Royal Botanic Garden Edinburgh
and
The University of Edinburgh

# Taxonomy, distribution and functional traits in *Themeda* Forssk. (Poaceae).

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## Abstract

$C_4$ grasses dominate warm-climate grasslands and savannas, which cover about 20% of global land surface and where $C_4$ grasses are the most important group of in terms of species richness, abundance and economic importance. This thesis addresses the debate of whether temperature or precipitation limit the distribution of $C_4$ grasses and investigates whether widespread, dominant $C_4$ grasses are more variable in their functional traits.

I used herbarium specimens to investigate the distribution and trait variation within *Themeda* Forssk., which inhabits tropical and subtropical regions across Africa, Asia and Oceania. Niche modelling was used to identify the environmental variables that limit species distributions. The distribution of three species responds mainly to variables of temperature, but the distribution of six other species is more related to precipitation. Therefore, this study demonstrates that within *Themeda* both factors are critical.

Analysis of traits showed that the widespread *T. triandra* is the most variable species and that within this species traits showed weak correlations with individual environmental variables. A linear model including mean annual temperature, mean annual rainfall and temperature seasonality explained 21.55% of the variation in height, comparing well to a global study of more than 7000 plant species.

# INTRODUCTION AND AIMS

$C_4$ is a specialized pathway that increases the efficiency of photosynthetic processes while minimizing photorespiration in environments with high-temperatures and/or low-$CO_2$ levels (Edwards & Smith, 2010). Thus, $C_4$ species have a strong competitive advantage under conditions of drought, high temperatures, and nitrogen or $CO_2$ limitation (Sage, 2004). Plants with this type of pathway comprise only the 3% of vascular species (Sage, 2004), but at the same time they account for 20-25% of terrestrial photosynthesis (Still *et al.*, 2003) and include some economically important species (e.g. maize, sugarcane, sorghum). Sixty percent of $C_4$ species are grasses, which dominate grassland and savannas in tropical and subtropical areas, covering about 20% of the global land surface (Edwards & Smith, 2010).

Despite their importance, a number of questions regarding the distribution and ecology of $C_4$ grasses remain unanswered. An accepted paradigm about the distribution of $C_4$ species establish that they were favoured in high temperature environments, because of physiological advantages that the $C_4$ pathway confers in such environments (Sage, 2004). However, more recent studies have pointed to a key role of precipitation in the evolution and current distribution of $C_4$ grasses (Edwards & Smith, 2010). Much of the research about $C_4$ species has focused on large taxonomic groups such as the entire Poaceae family. However, studies at a more detailed taxonomic scale between species in one genus, or even within single species, might be a fruitful way to approach the debate of what limits the distribution of $C_4$ grasses.

This thesis contains a detailed study of the species of the $C_4$ grass genus *Themeda* Forssk., which is an important element of tropical and subtropical grasslands throughout Africa, Asia and Oceania (Clayton *et al*., 2014), with the goal to understand what environmental factors limit their distribution. In addition it addresses the key question of whether grass species that are widely distributed, such as the widespread species *T. triandra* Forssk., are more variable in their functional traits, such as plant height and leaf size. The study of functional traits, attributes of organisms that are known to be important to plant fitness and are associated with many important ecological processes and services, has become important in ecology (Violle *et al*., 2007). These traits are usually measured in the field, but specimens in herbaria might represent a rich resource for trait-based studies, and the use of herbarium-measured traits in *Themeda* is explored in this thesis.

In conducting the research presented in this thesis, it became clear that the greatest barrier to studies of trait variation at species-level was the high morphological polymorphism within *Themeda*, and the consequent inadequate taxonomy of the genus, which makes species identification difficult, resulting in many wrongly identified specimens in herbaria. This is very problematic because delimitation of meaningful biological entities is an essential pre-requisite for species-level biogeography.

In this general context of investigating the distribution, ecology and functional traits of species of $C_4$ grasses in a genus (*Themeda*) that requires a taxonomic overview, this thesis:

- In Chapter 1 summarizes the dispersed knowledge regarding the taxonomy of *Themeda*, providing a taxonomic overview of the genus and making necessary changes to species boundaries

- In Chapter 2, studies the distribution of *Themeda* at the levels of genus and species and the environmental factors that govern their distributions, through the use of niche modelling.

- In Chapter 3 aims to address whether widespread $C_4$ species are more variable in their functional traits, and how these traits are related to key environmental variables.

# LIST OF CONTENTS

Chapter 1. Evaluation of the taxonomy of *Themeda*

Chapter 2. Distribution and biogeography of *Themeda*

2.2. Materials and methods

2.3. Results

Chapter 3. Functional traits in *Themeda*

3.2. Materials and methods

3.3. Results

## LIST OF FIGURES

# LIST OF TABLES

# CHAPTER 1. EVALUATION OF THE TAXONOMY OF *THEMEDA*

## 1.1. INTRODUCTION

The genus *Themeda* Forssk. (Poaceae, Panicoideae, Andropogoneae) comprises annual and perennial herbs distributed across tropical and temperate areas of Africa, Asia and Oceania (Clayton *et al*., 2014). *Themeda* has been recorded as introduced in Polynesia, North and South America (MacKee, 1994; Barkworth *et al*., 2003; Clayton *et al*., 2014). The number of accepted species is unclear because there has never been a full taxonomic revision of the genus. Although Nanxian (1998) revised the nomenclature of 33 accepted species, he did not include species descriptions or the taxonomic reasons to consider names as accepted or synonyms. In this respect, there is only one recent comprehensive taxonomic account for the genus by Clayton *et al.* (2014) which recognises 27 species.

*Themeda* belongs to the tribe Andropogoneae, and possesses the characteristic combination of sessile and pedicelled spikelets arranged in pairs or triads, where the pedicelled member is usually male or sterile and the palea of the fertile spikelet is absent or minute (Watson & Dallwitz, 1992). *Themeda* shares these characters with *Heteropogon* Pers. and *Iseilema* Andersson, which are considered the most closely related genera (Moulik, 1997). All plants in Andropogoneae use the $C_4$ photosynthetic pathway. $C_4$ is a specialized pathway that increases the efficiency of photosynthetic processes while minimizing photorespiration in environments with high-temperatures and/ or low-$CO_2$ levels, being the reason why $C_4$ grasses dominate in tropical and subtropical areas (Watson & Dallwitz, 1992; Edwards & Smith, 2010).

*Themeda triandra* Forssk. is a dominant and important grass species that is native across Africa, Asia and Oceania (Clayton *et al*., 2014). With its broad distribution across tropical and subtropical regions, this species inhabits a variety of climates and soil types of grasslands and savannas (Russell *et al*., 1991; Jessop *et al.*, 2006, Snyman *et al.*, 2013). *Themeda triandra* resprouts post fire and its persistence as a dominant grass species in any of its habitats relies on periodical burning (Morgan & Lunt, 1999; Bond *et al.*, 2003). *Themeda triandra* is a highly palatable species, especially when young and because of this it often becomes eliminated from habitats that are overgrazed or where fire has been excluded, hence its presence in habitats is considered an indicator of grassland health (Dackwerts, 1993). *Themeda triandra* plays an important economic role where it is found, as feed for livestock and wildlife (McNaughton, 1985; Morgan & Lunt, 1999), and the loss of this species from grasslands and savannas negatively affects biodiversity and soil health (du Preez & Snyman, 1993; Mills *et al.*, 2005).

Given the importance of *T. triandra*, it has been the subject of several studies addressing its ecological role and conservation (see Snyman *et al.*, 2013 for a comprehensive summary). However, there has been no attempt to clarify the taxonomic problems derived from the morphological polymorphism that this species exhibits (Russell *et al.*, 1991; Jessop *et al.*, 2006; Schouliang & Phillips, 2006; van Oudtshoorn, 2012). It is possible that the polymorphism of the species is related to variation in chromosome number. The basic chromosome number of *T. triandra* is x=10 (Fossey & Liebenberg 1987) but diploid, triploid, tetraploid, pentaploid and hexaploid populations have been recorded in southern Africa and Australia (Hayman, 1960; Liebenberg, 1986).

Due to this morphological variability, regional forms have been described as species or varieties within *T. triandra*. However, according to Russell *et al*. (1991: 335), the characters used to support these regional forms “are poorly correlated with other attributes such as distribution, habitat and chromosome number”. Currently, more than 70 names are believed to be synonyms of *T. triandra*, although with different levels of confidence (Clayton *et al*., 2014). Examples of regional forms that have been considered distinct species are *Themeda australis* (R.Br.) Stapf and *Themeda japonica* (Houtt.) Tanaka. The former has been applied to populations in Australia (Snyman *et al.*, 2013), while the latter has been applied to China, Korea and Japan (Hsu *et al.*, 2000). Both names are still accepted in some herbaria and publications (Wheeler *et al.*, 1982; Nanxian, 1998; Hsu *et al.*, 2000), whereas other authors consider these names as synonyms of *T. triandra* because of the similarities within the same distributional range (Jessop *et al.*, 2006; Schouliang & Phillips, 2006; Snyman *et al.*, 2013).

The delimitation of *T. triandra* from some other *Themeda* species is also difficult. For example, according to Schouliang & Phillips (2006), the name *Themeda arguens* (L.) Hack. has been incorrectly applied to several specimens of *T. triandra* from Yunnan province, China.

In other cases found during this research project, specimens are commonly classified as *T. triandra* that better match *T. arguens* and *Themeda quadrivalvis* (L.) Kuntze.

Given the taxonomic uncertainty in the genus, any attempt to study the biogeography and ecology of *Themeda* should consider, as an initial point, the examination of species delimitation. In particular, given the wide distribution and importance of *T. triandra*, examining similarities and differences between it and similar species is crucial. A global overview of the taxonomy of the genus would help to identify which characters define *T. triandra* as a single species and which ones are parts of the variability displayed across its distribution.

The present chapter has the aim to bring together the dispersed knowledge regarding the taxonomy of *Themeda* in a single document. In the results, key characters of the genus and 26 species are presented. Characters mentioned by different authors, which I also found useful in the determination of herbarium specimens are listed.

