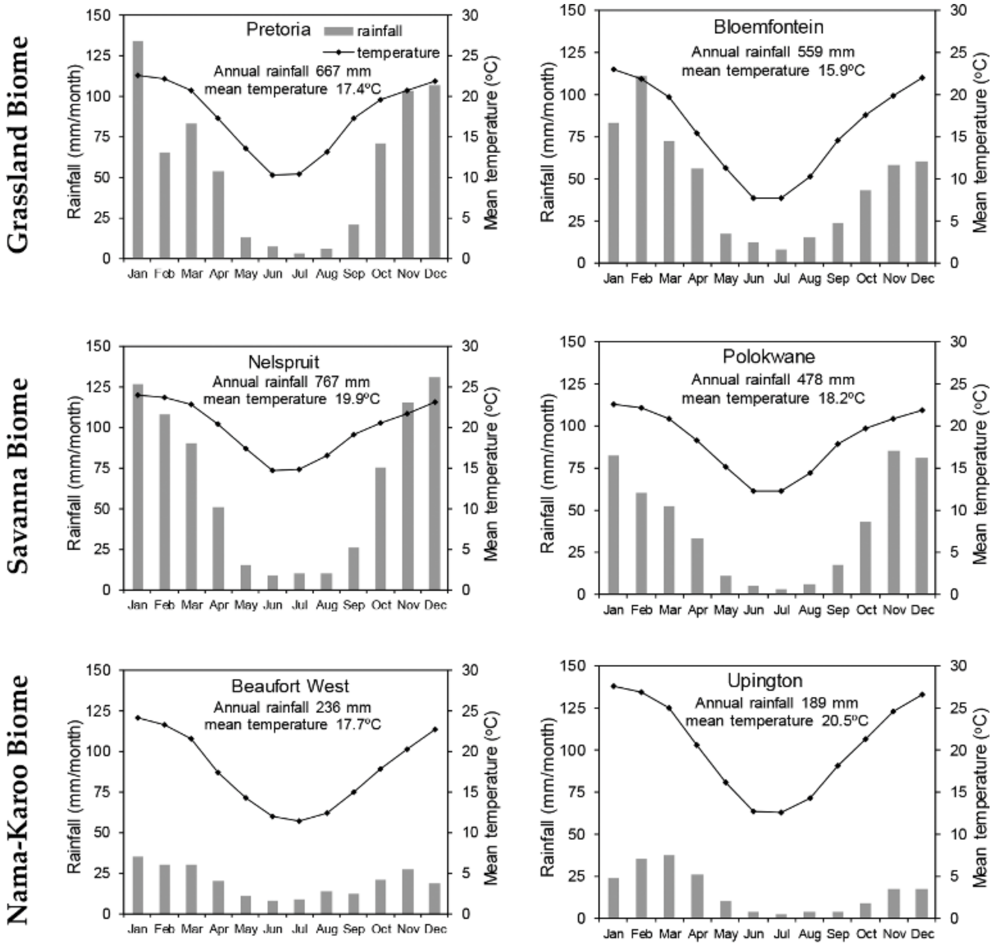

Figure 7. Rainfall and temperature for selected locations in the three representative biomes of South Africa [54].

areas, while the more arid savanna is dominated by microphyllous species where numerous *Vachellia* (and *Senegalia*) species dominate the tree component, but *Colophospermum mopane* is the broad-leaved exception [55].

The areas of the Savanna biome where *V. karroo* occurs are mainly in the Limpopo and North-West Provinces (**Figure 9**), and vast communities of *V. karroo* also occur in the Kalahari region in the Northern Cape Province. It can also be found in parts of the Eastern Cape and Western Cape Provinces. *V. karroo* communities can be encountered on predominantly sandy soils on bottomlands, footslopes, and mountain slopes. They can also be found as riparian thicket on clayey soils along stream and riverbanks.

Communities that make up this vegetation type are listed in **Table 3**, with the two most prominent as follows: The first is the *Acacia karroo–Panicum maximum* Open Woodland [62]

Figure 8. Savanna near Kimberley (top) and at Mokala National Park (middle, bottom), Northern Cape, South Africa (photos: M. Dingaan).