## 1.2. MATERIALS AND METHODS

The results presented in this chapter are based on the study of taxonomic descriptions and herbarium material from the Royal Botanic Garden Edinburgh and Kew. The lack of a comprehensive revision of the genus meant that consultation of numerous sources was necessary to obtain descriptions for the 27 species accepted by Clayton *et al.* (2014). Sources consulted were original descriptions, floras and field guides from across the distribution of *Themeda* (Maiden, 1898; Bor, 1941; Reeder, 1948; Bor, 1952; Jansen, 1952; Backer & Bakhuizen Van Den Brink, 1968; Bor, 1968; Lazarides, 1970; Hsu, 1978; Cope, 1982; Wheeler *et al.*, 1982; Britto & Matthew, 1983; Müller, 1984; Liang, 1987; Sreekumar & Nair, 1987; Zhuang & Chen, 1989; Russell *et al.*, 1991; Phillips, 1995; Moulik, 1997; Mathew, 1999; Hsu *et al.*, 2000; Noltie, 2000; Potdar *et al.*, 2003; Duistermaat, 2005; Jessop *et al.*, 2006; Schouliang & Phillips, 2006; Cope, 2007; Kabeer & Nair, 2009; van Oudtshoorn, 2012; Clayton *et al.*, 2014; for more detail see Appendix 1). From these references, a list of characters and their states were identified for each species. All this information was recorded in a database, making it accessible in a single source. Morphological characters were then studied in over 1,996 specimens (486 specimens from Edinburgh and 1,510 specimens from Kew), including type material. Specimens were examined using a dissecting kit and stereoscope. The examination of available herbarium material was crucial for the identification of characters useful in the taxonomy of the genus, and in building the list of diagnostic characters for each species.

Diagnostic characters of the genus and species are accompanied by lists of major synonyms and notes about taxonomy, for example how species that are morphologically similar can be separated. Under "major synonyms" are the names frequently found on herbarium specimens, which based on the present research are considered to be synonyms.

The identification of *Themeda* species cannot be addressed by single characters. Instead, the species can be recognized by the unique combination of characters listed in this section.

Morphological terminology used in this chapter follows Beentje (2010), Phillips (1995) and Wheeler *et al.* (1982). For a better understanding of the taxonomy of the genus, some of the morphological terms and concepts used within this chapter are summarised here.

*Culm*

The upright stem of a grass, which bears roots, leaves and inflorescence.

*Inflorescence*

The part of a grass that bears a number of spikelets, including bracts and branches. *Compound inflorescence*: referring to inflorescences made up of a number of small constituent inflorescences, where there are two orders of branching.

*Spikelet*

The basic unit of a grass inflorescence; each one has two glumes supporting one or more florets. Spikelets can be attached to the branches directly (sessile) or by pedicels.

*Callus* (plural calli)

A hard projection  at the base of a spikelet, indicating a disarticulation point.

*Raceme*

An unbranched axis bearing two or more spikelets.

*Spathate racemes*

Racemes subtended by spathes or spatheoles. *Spathe*: a bract or modified bladeless leaf subtending the inflorescence or part of it. *Spatheole*: the uppermost spathe supporting the racemes within the compound inflorescence of some Andropogoneae.

*Involucral spikelets*

A group of four spikelets arranged in two pairs, arising at the base of each raceme and forming an involucre about the fertile spikelet. Pairs of spikelets can be inserted at the same of different levels. Some authors also use the term *homogamous spikelets*, as they have a similar appearance.

*Spikelet pairs*

Comprise two spikelets arising from the same node, one pedicelled and one sessile, which is fertile. This arrangement is characteristic of the tribe Andropogoneae. Also called *heterogamous spikelets*, as they present different morphology.

*Triad*

A group of three spikelets arising from the same node, two pedicelled and one sessile, which is fertile. This arrangement is characteristic of the tribe Andropogoneae.

*Awn*

Appendage ending an organ. In *Themeda*, the appendage arises from the tip of the upper lemma. Its shape can be straight or geniculate, if geniculate it is divided into the *column* and the *bristle*. *Column:* the lower portion of a geniculate awn. *Bristle*: the upper portion of a geniculate awn; it can be also applied to a very slender awn.

## 1.3. A BRIEF TAXONOMIC CONSPECTUS OF *THEMEDA*.

***Themeda***, Fl. Aegypt.-Arab.: 178 (1775).

*Major synonyms*

*Anthistiria* L.f.

*Diagnostic characters*

- Plants annual or perennial,
- Inflorescence simple or compound.
- Presence of spathate racemes.
- Racemes bearing 7-17 spikelets (4 involucral spikelets + 0-5 pairs + triad).
- Involucral spikelets paired and sessile, not deciduous with the fertile spikelet.
- Callus of the fertile spikelet usually pointed.
- Upper lemma usually awned.

*Notes*

Similar to *Heteropogon* and *Iseilema*, with which *Themeda* shares the following characters: spikelets organised in pairs or triads, with one sessile and one or two pedicelled (at least one of these spikelets is bisexual), spathes are present most of the time and the upper lemma is usually awned, calli always present and florets with 3 stamens.

However, both genera differ from *Themeda* as follows: the inflorescence in *Heteropogon* is a spike, meaning that the spikelets are attached directly to the main axis, without forming racemes and lacking the involucral spikelets (Moulik, 1997; Watson & Dallwitz, 1992; Phillips, 1995).

*Iseilema* form racemes similar to those found in *Themeda*, with the difference that the involucral spikelets here are pedicellate and deciduous with the fertile spikelet (Wheeler *et al.*, 1982, Watson & Dallwitz, 1992).

**1. *Themeda anathera* (Nees ex Steud.) Hack.**, Monogr. Phan. [A.DC. & C.DC.] 6: 669 (1889).

*Major synonyms*

*Anthistiria anathera* Nees ex Steud.

*Diagnostic characters*

- Plant perennial up to 120 cm tall.
- Culms slender; arising from slender rhizomes.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9-13 spikelets (4 involucral spikelets + 1-3 pairs + triad).
- Involucral spikelets 5–8 mm long; glabrous or densely covered with long, stiff and white hairs (with tubercles at the base), towards the margins.
- Fertile spikelets 5-7 mm long; subglabrous or densely covered with soft hairs.
- Awns present or absent, if present strait and up to 1 cm long.

*Notes*

This Himalayan species can be confused with *T. hookeri* or *T. tremula*, giving its slender habit. However, it is the only one with awnless racemes.

According to Cope (1982), *Themeda anathera* shows a great deal of variation in the indumentum of the spikelets, from glabrous to being covered with tuberculate based hairs. This situation has been confirmed by examination of herbarium specimens, especially from Afghanistan (Griffith 199, Neubauer 811 & 996; at K).

**2. *Themeda arguens* (L.) Hack.**, Monogr. Phan. [A.DC. & C.DC.] 6: 657 (1889).

*Major synonyms*

*Anthistiria arguens* (L.) Willd.

*Diagnostic characters*

- Plant annual up to 180 cm tall.
- Culms robust.

- Compound inflorescence, made up of dense clusters of spathate racemes.
- Racemes bearing 7 spikelets (4 involucral spikelets + 0 pairs + triad).
- Involucral spikelets 6–10 mm long; glabrous.
- Fertile spikelets 8-10 mm long; subglabrous, with few short hairs, towards the apex.
- Awns always present, geniculate and 5-9 cm long.

*Notes*

This species can be recognised by its annual habit, with dense cluster of racemes enclosed by long sphates (up to 4 cm) and the presence of involucral spikelets consisting only of the lower glume. It is similar to *T. triandra*, but according to Schouliang & Phillips (2006) it can be distinguished by its glabrous leaf sheaths, blunter leaf blades and involucral spikelets made of the lower glume only. In my opinion, the indumentum in the leaf sheaths can be absent or present; this is also noted by Duistermaat (2005) and Reeder (1948). Leaf blades are similar among all species of *Themeda* and I could not use the morphology of this as a characterto identify species or groups within the genus.

**3. *Themeda arundinacea* (Roxb.) A.Camus**, Fl. Indo-Chine [P.H. Lecomte *et al*.] 7: 363 (1922).

*Major synonyms*

*Themeda subsericans* (Nees ex Steud.) Ridl.

*Diagnostic characters*

- Plant perennial up to 600 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7-11 spikelets (4 involucral spikelets + 0-2 pairs + triad).
- Involucral spikelets 12–20 mm long; densely covered with long, stiff and tawny hairs (with tubercles at the base).
- Fertile spikelets 7-10 mm long; densely covered with brown hairs.
- Awns always present, geniculate and 4-9 cm long.

*Notes*

Similar to *T. gigantea*/*T. intermedia*, as the involucral spikelets are densely covered with tawny hairs, but *T. arundinacea* has well-developed awns.

### 4. ***Themeda avenacea*** **(F.Muell.) T.Durand & B.D.Jacks.**, Index Kew. Suppl. 1: 424 (1906).

*Major synonyms*

*Anthistiria avenacea* F. Muell.

*Diagnostic characters*

- Plant perennial up to 200 cm tall.
- Culms robust; arising from a silky-hairy or woolly base.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7-9 spikelets (4 involucral spikelets + 0-1 pairs + triad).
- Involucral spikelets 20–30 mm long; glabrous.
- Fertile spikelets 13-17 mm long; densely covered with brown hairs.
- Awns always present, geniculate and 4-10 cm long.

*Notes*

This species is characterised by its yellowish culms arising from silky-hairy or woolly bases and with large involucral spikelets (20-30 mm).

### 5. ***Themeda caudata*** **(Nees ex Hook. & Arn.) A.Camus**, Fl. Indo-Chine [P.H. Lecomte *et al*.] 7: 364 (1922).

*Major synonyms*

*Themeda longispatha* (Hack.) Raiz & Jain

*Diagnostic characters*

- Plant perennial up to 600 cm tall.
- Culms robust; arising from a rootstock.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9-11 spikelets (4 involucral spikelets + 1-2 pairs + triad).

- Involucral spikelets 10–15 mm long; sparsely covered with short hairs (without tubercles at the base).
- Fertile spikelets 9-10 mm long; densely covered with brown hairs.
- Awns always present, geniculate and 4-8 cm long.

*Notes*

Similar to *T. villosa* in its general morphology and involucral spikelets that are sparsely covered with hairs. However, *T. caudata* has racemes with well-developed awns, which *T. villosa* lacks.

**6. *Themeda cymbaria* Hack.**, Monogr. Phan. [A.DC. & C.DC.] 6: 668 (1889).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 250 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7-9 spikelets (4 involucral spikelets + 0-1 pairs + triad).
- Involucral spikelets 5–8 mm long; glabrous or sparsely covered with short, weak and white hairs (with tubercles at the base).
- Fertile spikelets 4-6 mm long; densely covered with stiff hairs.
- Awns always present, geniculate and up to 2 cm long.

*Notes*

Similar to *T. sabarimalayana*. According to Sreekumar & Nair (1987), this species can be recognised by its sheaths bearded on one margin and involucral spikelets entirely glabrous. I found that the first character was difficult to observe in herbarium specimens and involucral spikelets are not always glabrous; sometimes they have tuberculate-based hairs. However, I do agree with the description that this species can be recognised by the length of the sessile spikelets (4-6 mm) and callus hairs being white.

**7. *Themeda gigantea* (Cav.) Hack. ex Duthie**, Fodder Grasses N. India: 89 (1888).

*Major synonyms*

*Anthistiria gigantea* Cav.

*Diagnostic characters*

- Plant perennial up to 400 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7(-9) spikelets (4 involucral spikelets + 0(-1) pairs + triad).
- Involucral spikelets 5-8 mm long; densely covered with long, stiff and tawny hairs (with tubercles at the base).
- Fertile spikelets 6.5-7 mm long; densely covered with brown hairs.
- Awns present or absent, if present straight and up to 1 cm long.

*Notes*

The distinction of this species from *T. intermedia* is difficult and in this project it has not proven possible to resolve their boundaries. There may be a single species because they both share many characters, but I consider them separate here following Clayton *et al.* (2014).

**8. *Themeda helferi* Hack.**, Monogr. Phan. [A.DC. & C.DC.] 6: 665 (1889).

*Major synonyms*

*Anthistiria helferi* Munro ex Hack.
*Themeda ciliata* subsp. *helferi* (Hack.) A.Camus

*Diagnostic characters*

- Plant annual up to 30 cm tall.
- Culms slender.
- Compound inflorescence, made up of dense clusters of spathate racemes.
- Racemes bearing 7 spikelets (4 involucral spikelets + 0 pairs + triad).

- Involucral spikelets 4–5 mm long; densely covered with long, stiff and white hairs (with tubercles at the base), towards the apex.
- Fertile spikelets ca. 4 mm long; densely covered with soft and thin hairs.
- Awns always present, geniculate and 3-5 cm long.

*Notes*

This annual species produces clusters of racemes from the bottom of the plant. Essentially, the whole plant comprises a short culm and a very large inflorescence.

Some authors considers this species as an intraspecific variety of *T. quadrivalvis* (Bor, 1960; Moulik, 1997)

**9. *Themeda hookeri* (Griseb.) A.Camus**, Bull. Mus. Hist. Nat. (Paris) 26: 425 (1920).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 90 cm tall.
- Culms slender; arising from slender rhizomes.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9-11 spikelets (4 involucral spikelets + 1-2 pairs + triad).
- Involucral spikelets 10–19 mm long; glabrous or sparsely covered with long and stiff hairs (without tubercles at the base).
- Fertile spikelets ca. 7 mm long; subglabrous or densely covered with soft and thin hairs, towards the apex.
- Awns always present, geniculate and 2-5 cm long.

*Notes*

Like *T. anathera*, this is a slender, Himalayan species. However, it can be recognised because it has few racemes, which are all borne singly from the upper leaf axils instead of being gathered into spathate clusters (Schouliang & Phillips, 2006). Racemes are always awned, once or twice.

**10. *Themeda huttonensis* Bor**, Indian Forest Rec., Bot. 1: 96 (1938).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 100 cm tall.
- Culms slender.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9 spikelets (4 involucral spikelets + 1 pair + triad).
- Involucral spikelets 11–12 mm long; sparsely covered with short and thin hairs (without tubercles at the base).
- Fertile spikelets ca. 6 mm long; subglabrous, with few short hairs, towards the apex.
- Awns always present, geniculate and 2-3 cm long.

*Notes*

This slender species is characterised by its racemes that are scattered throughout the plant and the involucral spikelets that are twice the length of the fertile spikelet.

**11. *Themeda idjensis* Jansen**, Acta Bot. Neerl. 1: 482 (1952).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 600 cm tall.
- Culms robust.

- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7 spikelets (4 involucral spikelets + 0 pairs + triad).
- Involucral spikelets 12-15 mm long; glabrous.
- Fertile spikelets 8-10 mm long; densely covered with brown hairs.
- Awns always present, geniculate and up to 6 cm long.

*Notes*

I have not seen material of this species, but based on characters of height and indumentum in the involucral spikelets described by Jansen (1952) and Backer & Bakhuizen Van Den Brink (1968), I infer a close morphological appearance to *T. caudata* and *T. villosa*. Characters that should help to recognise *T. idjenensis* from these two species are the number of spikelets in the racemes and the length of the involucral spikelets.

**12. *Themeda intermedia* (Hack.) Bor**, Indian Forest Rec., Bot. 1: 96 (1938).

*Major synonyms*

*Themeda gigantea* var. *intermedia* Hack.

*Diagnostic characters*

- Plant perennial up to 500 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7-11 spikelets (4 involucral spikelets + 0-2 pairs + triad).
- Involucral spikelets 10–14 mm long; densely covered with long, stiff and tawny hairs (with tubercles at the base).
- Fertile spikelets 7-9 mm long; densely covered with brown hairs.
- Awns present or absent, if present strait and up to 1 cm long.

*Notes*

See notes under *T. gigantea*.

**13.** ***Themeda minor*** **L.Liou**, Fl. Xizang. 5: 343 (1987).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 50 cm tall.
- Culms slender; arising from scaly rhizomes.
- Compound inflorescence, made up of dense clusters of spathate racemes.
- Racemes bearing 7 spikelets (4 involucral spikelets + 0 pairs + triad).
- Involucral spikelets 4–5 mm long; sparsely covered with long, soft and white hairs (with tubercles at the base).
- Fertile spikelets ca. 4 mm long; densely covered with soft hairs.
- Awns always present, strait and up to 0.4 cm long.

*Notes*

I have not seen specimens of this species but according to Liang (1987), *T. minor* is characterized by slender culms, leaves covered tuberculate-based hairs and racemes with a short and straight awn.

**14.** ***Themeda mooneyi*** **Bor**, Kew Bull. 1951(3): 451 (1952).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 50 cm tall.
- Culms slender.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9 spikelets (4 involucral spikelets + 1 pair + triad).
- Involucral spikelets ca. 11 mm long; densely covered with long, soft and white hairs (with tubercles at the base).
- Fertile spikelets ca. 6.5 mm long; densely covered with reddish hairs.

- Awns always present, geniculate and 2-5 cm long.

*Notes*

In my opinion, this species could be confused with *T. hookeri*, because of its slender habit and the similar size and appearance of the racemes, which have more than one awn in both cases. However, the involucral spikelets in *T. mooneyi* are always densely covered by long, soft and white hairs with tubercles at the base, whereas *T. hookeri* has involucral spikelets which can be glabrous or with sparsely stiff hairs without tubercles at the base.

### 15. ***Themeda novoguineensis* (Reeder) Jansen**, Acta Bot. Neerl. 1: 483 (1952).

*Major synonyms*

*Themeda gigantea* var. *novoguineensis* Reeder

*Diagnostic characters*

- Plant perennial up to 400 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 7(-9) spikelets (4 involucral spikelets + 0(-1) pairs + triad).
- Involucral spikelets 8–9 mm long; glabrous.
- Fertile spikelets 4-6 mm long; densely covered with stiff hairs.
- Awns always present, geniculate and 2-5 cm long.

*Notes*

*Themeda novoguinensis* has glabrous involucral spikelets similar to those found in *T. caudata* and *T. villosa*. However, *T. novoguinesis* has shorter fertile spikelets (up to 6 mm), which are densely covered with stiff hairs.

**16.** ***Themeda pseudotremula*** **Potdar, Salunkhe & S.R.Yadav**, Kew Bull. 58(1): 243 (2003).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 200 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9(-11) spikelets (4 involucral spikelets + 1(-2) pairs + triad).
- Involucral spikelets 7-9 mm long; densely covered with hairs (with tubercles at the base).
- Fertile spikelets 2.5-3 mm long; densely covered with stiff and reddish hairs.
- Awns always present, geniculate and 2-3 cm long.

*Notes*

I have not seen material of this species. According to Potdar *et al.* (2003), *T. pseudotremula* is similar to *T. tremula* in its habit and general appearance, but it differs from the latter in the indumentum present in the awns and the fertile spikelets.

**17.** ***Themeda quadrivalvis*** **(L.) Kuntze**, Revis. Gen. Pl. 2: 794 (1891).

*Major synonyms*

*Anthistiria ciliata* L.f.
*Themeda ciliata* (L.f.) Hack.

*Diagnostic characters*

- Plant annual up to 200 cm tall.
- Culms robust.
- Compound inflorescence, made up of dense clusters of spathate racemes.
- Racemes bearing 7 spikelets (4 involucral spikelets + 0 pairs + triad).
- Involucral spikelets 4-6(6.5) mm long; densely covered with long, stiff and white hairs (with tubercles at the base), towards the apex.

- Fertile spikelets 4-6 mm long; subglabrous, with few short hairs, towards the apex.
- Awns always present, geniculate and 2-5 cm long.

*Notes*

This species is usually confused with *T. triandra* because of its dense clusters of racemes and involucral spikelets covered with tuberculate-based hairs towards the apex. However, *T. quadrivalvis* has an annual habit and involucral spikelets which are always smaller (up to 6 mm) than those found in *T. triandra*.

**18. *Themeda sabarimalayana* Sreek. & V.J.Nair**, Bull. Bot. Surv. India 29(1-4): 127 (1989).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 200 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9-11 spikelets (4 involucral spikelets + 1-2 pairs + triad).
- Involucral spikelets 4-8 mm long; glabrous or sparsely covered with hairs (without tubercles at the base).
- Fertile spikelets 5-6 mm long; covered with soft hairs; callus hairs reddish.
- Awns always present, geniculate and 1-3 cm long.

*Notes*

Only one specimen of this species was examined, which is an isotype (Sreekumar 69433; at K). *Themeda sabarimalayana* looks superficially like *T. cymbaria*, but the former has bigger fertile spikelets, reddish hairs in the callus and the lower and upper glumes truncate and dentate at the apex (Sreekumar & Nair, 1987).

**19. *Themeda saxicola* Bor**, Kew Bull. 1951(3): 452 (1952).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 35 cm tall.
- Culms slender; arising from a woody base.
- Simple inflorescence, made up of a raceme at the end of the culm.
- Racemes bearing 9 spikelets (4 involucral spikelets + 1 pair + triad).
- Involucral spikelets 11–15 mm long; glabrous.
- Fertile spikelets 7.5-8 mm long; densely covered with stiff hairs.
- Awns always present, geniculate and up to 3 cm long.

*Notes*

The most easily distinguishable species of the genus, which has solitary racemes at the end of each culm.

**20. *Themeda strigosa* (Ham. ex Hook.f.) A.Camus**, Bull. Mus. Hist. Nat. (Paris) 26: 423 (1920).

*Major synonyms*

*Anthistiria strigosa* Buch.-Ham. ex Hook.f.

*Diagnostic characters*

- Plant perennial up to 150 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9-11 spikelets (4 involucral spikelets + 1-2 pairs + triad).
- Involucral spikelets 3–5 mm long; densely covered with long, stiff and white hairs (with big tubercles at the base).
- Fertile spikelets ca. 3.5 mm long; densely covered with stiff hairs.
- Awns always present, geniculate and up to 1 cm long.