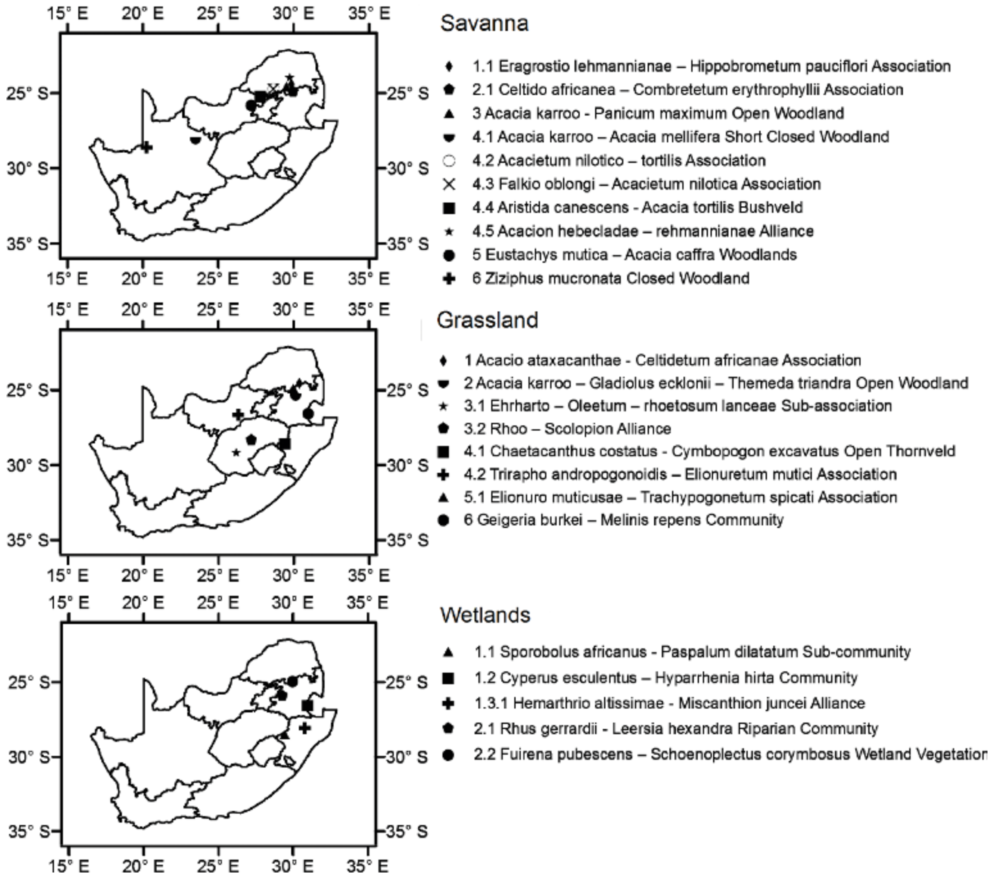

Figure 9. Distribution of selected *Vachellia karroo* communities.

found mainly along the banks of Ngwaritzi and Olifants Rivers south of Polokwane in the Limpopo Province. The second is the *Panico maximi–Acacietea tortilis* Class, described by Winterbach et al. [59] as microphyllous thorny bushveld that is associated with dark, clayey soils in low-lying areas. Other communities in the savanna where *V. karroo* occurs include the *Kirkia wilmsii–Terminalia prunioides* Closed Mountain Bushveld described by Siebert et al. [61]. This vegetation occurs within the Sekhukhuneland Centre of Plant Endemism (SCPE), which stretches from the Limpopo Province into the Mpumalanga Province and includes towns such as Roossenekal, Steelpoort and Sekhukhune. The vegetation is predominantly restricted to the warm slopes and valleys of undulating hills and mountains.

4.2. Grassland communities

The South African Grassland biome is part of the global temperate grassland biome [69]. It is the third largest biome in the country and covers 25.71% of South Africa [57] The biome is