*Notes*

This species has some of the smallest spikelets of all species within *Themeda* and the involucral spikelets are covered with large tubercles at the base of each hair.

**21.** ***Themeda tremula*** **(Nees ex Steud.) Hack.**, Monogr. Phan. [A.DC. & C.DC.] 6: 667 (1889).

*Major synonyms*

*Anthistiria tremula* Nees ex Steud.

*Diagnostic characters*

- Plant perennial up to 140 cm tall.
- Culms slender.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9 spikelets (4 involucral spikelets + 1 pair + triad).
- Involucral spikelets 5–8 mm long; densely covered with long, stiff and white hairs (with tubercles at the base).
- Fertile spikelets ca. 3.5 mm long; sparsely covered with soft and brownish-white hairs.
- Awns always present, geniculate and up to 1 cm long.

*Notes*

This slender species is characterised by small racemes and involucral spikelets that are densely covered by long and white hairs.

**22.** ***Themeda triandra*** **Forssk.**, Fl. Aegypt.-Arab.: 178 (1775).

*Major synonyms*

*Themeda australis* (R.Br.) Stapf
*Themeda brachyantha* (Boiss.) Trab.
*Themeda forskalii* Hack.
*Themeda laxa* (Andersson) A.Camus

*Diagnostic characters*

- Plant perennial up to 300 cm tall.
- Culms robust; arising from a knotty rootstock.
- Compound inflorescence, made up of dense clusters of spathate racemes.
- Racemes bearing 7 spikelets (4 involucral spikelets + 0 pairs + triad).
- Involucral spikelets 6–14 mm long; glabrous or densely covered with long, stiff and white hairs (with tubercles at the base), towards the apex.
- Fertile spikelets 6-11 mm long; subglabrous, with few short hairs, towards the apex.
- Awns always present, geniculate and 2-7 cm long.

*Notes*

*Themeda triandra* is usually confused with *T. arguens* and *T. quadrivalvis* in herbarium specimens, as they all have dense fascicules of racemes, where each raceme has seven spikelets. However, *T. triandra* is a perennial plant, unlike *T. arguens* and *T. quadrivalvis*. The involucral spikelets of *T. triandra* are always bigger than those found in *T. quadrivalvis*, and the clusters of racemes are often drooping.

Kabeer & Nair (2009) list several characters to distinguish *T. laxa* from *T. triandra*, most of which are related to the size of organs. However, all these characteristics have some degree of overlap between species (e.g. involucral spikelets in *T. laxa* are 7.5-8 mm long, while in *T. triandra* they are 7-12 mm long). The same authors also mention the number of racemes subtended by a spathe as a good character to support both species (*T. laxa* with 1-2 racemes per spathe and *T. triandra* with at least six racemes per spathe), but after seeing specimens of *T. triandra* from across its distribution, I have found some from Australia and South Africa with spathes subtending less than six racemes. Therefore, I have decided to consider *T. laxa* as a synonym of *T. triandra*, recognising all the overlapping characters.

**23. *Themeda trichiata* S.L.Chen & T.D.Zhuang**, Bull. Bot. Res., Harbin 9(2): 58 (1989).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 200 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9 spikelets (4 involucral spikelets + 1 pair + triad).
- Involucral spikelets 10-15 mm long; densely covered with short and soft hairs (without tubercles at the base).
- Fertile spikelets ca. 10 mm long; densely covered with soft and thin hairs.
- Awns always present, geniculate and 2-5 cm long.

*Notes*

Only two specimens of this species were examined. According to Zhuang & Chen (1989) and Schouliang & Phillips (2006), *T. trichiata* is similar to *T. yunnanensis* and *T. caudata*, but it differs because it is densely covered with long hairs on sheaths, culms, leaves and throughout the inflorescence, and in its shorter and more slender awns.

**24. *Themeda unica* S.L.Chen & T.D.Zhuang**, Bull. Bot. Res., Harbin 9(2): 56 (1989).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 250 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 13-17 spikelets (4 involucral spikelets + 3-5 pairs + triad).
- Involucral spikelets 25-40 mm long; densely covered with stiff and white hairs (with tubercles at the base), towards the margins.

- Fertile spikelets 7-10 mm long; densely covered with stiff and brown hairs.
- Awns always present, geniculate and 2-4 cm long.

*Notes*

I have not seen material of this species. Of the characters mentioned by Zhuang & Chen (1989), I think *T. unica* can be recognised by racemes with at least 13 spikelets (though this character can be sporadically found in *T. anathera* and *T. villosa*) and involucral spikelets as long as the awns.

**25. *Themeda villosa* (Lam.) A.Camus**, Fl. Indo-Chine [P.H. Lecomte *et al*.] 7: 364 (1922).

*Major synonyms*

*Themeda gigantea* var. *villosa* (Lam.) Hack.

*Diagnostic characters*

- Plant perennial up to 300 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9-11(13) spikelets (4 involucral spikelets + 1-2(3) pairs + triad).
- Involucral spikelets 9.5-14(-15.5) mm long; sparsely covered with short hairs (sometimes with tubercles at the base).
- Fertile spikelets 7-8 mm long; densely covered with brown hairs.
- Awns always present, strait or geniculate and up to 1 cm long.

*Notes*

This species can be confused with *T. caudata* given its general morphology and similar indumentum in the involucral spikelets. However, *T. villosa* has smaller awns (up to 1 cm long), which can be strait or geniculate.

**26. *Themeda yunnanensis* S.L.Chen & T.D.Zhuang**, Bull. Bot. Res., Harbin 9(2): 58 (1989).

*Major synonyms*

None.

*Diagnostic characters*

- Plant perennial up to 100 cm tall.
- Culms robust.
- Compound inflorescence; racemes not forming clusters.
- Racemes bearing 9 spikelets (4 involucral spikelets + 1 pair + triad).
- Involucral spikelets ca. 15 mm long; densely covered with long, soft and white hairs (with tubercles at the base).
- Fertile spikelets ca. 10 mm long; densely covered with soft, thin and brown hairs.
- Awns always present, geniculate or bigeniculate and 3-6 cm long.

*Notes*

I have not seen material of this species. Zhuang & Chen (1989) describe it as similar to *T. arundinacea* because of the habit, but differing from the latter in the number of spikelets per raceme and the colour of the hairs that cover the involucral spikelets.

According to Schouliang & Phillips (2006) it is most similar to *T. mooneyi* as both species have the same number of spikelets per raceme and involucral spikelets covered with white hairs, but *T. yunnanensis* is distinguished by having longer involucral and fertile spikelets.

## 1.4. Conclusion

In this study I recognise 24 of the 27 species listed in Clayton *et al.* (2014) (*T. anathera*, *T. arguens*, *T. arundinacea*, *T. avenacea*, *T. caudata*, *T. cymbaria*, *T. helferi*, *T. hookeri*, *T. huttonensis*, *T. idjensis*, *T. minor*, *T. mooneyi*, *T. novoguineensis*, *T. pseudotremula*, *T. quadrivalvis*, *T. sabarimalayana*, *T. saxicola*, *T. strigosa*, *T. tremula*, *T. triandra*, *T. trichiata*, *T. unica*, *T. villosa*, *T. yunnanensis*).

The name *T. laxa* has been reduced to a synonym of *T. triandra*, as I found several morphological similarities in the size of organs and number of racemes per spathe between specimens attributed to these species. This is in accordance with Noltie (2000), who considers *T. laxa* as a variety of *T. triandra*.

It is not clear if *T. gigantea* and *T. intermedia* are one or two different species. A detailed study of characters from specimens across the range of both species is needed in order to resolve their boundaries. Such as task goes beyond the scope of this project.

The information presented in this chapter has been useful to understand the morphological limits of *T. triandra* and other species which are often misidentified in herbaria. The overview of the taxonomy of the *Themeda* was needed in order to identify meaningful biological entities for the research presented in the following chapters.

# CHAPTER 2. DISTRIBUTION AND BIOGEOGRAPHY OF THEMEDA

## 2.1. INTRODUCTION

Grasses are the most important group of herbaceous plants in global savannas and drylands in terms of species richness, abundance, and economic importance (Wheeler *et al.*, 1982; Scholes & Archer, 1997). There have been few attempts to examine the biogeography of $C_4$ grasses at a detailed, within genus, scale, partly because of the number of independent origins of $C_4$ grasses (Edwards *et al*., 2010), which means many separate studies within different genera may be needed to make general conclusions. However, perhaps the greatest barrier to such studies is the high morphological polymorphism within grass genera and the resulting complexities associated with resolving their taxonomy, as demonstrated in Chapter 1, which is an essential pre-requisite for species-level biogeography. *Themeda* has a broad distribution across tropical and subtropical regions (Clayton *et al*., 2014) and according to the literature, the highest species diversity should be found in India, where about 18 species have been described (Moulik, 1997; Clayton *et al.*, 2014). While it is known that *Themeda* is distributed across these regions there has been no appraisal of the biogeography of the genus or the factors that govern its distribution.

As a first approach, an assessment of the factors limiting the distribution of *Themeda* can be related to factors limiting grasses with the same $C_4$ photosynthetic pathway. $C_4$ grasses are restricted to low latitudes and altitudes (Edwards *et al.*, 2010), and within these areas they are found in arid and open canopied environments (Edwards & Smith, 2010; Pau *et al.*, 2013). Because these patterns correlate best with temperature the research into the distribution of $C_4$ grasses has primarily focussed in this factor (Teeri & Stowe, 1976; Hattersley, 1983; Vogel *et al.*, 1986). Hence, $C_4$ grasses are considered to dominate regions of high mean annual temperature and where seasonality is primarily a product of variation in rainfall not temperature. In addition to favourable temperatures, $C_4$ plants require sufficient precipitation during the warm growing season (Teeri & Stowe, 1976; Paruelo & Lauenroth, 1996; von Fischer *et al.*, 2008). Thus, warm season precipitation and drought tolerance should also be important in the distribution of $C_4$ grasses. However, in an assessment of the distribution of $C_4$ grasses across Hawaii, Edwards & Smith (2010) found no significant correlation with any of the variables of temperature considered in their study, but they found a strong relationship between the presence of $C_4$ grasses and mean annual rainfall. Edwards &Smith (2010) considered that rainfall is likely to have had a strong indirect effect on the evolution and biogeography of $C_4$ grasses by limiting overstorey woody plant growth, thereby facilitating the high light and warmer environments needed to drive the $CO_2$ concentrating mechanism in $C_4$ grasses. In fact, Edwards & Smith (2010) go so far as to suggest that distributional patterns of $C_4$ grasses associated with temperature may, in part, be a biogeographic legacy.

Investigating the biogeography of *Themeda* species might be illuminating to address whether temperature or rainfall are the most important determinants of distribution. In particular, understanding the biogeography of *T. triandra* could be especially illuminating. *Themeda triandra* is a key dominant species in tropical grasslands and savannas of Australia, Asia, the Middle East and Africa (Russell *et al*., 1991; Jessop *et al.*, 2006, Snyman *et al.*, 2013). It follows that the factors that limit savanna vegetation are likely to be important in limiting *T. triandra*. Climate, hydrology, herbivory, fire and soil characteristics are all known to influence the distribution of savanna (Tinley, 1982; Furley, 1992; Hopkins, 1992; Ruggiero *et al.*, 2002; Bond, 2008). According to Stott (1988), South-East Asian savannas are present in climates with a range of 800 - 2000 mm mean annual precipitation and a dry season of 5–7 months. Schimper (1903) and Sarmiento (1984) considered that rainfall seasonality limits the growing of woody plants preventing the occurrence of closed-canopy forests. Lehmann *et al.* (2011) and Staver *et al*. (2011) both found that interactions between precipitation seasonality, mean annual rainfall and fire also prevent the recruitment of woody plants. However, the common aspect to all of these studies is that they consider the limits of savanna from the ecological standpoint of woody plants. Yet, the presence and abundance of $C_4$ grasses is the functional defining feature of savanna (Lehmann *et al.*, 2011). Within the tropical zone, seasonality of precipitations and mean annual rainfall are the critical drivers of the distribution of vegetation (C. Lehmann, UoE, pers. comm.) therefore it follows that these factors are likely to be important in limiting the distribution of a key species this of biome.

Niche models based on environmental information are a powerful tool to understand the distribution of species and provide insight into understanding the biogeography and ecology of species (Peterson, 2001; Guisan & Thuiller, 2005). There are known limitations to niche modelling as being correlative rather than causative in terms of the relationship between environment and distribution (Guisan & Thuiller, 2005). However, such models provide important information allowing us to distinguish differences in the environmental space of closely related or physiologically similar species (Pliscoff, 2013).

In this chapter I assess the distribution of *Themeda* at the levels of genus and species. Additionally, I studied the environmental factors correlated with the distribution of nine species of *Themeda* through the use of niche modelling. This includes the establishment of differences and similarities between the environmental space of *T. triandra* and other congeneric species.

## 2.2. MATERIALS AND METHODS

### 2.2.1. Database

To assess the distribution of *Themeda* and its species, I developed a database of herbarium specimens from the Royal Botanic Garden Edinburgh and the Royal Botanic Gardens, Kew. The collections of *Themeda* specimens at Edinburgh and Kew differ substantially in size, geographic coverage and number of species. Thus, the procedure to transfer the information to the database was different. From the Edinburgh herbarium, I recorded the data from all available 486 specimens into the main database of the institution (BG-Base) and then exported these data to a database I developed for this project. At Kew, the collection of *Themeda* was more than four times the size of the collection at Edinburgh. Hence, I first explored the collection to determine the approximate number of specimens and species at this herbarium. This was important to identify specimens of six species without samples at Edinburgh (*T. huttonensis, T. mooneyi, T. novoguinensis, T. sabarimalayana, T. saxicola* and *T. trichiata*), all of which were completely sampled from all specimens collected across their narrow distributions. The remaining 14 species are more widespread and for these, I selected specimens to sample based on their reproductive stage, availability of characters to identify species (or at least the genus) and the presence of a traceable locality or geographical area on the labels. Specimens were then recorded using photos of specimen labels.

For each specimen examined the following information was recorded:

- Species name
- Country
- Province or district
- Locality
- Geographic coordinates
- Altitude
- Notes about habitat, vegetation, and soil
- Collector and collector number
- Date of collection
- Label headings (when a flora of a country or province was mentioned; e.g. Flora of Kweichow).

All of this information was extracted from the herbarium labels, except the species name, which was determined using the characters in Chapter 1.

The final database compiles data of 1,996 specimens of *Themeda* from across Africa, Asia and Oceania. The list of species and number of records are shown in Table 1.

| **Species** | **Number of specimens recorded on the database** | | |
|---|---|---|---|
| | **E** | **K** | **Total** |
| *Themeda anathera* | 39 | 40 | 79 |
| *Themeda arguens* | 15 | 120 | 135 |
| *Themeda arundinacea* | 36 | 55 | 91 |
| *Themeda avenacea* | 1 | 67 | 68 |
| *Themeda caudata* | 30 | 35 | 65 |
| *Themeda cymbaria* | 11 | 20 | 31 |
| *Themeda helferi* | 2 | 3 | 5 |
| *Themeda hookeri* | 6 | 9 | 15 |
| *Themeda huttonensis* | 0 | 5 | 5 |
| *Themeda intermedia-gigantea* | 14 | 37 | 51 |
| *Themeda mooneyi* | 0 | 4 | 4 |
| *Themeda novoguinensis* | 0 | 4 | 4 |
| *Themeda quadrivalvis* | 27 | 42 | 69 |
| *Themeda sabarimalayana* | 0 | 1 | 1 |
| *Themeda saxicola* | 0 | 2 | 2 |
| *Themeda strigosa* | 1 | 2 | 3 |
| *Themeda tremula* | 8 | 46 | 54 |
| *Themeda triandra* | 234 | 856 | 1,090 |
| *Themeda trichiata* | 0 | 2 | 2 |
| *Themeda villosa* | 37 | 119 | 156 |
| *Themeda sp.* | 25 | 41 | 66 |
| **Total** | **486** | **1,510** | **1,996** |

Table 1. *Themeda* species and number of specimens recorded into the database

This comprehensive database, while sufficient to map the distribution of the genus and species to a country level, was insufficient to perform either niche modelling or an analysis of the intraspecific variation in functional traits (described in Chapter 3). Both of these analyses require georeferenced data. Hence, geographic coordinates for all localities recorded in the database were gathered. During the georeferencing process, six sources were consulted:

- GeoNames database (www.geonames.org)
- Google Earth 7.1.2.2041 (Google Inc., 2013)
- Fuzzy Gazetteer (http://isodp.hof-university.de/fuzzyg)
- Wikimapia (www.wikimapia.org)
- An unpublished database of Flora of Nepal (B. Adhikari, RBGE, pers. comm.)
- An unpublished gazetteer of Bhutan and India (H. Noltie, RBGE, pers. comm.)

Coordinates extracted from specimen labels were verified using the same cited sources. Pairs of coordinates (latitude and longitude) of each place were recorded in degrees, minutes and seconds. At the end of this process, more than the 91% of the database was georeferenced. The number of records with coordinates adopted from each source can be seen in Table 2.

| **Source** | **Type of source** | **Number of records with coordinates** |
|---|---|---|
| GeoNames Database | Online gazetteer | 1,549 |
| Specimen's labels | ------------------- | 175 |
| GoogleEarth | Software | 94 |
| Flora of Nepal database | Private database | 5 |
| Wikimapia | Online gazetteer | 2 |
| Gazetter of Bhutan and India | Private gazetteer | 2 |
| The Fuzzy Gazetteer | Online gazetteer | 1 |
| | **Total** | **1,828** |

Table 2. Number of records with geographic coordinates by source and total

Specimen records with coordinates were classified into two groups according to the resolution of the geographic information, depending on whether coordinates referred to a precise locality (populated place, bay, mountain, etc.) or an area (mountain ranges, provinces, districts, etc.). According to this classification, 1,572 specimen records referred to a precise location. Records without geographic coordinates could generally be explained by localities which could not be found (e.g. Zeisphoon in Oman) or there was repetition of the locality name within the same district, province or country (e.g. Epping in New South Wales, Queensland, Tasmania and Victoria). In these instances, specimen labels did not have the necessary information to determine a correct location.

### 2.2.2. Distribution maps based in collections

The final database of 1,828 georeferenced records was then used to create distribution maps of the genus, species and species diversity. Distribution of the species diversity was determined by both country and using cells of 4° x 4° latitude and longitude, and maps were created using ArcGIS v. 9.3 (Esri, 2008). Topographic surface used in these maps was created on the same software, from the 30 arc-seconds Digital Elevation Model (DEM), available via WorldClim (http://www.worldclim.org/).

The distributions of 19 species are described. For each species I mention latitudinal and longitudinal range, countries where it is found, habitat preferences and altitudinal range. Habitat preferences and altitudinal range were gathered from specimen labels and literature (Jansen, 1952; Bor, 1960; Backer & Bakhuizen Van Den Brink, 1968; Hsu, 1978; Britto & Matthew, 1983; Sreekumar & Nair, 1987; Phillips, 1995; Moulik, 1997; Mathew, 1999; Noltie, 2000; Duistermaat, 2005; Jessop *et al.*, 2006; Schouliang & Phillips, 2006; Cope, 2007; Kabeer & Nair, 2009; van Oudtshoorn, 2012).

### 2.2.3. Niche models

Of the original 1,996 records in the database, a subset of 1,488 records was selected for use in niche models. This subset comprises all records determined at species level and with precise locations. This number of records was further reduced to unique localities to avoid redundancy caused by duplication (where two or more records were recorded as having the same geographic coordinates for a species). After this, a final subset of 1,147 unique localities for 19 species was obtained (Table 3).

| **Species** | **Number of records with coordinates** | **Number of unique Localities** |
|---|---:|---:|
| *Themeda anathera* | 52 | 39 |
| *Themeda arguens* | 100 | 78 |
| *Themeda arundinacea* | 65 | 41 |
| *Themeda avenacea* | 65 | 51 |
| *Themeda caudata* | 41 | 30 |
| *Themeda cymbaria* | 17 | 16 |
| *Themeda hookeri* | 8 | 6 |
| *Themeda huttonensis* | 4 | 2 |
| *Themeda mooneyi* | 4 | 1 |
| *Themeda novoguinensis* | 3 | 3 |
| *Themeda quadrivalvis* | 50 | 43 |
| *Themeda sabarimalayana* | 1 | 1 |
| *Themeda saxicola* | 2 | 1 |
| *Themeda strigosa* | 2 | 1 |
| *Themeda tremula* | 48 | 32 |
| *Themeda triandra* | 921 | 729 |
| *Themeda trichiata* | 1 | 1 |
| *Themeda villosa* | 103 | 71 |
| **Total** | **1,487** | **1,146** |

Table 3. Number of records with coordinates and unique localities by species

Following Pliscoff (2013), only the species with more than 20 unique localities were modelled. The final dataset encompasses 1,114 unique localities corresponding to the distributions of nine species (*T. anathera*, *T. arguens*, *T. arundinacea*, *T. avenacea*, *T. caudata*, *T. quadrivalvis*, *T. tremula*, *T. triandra* and *T. villosa*).