Community	Location and habitat	Refs.
1. *Englerophyto magalismontani–Acacietea caffrae* Class	Found on slopes of Waterberg, Magaliesberg, Witwatersrand, Suikerbosrand mountains (Limpopo) Mainly on sandy soils	[59]
1.1. *Eragrostio lehmannianae–Hippobrometum pauciflori* Association	Sekhukhuneland (SCPE) (Limpopo/Mpumalanga) Occurs as scattered thickets in large river valleys, dongas or eroded areas Sandy soils, mainly Hutton form	[60]
2. *Kirkia wilmsi–Terminalia prunioides* Closed Mountain Bushveld	Sekhukhuneland (SCPE) (Limpopo/Mpumalanga) Restricted to warm slopes and valleys of undulating hills and mountains Soils are generally clayey Surface rocks are predominant	[61]
2.1. *Celtido africanea–Combretetum erythrophyllii* Association	Closed riparian thicket to forest found in valleys along large rivers such as the Steelpoort and Olifants Red loam Oakleaf soils	[60]
3. *Acacia karroo–Panicum maximum* Open Woodland	Polokwane (formerly Pietersburg), Limpopo	[62]
3.1. *Sporobolus ioclados–Gymnosporia buxifolia* Short Closed Woodland	Occurs along the banks, floodplains of the Ngwaritzi and Olifants Rivers Deep clayey, poorly drained soils Oakleaf, Dundee, and Valsrivier forms	[62]
3.2. *Commiphora africana–Digitaria velutina* Low Open Woodland	Found on plains, along the upper banks of the Ngwaritzi River and along the ridges Shallow, well-drained sandy soils Hutton and Glenrosa forms	[62]
4. *Panico maximi–Acacietea tortilis* Class	Waterberg, Soutpansberg and Pietersburg Plateaus (Limpopo) Dark, clayey soils	[59]
4.1. *Acacia karroo–Acacia mellifera* Short Closed Woodland	Rhino Ranch, Lephalale (formerly Ellisras), Limpopo Clayey soils of the Arcadia form	[63]
4.2. *Acacietum nilotico–tortilis* Association	Nylsvley Nature Reserve, Limpopo Found on flat bottomlands, typically on calcareous alluvium Soils mainly Oakleaf, Valsrivier, and Arcadia forms	[64]
4.3. *Falkio oblongi–Acacietum nilotica* Association	Nylsvley Nature Reserve, Limpopo Found on bottomland Vertic soils of the Arcadia form	[64]
4.4. *Aristida canescens–Acacia tortilis* Bushveld	Borakalalo Nature Reserve (BNR), North-West	[64]
4.4.1. *Acacia erubescens–Acacia luederitzii–Plectranthus madagascariensis* Thornveld	Dry to moderately dry habitat Sandy, sometimes clayey soils	[65]
4.4.2. *Perotis patens–Terminalia sericea* Woodland	Found on southern section of BNR Sandy soils	[66]

Community	Location and habitat	Refs.
4.4.3. *Ziziphus mucronata–Acacia karroo* Woodland Note: Although this community is similar to the communities of the *Vachellia karroo* Class suggested by Dingaan [54] in that it is *Vachellia karroo*–dominated riparian vegetation, it shows more affinity towards communities of the *Panico maximi–Acacietea tortilis* and is hence correctly included by Winterbach [64] in this class	Situated on the banks of the Moretele River and tributaries (BNR) Loamy to clayey soils, sandy soils in some tributaries	[65]
4.5. *Acacion hebecladae–rehmannianae* Alliance	Vicinity of Turfloop Dam, Limpopo Mainly occurs along streams and adjacent areas Clayey soils	[64]
5. *Eustachys mutica–Acacia caffra* Woodlands	Kgaswane Mountain Reserve (formerly Rustenburg Nature Reserve), North-West Found on slopes of the Magaliesberg Also on flat surfaces with clay-loam soils	[67]
6. *Ziziphus mucronata* Closed Woodland	Augrabies Falls National Park, Northern Cape Associated with drainage lines, floodplains and islands of the Orange River Dominant soil forms are Dundee and Oakleaf	[68]

Table 3. Classification and habitat features of savanna communities.

found mainly on the high central plateau (Highveld) comprising the Free State and Gauteng Provinces and is also found in parts of Mpumalanga Province and the inland areas of KwaZulu-Natal and Eastern Cape Provinces. Most of the large urban areas are concentrated in the biome, and consequently, the grassland biome has the greatest urban population density in South Africa [57]. The urban expansion, coupled with conversion of natural grassland to cultivated land, has resulted in a huge decline in biodiversity in this biome [70]. Most of the grassland is converted for the production of crops such as maize, wheat, sorghum and sunflower. Compared to the savanna, conservation of grasslands is relatively low with only 1.12% of the biome conserved [57].

The distribution of the biome is determined by an interplay of climate, topography, fire and grazing [71]. The overall extent of the biome is mainly determined by climate, especially the amount of summer rainfall and minimum winter temperatures [69]. The grass dominance is maintained by frosts, fire and grazing, which also prevent the establishment of trees [56]. However, the role of fire in maintaining grassland is greater in humid (>650 mm of annual rainfall) than semi-arid regions (<650 mm of annual rainfall) [69, 71]. The biome is limited to altitudes varying from near sea level to 2850 m above sea level; the winters are cold, dry with frequent occurrences of frost; rainfall varies spatially from 400 to 2500 mm per annum and occurs mainly during the summer season [57, 69]. The topography is mainly flat to slightly undulating and may include mountainous regions [69].

The biome comprises grasslands that are dominated by a single layer of grasses (**Figure 10**), with forbs forming an important but usually not dominant component. The dominant grasses in the biome are of the genera *Andropogon, Cymbopogon, Diheteropogon, Heteropogon, Hyparrhenia, Monocymbium, Schizachyrium, Themeda, Trachypogon* and *Tristachya* [69]. Trees are generally absent, except in a few localised habitats. The woody component is usually limited to higher

Figure 10. Grasslands near Bloemfontein (top), Bethlehem (middle) and Winburg (bottom), Free State Province, South Africa (photos: M. Dingaan).

moisture areas such as hills, gullies, valley slopes and is also found on azonal alluvial soils. The woody species often found in grassland are *V. karroo, V. sieberiana,* species of *Protea, Cussonia, Diospyros, Gymnosporia* and many more. Some of these trees and shrubs can tolerate frequent fires by being serotinous and through their ability to resprout after fires [69]. The Grassland biome can be divided into two classes (sweet and sour grasslands), based on moisture availability and palatability to livestock. Sweet grasslands (locally known as sweetveld) are dry grasslands that occur on base-rich soils at lower altitudes and remain palatable and nutritious throughout the year. Sour grasslands (sourveld) are moist grasslands generally found on leached soils at higher altitudes, which are palatable only in spring and summer [69, 72].

Vachellia karroo occurs throughout the biome and often encroaches on degraded grasslands. It is found on plains where soils are sufficiently deep, as well as in sheltered sites on the slopes, where habitat conditions are relatively moist. Communities where it is found are listed in **Table 4** and the two most prominent are as follows: The first is the *Themeda*

Community	Location and habitat	Refs.
1. *Acacio ataxacanthae–Celtidetum africanae* Association	North-eastern Mpumalanga and south eastern Limpopo Mountain sourveld on dry dolomitic regions Rock outcrops near or on the bottom of valleys Some protected areas on valley sides	[73]
2. *Acacia karroo–Gladiolus ecklonii–Themeda triandra* Open Woodland	Northern Mpumalanga Belfast-Lydenburg-Dullstroom area Plains and slopes Diverse soil types and forms	[74]
3. *Rhoetea erosae* Class Originally described by Werger [75] In present classification, it represents the shrub communities of southern and eastern Free State as described by Du Preez and Bredenkamp [76]	(i) Shrub communities occurring along the Upper Orange River Valley (ii) Shrub communities typical of the talus slopes of mountains, dolerite hills and ridges Also includes grassy shrubland communities on low dolerite outcrops	[75] [77]
3.1. *Ehrharto–Oleetum–rhoetosum lanceae* Sub-association Part of the *Chrysocomo–Selagenea albidae* sub-class [77]	Bloemfontein, Free State Province Relatively moist habitats found in gorges and drainage lines on the slopes of dolerite hills	[77]
3.2. *Rhoo–Scolopion* Alliance Synonym: *Grewio–Isoglossion grantii* Alliance Du Preez [77] Part of the *Rhoo–Rhoicissenea tridentatae* sub-class proposed by Du Preez [77]	Willem Pretorius Nature Reserve, Winburg-Ventersburg area, Free State Province Shrubland occupying plateaus and steep slopes of dolerite hills, rocky outcrops of the Beaufort Formation	[78]
4. *Themeda triandra–Eragrostis plana* Class	Moist grasslands of the plains High altitudes and high rainfall	[76]
4.1. *Chaetacanthus costatus–Cymbopogon excavatus* Open Thornveld Described by Robbeson [79] as Open Thornveld, a variation of Acocks' [27] Southern Tall Grassveld	North-western KwaZulu-Natal Includes the towns Estcourt, Colenso and Ladysmith, as well as Bergville and Winterton Plains adjacent to the footslopes of the Drakensberg Soils mostly shallow, sandy or sandy loam	[79]
4.1.1. *Hermannia depressa–Anthospermum rigidum* Sub-community	Slopes and footslopes of rocky hills Deep sandy soils	[79]