Niche modelling for the nine selected species was performed using MaxEnt v. 3.3.3k (Phillips *et al.*, 2004; http://www.cs.princeton.edu/~schapire/maxent/). This software predicts habitat suitability of an organism using records of presence and environmental information. To achieve these results, MaxEnt implements an algorithm based on the principles of maximum entropy (Phillips *et al.*, 2006; Elith *et al.*, 2011). In comparison with other methods, the results obtained with MaxEnt are consistently robust, especially with few presence records (Elith *et al.*, 2006; Hernandez *et al.*, 2006). MaxEnt has been characterized as a flexible method, as the analysis can be performed varying a number of parameters which produce different levels of detail in the results (Pau *et al.*, 2013). Another example of its flexibility is related to the number and type of environmental information that can be incorporated in the analysis. MaxEnt can be performed using a wide range of environmental layers, which can be continuous (e.g. altitude) or categorical (e.g. type of soil). According to Elith *et al.* (2011), the software can manage a large set of correlated variables and still provide robust results. However, the inclusion of irrelevant environmental information is not recommended, as the algorithm will force the inclusion of these variables leading to overfitting of the model. For the reasons enumerated above, MaxEnt has been widely used since was developed and the range of studies using this software covers all possible applications related to distributional patterns (Baldwin, 2009; Pliscoff, 2013).

Environmental surfaces used in this analysis were obtained from the WorldClim database (Hijmans *et al.*, 2005; http://www.worldclim.org/). Climate data were used at a resolution of 2.5 arc-minutes (altitude and 19 bioclimatic surfaces; see Table 4 for detailed list of the correlates). The size and format of each surface was edited in ArcGIS v. 9.3 (Esri, 2008) and clipped to the following extreme coordinates: 50°S – 50°N and 30°W – 180°E. The area enclosed by these coordinates comprised the maximum extension of the genus and includes the African continent, tropical and subtropical Asia and Oceania.

| Code | Name of the variable |
|---|---|
| Bio1 | Annual mean temperature |
| Bio2 | Mean diurnal range (mean of monthly (max temp - min temp)) |
| Bio3 | Isothermality (bio2/bio7) (* 100) |
| Bio4 | Temperature seasonality (standard deviation *100) |
| Bio5 | Max. temperature of warmest month |
| Bio6 | Min. temperature of coldest month |
| Bio7 | Temperature annual range (bio5-bio6) |
| Bio8 | Mean temperature of wettest quarter |
| Bio9 | Mean temperature of driest quarter |
| Bio10 | Mean temperature of warmest quarter |
| Bio11 | Mean temperature of coldest quarter |
| Bio12 | Annual precipitation |
| Bio13 | Precipitation of wettest month |
| Bio14 | Precipitation of driest month |
| Bio15 | Precipitation seasonality (coefficient of variation) |
| Bio16 | Precipitation of wettest quarter |
| Bio17 | Precipitation of driest quarter |
| Bio18 | Precipitation of warmest quarter |
| Bio19 | Precipitation of coldest quarter |

Table 4. List of bioclimatic variables used for niche models

To identify variables with a low participation in the models I ran MaxEnt using its default parameters and including all 20 correlates. These results showed two variables with minimal contribution (< 0.3%) to the models (mean temperature of driest and warmest quarter). Therefore, these two variables were excluded from subsequent analyses. I also found a medium (~ 7%) to high (~20%) contribution of altitude to the niche models of four species. According to Austin & Smith (1989), altitude has no direct physiological basis for predicting plant distribution. However, it has been used as an indirect gradient because it captures some of the variation among temperature, moisture, solar radiation and $CO_2$ levels (Pau *et al.*, 2013). Hence, I performed the analysis again without altitude to determine the degree to which the contribution of this variable was adopted by other related variables (e.g. mean annual temperature) across all species.

During the run without altitude, 17 environmental correlates were assessed. Based on this analysis, seven variables were identified as irrelevant to the models or as being overly correlated with other environmental variables in the models. Temperature annual range, mean temperature of wettest quarter and mean temperature of the coldest quarter made only marginal contributions to model fit. Additionally, these temperature variables were correlated with isothermality and mean annual temperature (C. Lehmann, UoE, pers. comm.). Another four variables were considered highly correlated to precipitation of warmest quarter (precipitation of the wettest month and precipitation of the warmest quarter) or precipitation of coldest quarter (precipitation of the driest month and precipitation of the driest quarter) (C. Lehmann, UoE, pers. comm.). Hence, precipitation of the wettest month, precipitation of the warmest quarter, precipitation of the driest month and precipitation of the driest quarter, were not used in the final analysis. Regarding altitude, I found that it has its own independent meaning within the models and hence altitude remained in the final model set.

A final set of 11 environmental correlates was used to model the environmental niche models of the nine species: altitude, mean annual temperature, mean diurnal range of temperature, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation seasonality, precipitation of warmest quarter and precipitation of the coldest quarter. These final 11 variables were selected based on my biological and ecological understanding of *Themeda*, to minimise correlations among environmental correlates within the models and to capture information about both mean and extreme climate conditions. Mean annual temperature, temperature seasonality, diurnal range and isothermality are known as key to the limiting the global distribution of $C_4$ grasses (C. Lehmann, UoE, pers. comm.). Mean annual precipitation is also considered as key to the distribution of $C_4$ grasses (Sage & Kubien, 2007, Edwards *et al.*, 2010; Edwards & Smith, 2010; Pau *et al.*, 2013). Rainfall seasonality is considered as key to understanding the limits of savanna (Lehmann *et al*., 2011). While other variables such as precipitation of warmest quarter and precipitation of the coldest quarter are representative of moisture available during the growing season.

For each of the nine species, ten replicates were executed using the default parameters and the ten replicates are synthesized by MaxEnt to produce a consensus model. The predictive accuracy of each consensus model was evaluated using an AUC value (area under the curve), calculated by MaxEnt. AUC values provide a measure of model accuracy relative to the ability of the model to predicts the occurrence of an organism across a landscape. These values typically range from 0.5–1.0, where values close to 0.5 indicate a fit no better than that expected by random, while a value of 1.0 indicates a perfect fit (Baldwin, 2009).

The consensus models are provided as maps of habitat suitability, at the same resolution of the environmental layers used and with values ranging from 0 (not suitable) to 1 (maximum suitability). These consensus were imported to ArcGIS v. 9.3, and niche suitability values reclassified.

The analysis regarding the relative importance of each environmental correlate was determined via their percent contribution to model fit, also known as jackknife test of variable importance.

## 2.3. RESULTS

### 2.3.1. Distribution of the genus

This section analyses the distribution of 1,828 specimens of *Themeda* representing 19 species. The distribution of five species was not considered in the results (Table 5), because I could not find specimens of these taxa in the herbaria consulted. However, based on the literature, the distribution of these five species is nested within the range of the remaining species described in this section (Table 5).

| Species | Country | Province | Source |
|---|---|---|---|
| *Themeda idjensis* | Indonesia | East Java | Jansen (1952) |
| *Themeda minor* | China | Xizang (Tibet) | Schouliang & Phillips (2006) |
| *Themeda pseudotremula* | India | Maharashtra | Potdar *et al.* (2003) |
| *Themeda unica* | China | Anhui, Zhejiang | Schouliang & Phillips (2006) |
| *Themeda yunnanensis* | China | Yunnan | Schouliang & Phillips (2006) |

Table 5. Distribution of species not sampled

*Themeda* is distributed across tropical and subtropical areas in the Old World (Figure 1). Its range covers more than 83° of latitude (42°51’S – 40°17’N) and 192° of longitude (12°30’W – 179°54’E), reaching areas with Mediterranean climate (south Mediterranean basin, western Cape in South Africa and western and south Australia). The genus is also present across a wide altitudinal range from sea level to 3,500 m in the Himalayan Mountains.

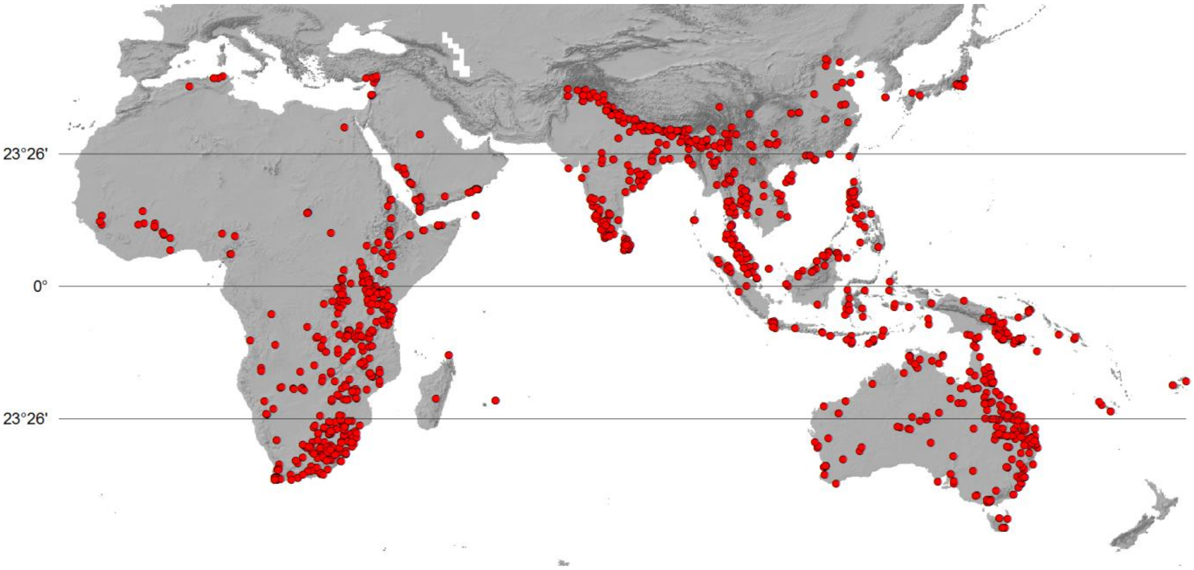

Figure 1. Distribution map of *Themeda*; based in collections from E and K.

### 2.3.2. Distribution of the species

Species have been organised into two groups according their distributional range. The first group comprise taxa with narrow distributions or present in only a single country, while the second group covers species with a broad distribution and present in two or more countries.

*Group 1. Taxa with narrow distribution*

***Themeda anathera* (Nees ex Steud.) Hack.** (Figure 2A).

Latitudinal range: 27°44’N – 34°57’N

Longitudinal range: 70°20’E – 95°38’E

Himalayan Mountains of Afghanistan, Pakistan and India and Nepal.