Community	Location and habitat	Refs.
4.1.2. *Hyparrhenia hirta–Themeda triandra* Grassland Community	Plains close to rocky hills Sandy and clayey soils	[79]
4.1.3. *Scabiosa columbaria–Aster peglerae* sub-variation	Open grassland on slopes of rocky hills Shallow soils of the Mispah form	[79]
4.2. *Trirapho andropogonoidis–Elionuretum mutici* Association	Ottosdal-Delareyville-Lichtenburg area, North-West Province High altitude grassland on midslopes Well-drained, sandy soils Mainly Hutton, Avalon and Mispah soil forms	[80]
i) *Helichrysum rugulosum–Conyza podocephala* Grassland	Pretoria and Heidelberg area, Gauteng Province Witbank, Mpumalanga Province Moist, deep soils on the undulating and flat plains Dominant soil forms are Glenrosa, Clovelly, and Hutton	[81]
5. *Tristachya leucothrix–Trachypogon spicatus* Class Synonym: *Harpochloo–Tristachyetea leucothrichis* Class Du Preez [77]	Korannaberg, Clocolan, Ficksburg, Bethlehem, Golden Gate, Platberg mountain near Harrismith, Free State Province Moist, high altitude mountain slopes and plateaus Sandy soils	[76]
6. *Geigeria burkei–Melinis repens* Community	Southeastern Mpumalanga Belfast–Barberton–Piet Retief–Wakkerstroom area Mountains and plains Associated with sandy loam soils Glenrosa the dominant soil form	[83]
6.1. *Acacia nilotica–Aristida congesta* Community	Found on strongly undulating plains Sandy to sandy loam soils Glenrosa soil form dominant	[83]
6.1.1. *Perotis patens–Hyperthelia dissoluta* Pure Short Closed Grassland Community	Found on slopes characterised by sandy to sandy loam soils Hutton and Glenrosa forms	[83]
6.1.2. *Pavetta edentula–Pellaea calomelanos* Low/Short Thicket Community	Occurs along the crest of strongly undulating plains Soils generally sandy to sandy loam, and rocky Mainly Glenrosa form	[83]
6.2. *Dombeya rotundifolia–Heteropogon contortus* Low/Short Thicket Community	Mountain vegetation associated with north facing slopes Sandy clay loam to sandy clay Glenrosa soils	-

Table 4. Classification and habitat features of grassland communities.

triandra–Eragrostis plana Class proposed and described by Du Preez and Bredenkamp [76] as moist grasslands of the plains at relatively high altitudes and high rainfall. The second is the *Geigeria burkei–Melinis repens* community; the individual communities that represent this vegetation type were identified and described by De Frey [83], but they are classified together under one major community for the first time in the present classification. This is vegetation of the mountains and plains of southeastern Mpumalanga, specifically the area comprising the towns of Belfast, Barberton, Piet Retief, and Wakkerstroom. It is associated with sandy loam soils, with Glenrosa as the dominant soil form.

4.3. Riparian thickets

The riparian thickets dominated by *V. karroo* are mainly associated with deep, clayey alluvial deposits that occur along stream and river banks (**Figure 11**) and occasionally on

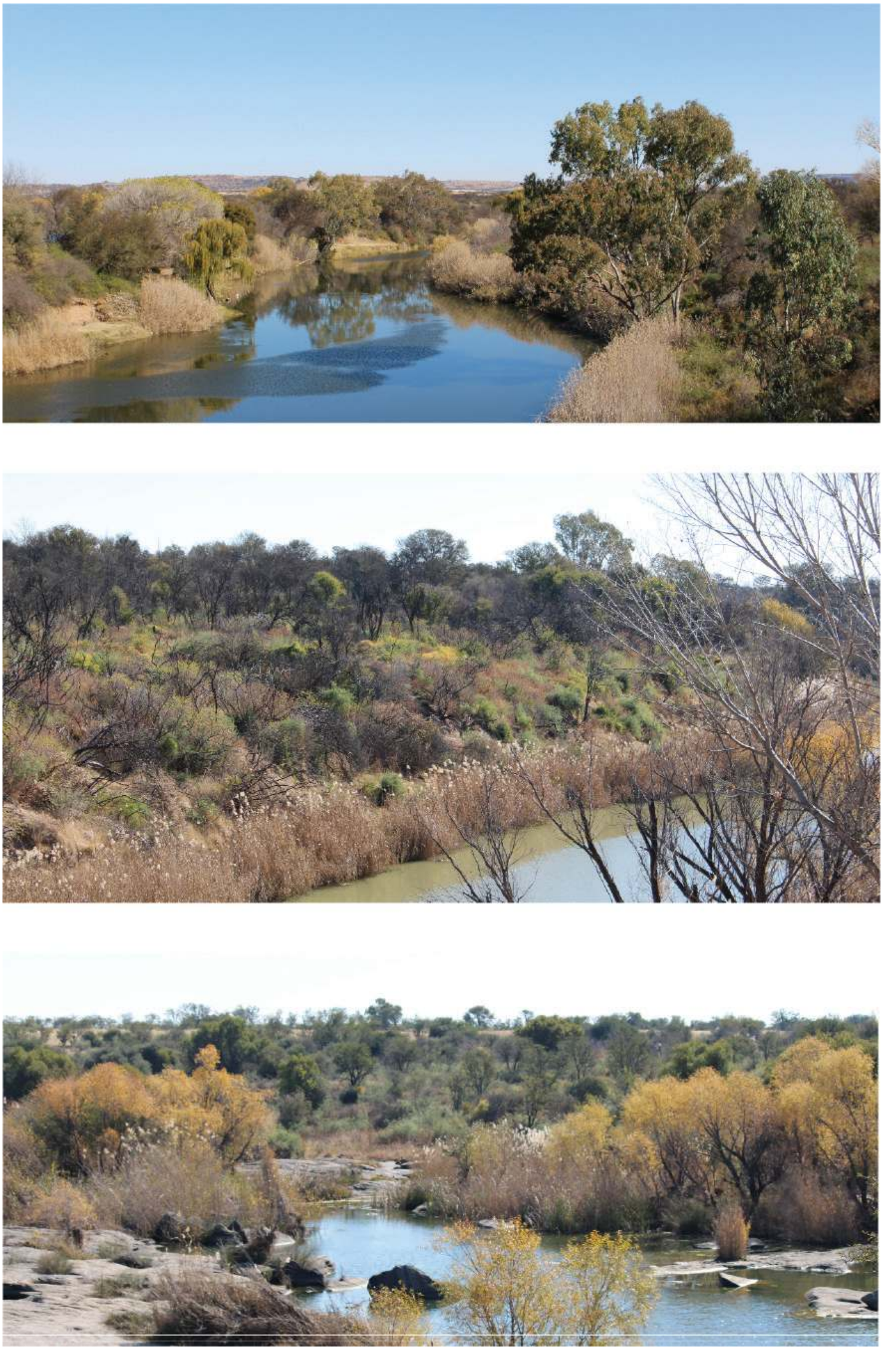

Figure 11. Riparian vegetation along the Modder River near Glen (top, middle) and Sand River near Ventersburg (bottom), Free State Province, South Africa (photos: M. Dingaan).

the river beds. The thickets also extend to the floodplains and bottomlands adjacent to the watercourses and also on gradual footslopes of hills and ridges. This vegetation type forms the core of the *Acacia* (*Vachellia*) *karroo* Class suggested and described in more detail by Dingaan [54].

4.4. Wetland communities

Wetland communities in which *V. karroo* is usually encountered are found in KwaZulu-Natal, Mpumalanga and Limpopo Province. Although these communities occur in both the Savanna and Grassland Biomes, we regard them as a distinct vegetation type because of their unique species composition. This vegetation type differs from the riparian thickets, which are mainly associated with clayey soils along rivers and streams. The wetland communities described here are generally associated with moist sandy soils and are dominated by grasses and forbs. *V. karroo* in these communities is the only notable woody species (**Figure 12**) but is not as prominent as in the riparian thickets.

Some of the major communities recognised within this vegetation type are as follows: The first is the *Hemarthria altissima* Class described by Du Preez and Bredenkamp [76] for the southern and eastern Free State. It represents vegetation of moist soils on marshes, stream-banks, riverbanks, dam edges, and vleis (shallow, seasonal wetlands). Although *V. karroo* is not present in communities described by Du Preez and Bredenkamp [76], it can be encountered in other wetland communities regarded as part of this class, namely those of the central-northern KwaZulu-Natal described by Eckhardt et al. [82]. The other distinct community is the *Fuirena pubescens–Schoenoplectus corymbosus* wetland vegetation described by Siebert et al. [61]. This wetland vegetation is found throughout the Sekhukhune Centre of Plant Endemism in Limpopo and Mpumalanga Provinces. It occurs on stream banks in valleys, in seepage areas on mountain slopes and also in wetlands on the mountain plateaus. It is associated with wet, vertic black clay soils. The main distinction between this vegetation and other *Vachellia karroo*-dominated riparian thickets is the absence of woody species such as *Ziziphus mucronata, Diospyros lycioides,* and *Rhus pyroides*, which are the usual companions of *Vachellia karroo* along the riverbanks. The wetland communities where *V. karroo* occurs are listed in **Table 5**.