Open and shaded areas with dry or wet soil (near watercourses); grassland and forest on mountain slopes, stream banks, roadsides and cultivated fields; 750 – 2700 m.

***Themeda avenacea* (F.Muell.) T.Durand & B.D.Jacks.** (Figure 2A).

Latitudinal range: 17°9’S – 35°0’S

Longitudinal range: 114°9’E – 152°44’E

Australia.

Open and shaded areas near watercourses; grassland slopes, open forest, and stream banks; 100 – 900 m.

***Themeda cymbaria* Hack.** (Figure 2A).

Latitudinal range: 6°25’N – 11°48’N

Longitudinal range: 76°30’E – 81°22’E

Western Ghats Mountains of Southwest India and Sri Lanka.

Open areas; grassland, forest edges, hillsides and stream banks; 30 – 1900 m.

***Themeda helferi* Hack.** (Figure 2A).

Latitudinal range: 13°N – 24°38’N

Longitudinal range: 98°50’E – 99°0’E

China (Yunnan) and Myanmar (Tanintharyi or Tenasserim)

Stream banks and roadsides (Yunnan); ca. 600 m.

***Themeda hookeri* (Griseb.) A.Camus** (Figure 2A).

Latitudinal range: 25°2’N – 31°45’N

Longitudinal range: 84°50’E – 102°43’E

Himalayan Mountains of India, Nepal and China.

Open and shaded areas; mountain slopes, rocky places and cultivated fields; 1100 – 3400 m.

***Themeda huttonensis* Bor** (Figure 2A).

Latitudinal range: 25°40’N – 26°0’N

Longitudinal range: 94°37’E – 95°0’E

Nagaland Mountains in India.

Hillsides, near watercourses and stream banks; ca. 1500 m.

***Themeda mooneyi* Bor** (Figure 2A).

Latitudinal range: 18°32’N – 18°34’N

Longitudinal range: 82°56’E – 82°58’E

Eastern Ghats in Odisha State, India. Recorded twice in the vicinity of Pottangi village.

Granite cliffs; 1000 – 1200 m.

***Themeda novoguineensis* (Reeder) Jansen** (Figure 2B).
Latitudinal range: 9°0’S – 10°11’S
Longitudinal range: 146°57’E – 149°23’E
Central province in Papua New Guinea.
Open areas; grassland, savanna, forest edges, stream banks; 10 – 50 m.

***Themeda sabarimalayana* Sreek. & V.J.Nair** (Figure 2B).
Latitudinal range: 9°21’N – 9°23’N
Longitudinal range: 77°7’E – 77°9’E
Western Ghats in the Kerala State, India. Recorded once around Sabarimala village.
Forest edges and hillsides; ca. 450 m.

***Themeda saxicola* Bor** (Figure 2B).
Latitudinal range: 18°56’N – 18°58’N
Longitudinal range: 83°3’E – 83°5’E
Eastern Ghats in the Odisha State, India. Recorded once in the vicinity of Raisili village.
Forest edges and hillsides; in shallow soil over granite gneiss; ca. 950 m

***Themeda strigosa* (Ham. ex Hook.f.) A.Camus** (Figure 2B).
Latitudinal range: 25°21’N – 25°23’N
Longitudinal range: 86°27’E – 86°29’E
Bihar State, India.
Open areas; forest and waste ground; altitude not recorded.

***Themeda tremula* (Nees ex Steud.) Hack.** (Figure 2B).
Latitudinal range: 6°18’N – 15°18’N
Longitudinal range: 74°18’E – 80°57’E
Western Ghats in Southwest India and Sri Lanka
Open areas with dry or wet soil (near watercourses); grassland, forest edges, steep cliffs and slopes near mountain tops, swamp banks, waste ground, roadsides and cultivated fields; 100 – 2100 m.

***Themeda trichiata*** **S.L.Chen & T.D.Zhuang** (Figure 2B).

Latitudinal range: 18°20’N – 19°0’N

Longitudinal range: 109°4’E – 109°30’E

Autonomous region of Guangxi and provinces of Hainan and Yunnan, China. In this study, only samples from Hainan were examined.

Open and dry areas; grasslands and mountain slopes; ca. 350 m.

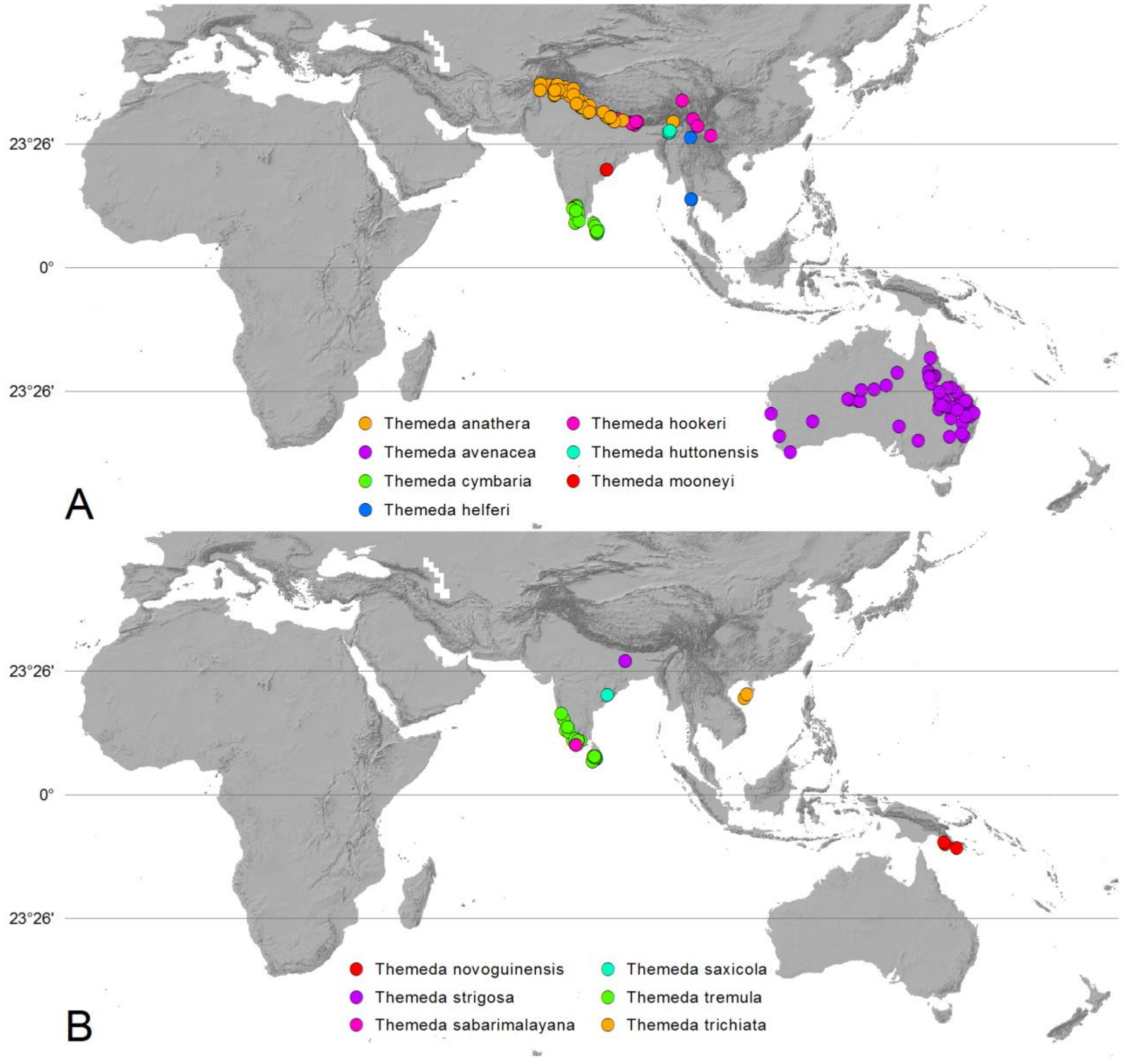

Figure 2. Distribution maps for taxa with narrow distribution. A. *Themeda anathera*, *Themeda avenacea*, *Themeda cymbaria*, *Themeda helferi*, *Themeda hookeri*, *Themeda huttonensis* and *Themeda mooneyi*; B. *Themeda novoguinensis*, *Themeda strigosa*, *Themeda sabarimalayana*, *Themeda saxicola*, *Themeda tremula* and *Themeda trichiata*.

*Group 2. Taxa with wide distribution*

***Themeda arguens*** **(L.) Hack.** (Figure 3A).

Latitudinal range: 27°0’S – 17°52’N

Longitudinal range: 80°35’E – 179°54’E

Open and shaded areas with dry or wet soil (near watercourses); grassland, savanna, open forest, swamp and forest edges, schist cliffs, stream banks, roadsides, railroads, cultivated fields; 0 – 1400 m.

***Themeda arundinacea*** **(Roxb.) A.Camus** (Figure 3B).

Latitudinal range: 2°42’N – 30°27’N

Longitudinal range: 87°1’E – 121°0’E

Open areas; grassland, open forest, swamp and forest edges, mountain slopes; stream banks, roadsides, cultivated fields; 10 – 2000 m.

***Themeda caudata*** **(Nees ex Hook. & Arn.) A.Camus** (Figure 3C).

Latitudinal range: 22°10’S – 30°23’N

Longitudinal range: 78°28’E – 166°32’E

Open areas with dry or wet soil; savanna, forest edges, hillsides, stream banks, roadsides, railroads, cultivated fields; 0 – 2500 m.

***Themeda quadrivalvis*** **(L.) Kuntze** (Figure 3D).

Latitudinal range: 20°18’S – 33°20’N

Longitudinal range: 44°3’E – 177°28’E

Open and shady areas with dry or wet soil (near watercourses); grassland, open forest, hillsides, stream banks, roadsides; 0 – 2000 m.

***Themeda triandra*** **Forssk.** (Figure 3E).

Latitudinal range: 42°51’S – 40°17’N

Longitudinal range: 12°30’W – 166°27’E

Open areas near watercourses; grassland, savanna, open forest, swamp edges, hillsides, stream banks, roadsides, cultivated fields, plantations; 0 – 3500 m.

***Themeda villosa* (Lam.) A.Camus** (Figure 3F).

Latitudinal range: 10°10’S – 30°43’N

Longitudinal range: 80°23’E – 128°16’E

Open areas near watercourses; savanna, swamp and forest edges, hillsides, stream banks, roadsides and margins of cultivated fields; 0 – 2500 m.