4.5. Nama-Karoo communities

The Nama-Karoo biome is the second-largest biome in South Africa, covering 28.35% of the country [57]. It occurs on the western half of South Africa, at altitudes ranging from 500 to 2000 m but most of the biome falls between 1000 and 1400 m [56, 57]. This is an arid biome, characterised by unreliable summer rain that varies between 100 and 520 mm per year [85]. The topography resembles extensive, flat to undulating plains dotted with hills and occasional mountains [57]. The dominant vegetation is a grassy, dwarf shrubland (**Figure 13**), comprising a mix of low shrubs, grasses, succulents, geophytes and annual herbs [56, 85]. The annuals on average comprise the highest number of species in the biome [86].

V. karroo in this karroid vegetation is found in southern Free State and some areas in the Eastern Cape. The vegetation is found in varied habitats, ranging from gentle slopes

Figure 12. Wetlands near Verkeerdevlei (top), Winburg (middle) and Ventersburg (bottom), Free State Province, South Africa (photos: M. Dingaan).

Community	Location and habitat	Refs.
1. *Hyparrhenia dregeana–Eragrostis plana* Wetland	KwaZulu-Natal and Mpumalanga Rivers and streams	-
1.1. *Sporobolus africanus–Paspalum dilatatum* Sub-community	North-western KwaZulu-Natal Estcourt-Colenso-Ladysmith area Occurs in riverbeds Deep, sandy loam to clayey soils	[79]
1.2. *Cyperus esculentus–Hyparrhenia hirta* Community	Mountain wetland of the Belfast-Barberton-Piet Retief-Wakkerstroom area, Mpumalanga Occurs in valley bottoms Sandy clay loam to sandy clay soils Katspruit dominant soil form	[83]
1.3. *Hemarthria altissima* Class	Southern and eastern Free State Restricted to marshes and stream banks on the plateaux of the Korannaberg Also found in the Willem Pretorius Game Reserve on riverbanks, dam edges and wetlands with permanent water	[77] [78]
1.3.1. *Hemarthrio altissimae–Miscanthion juncei* Alliance Originally described by Eckhardt et al. [82] as an alliance of the *Agrostis lachnantha–Eragrostis plana* Wetlands	Central-northern KwaZulu-Natal Helpmekaar-Utrecht-Louwsburg area Rivers and streams Alluvial sandy soil Predominantly Dundee form	[82]
2. *Conyza scabrida–Gomphostigma virgatum* Wetland	SCPE (Limpopo/Mpumalanga) and Witbank Nature Reserve(Mpumalanga) Occurs along rivers and streams, and in the rocky streambeds	–
2.1. *Rhus gerrardii–Leersia hexandra* Riparian Community	Witbank Nature Reserve, Mpumalanga Occurs along the banks of the Olifants River and in the rocky streambed Soils generally sandy, rocky and shallow Predominantly Glenrosa and Mispah soil forms.	[84]
2.2. *Fuirena pubescens–Schoenoplectus corymbosus* Wetland vegetation	Throughout SCPE, Limpopo/Mpumalanga Found on stream banks in valleys, in seepage areas on mountain slopes, and also in wetlands on the mountain plateaus Associated with wet, vertic black clay soils	[61]

Table 5. Classification and habitat features of wetland communities.

and plateaus in south-western Free State to rocky habitats on hot and dry slopes in the Eastern Cape. The presence of *V. karroo* in these karroid veld types can be ascribed to bush encroachment occurring as a result of overgrazing [27]. The plant communities where *V. karroo* occurs are part of the *Acacia (Vachellia) karroo* Class proposed and described in detail by Dingaan [54].

Figure 13. Nama-Karoo at Augrabies National Park (top, middle) and in Hopetown (bottom), Northern Cape Province, South Africa (photos: M. Dingaan).

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