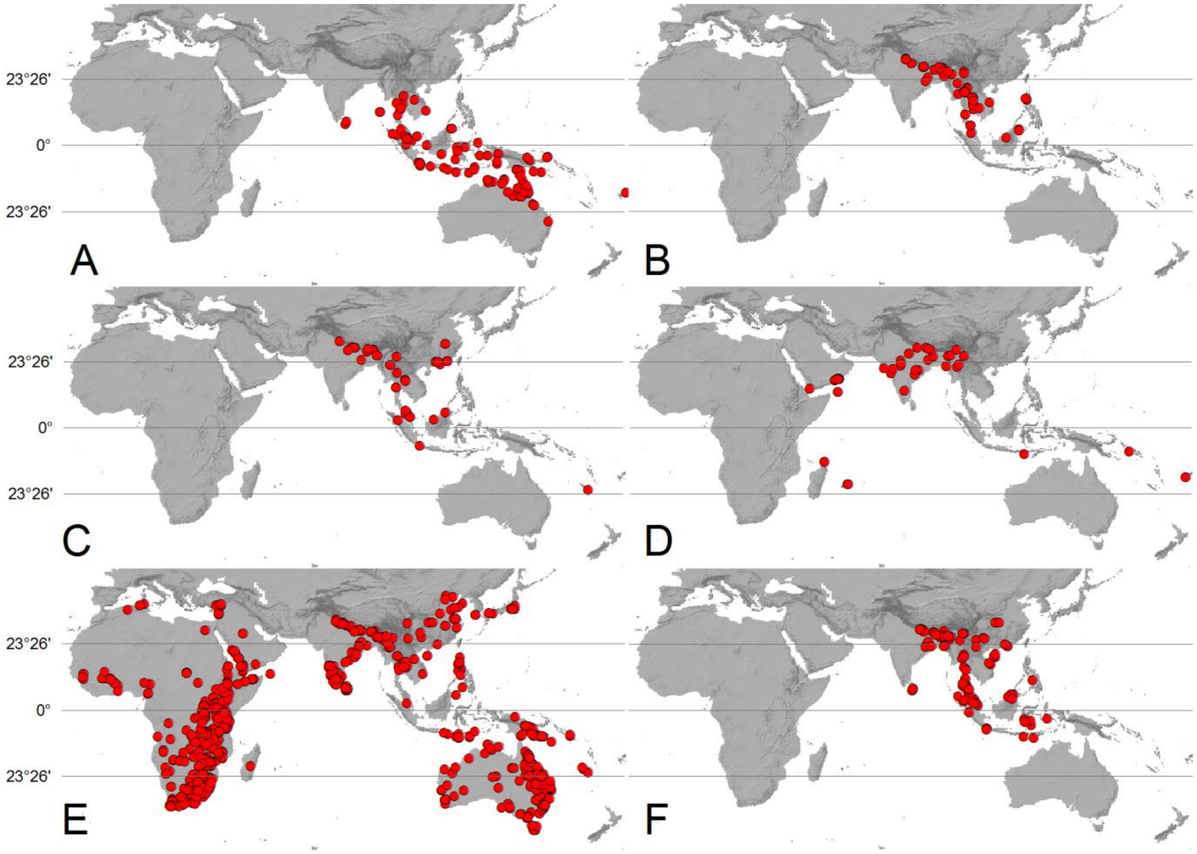

Figure 3. Distribution maps for taxa with wide distribution. A. *Themeda arguens*; B. *Themeda arundinacea*; C. *Themeda caudata*; D. *Themeda quadrivalvis*; E. *Themeda triandra*; F. *Themeda villosa*.

### 2.3.3. Distribution of species diversity

At a country level (Figure 4A), the centre of diversity is located in India, where 16 out of 19 species included in this analysis are found. The number of species per country then decreases gradually eastward with eight species in China to two in the Pacific Islands. However, to the west the number of species drops dramatically. Two species are found in the Middle East (*T. quadrivalvis* and *T. triandra*) and only *T. triandra* across continental Africa. If the species not included in this analysis are incorporated, the centre of diversity would not change. However, the number of taxa would change to 17 species in India, 11 in China and seven in Indonesia.

Country level results are influenced by country area. For example, high species richness in China and Indonesia is correlated with their geographic extension (bigger areas result in a bigger number of species). In comparison, the smaller area of Laos and Cambodia result in a low species richness values, though, in these countries the lack of collections should also be considered when interpreting patterns of species richness.

To counter the problems of this analysis by country, I also examined species richness using units of regular size of cells of 4°x4° latitude and longitude. These results mirror the same general trend described for countries (Figure 4B). However, the maximum number of species occurs across the eastern Himalayan region in Nepal, northeast India, Bhutan, and Myanmar, with five to six species.

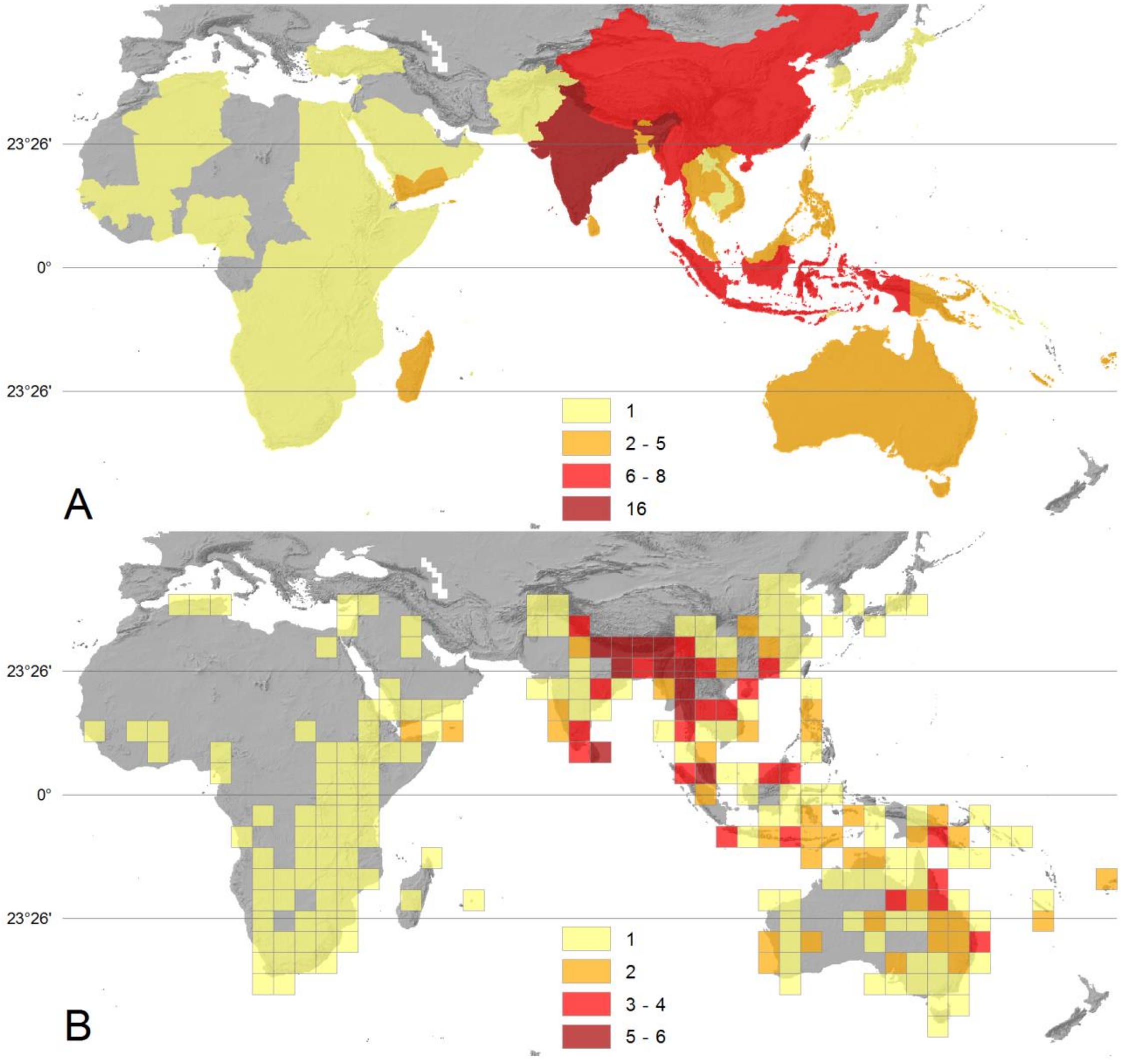

Figure 4. Number of species of *Themeda* by country and cells of 4° latitude x 4° longitude.

### 2.3.4. Niche models

Niche models were performed for nine species; one cosmopolitan (*T. triandra*), five regionally restricted (*T. arguens*, *T. arundinacea*, *T. avenacea*, *T. caudata*, *T. quadrivalvis* and *T. villosa*) and two endemics (*T. anathera* and *T. tremula*).

All models present AUC values <0.90, except *T. triandra* (Table 6), and this is likely to be due to > 500 values being used to define the niche model for this species.

| **Species** | **AUC values** | **Percent of contribution** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **Altitude** | **Bio1** | **Bio2** | **Bio3** | **Bio4** | **Bio5** | **Bio6** | **Bio12** | **Bio15** | **Bio18** | **Bio19** |
| *Themeda anathera* | 0.984 | 24.7 | 1.2 | 0.2 | 3.7 | 13.1 | 3.8 | 3.2 | 0.2 | 4.8 | 20.3 | 24.9 |
| *Themeda arguens* | 0.956 | 16.5 | 2 | 0.8 | 12.9 | 10.8 | 0 | 17.4 | 0.9 | 1.2 | 35.6 | 1.9 |
| *Themeda arundinacea* | 0.971 | 2.7 | 1 | 3.5 | 10.9 | 0.1 | 0.8 | 0.7 | 48.3 | 3.8 | 15.2 | 12.9 |
| *Themeda avenacea* | 0.973 | 4.5 | 3 | 8.7 | 24.6 | 20 | 1.8 | 0.2 | 2.7 | 1.6 | 12.8 | 20.1 |
| *Themeda caudata* | 0.939 | 2.5 | 0.2 | 0 | 2.3 | 0.4 | 0.2 | 0.2 | 26.7 | 0.9 | 60.2 | 6.4 |
| *Themeda quadrivalvis* | 0.916 | 1.8 | 7 | 21.6 | 17.4 | 19 | 0.3 | 0.5 | 8.1 | 2.3 | 9.7 | 12.1 |
| *Themeda tremula* | 0.994 | 7 | 0.1 | 9.7 | 24 | 4.2 | 0 | 0.2 | 30.4 | 0.4 | 0.2 | 23.8 |
| *Themeda triandra* | 0.882 | 9 | 15.2 | 0.5 | 8.1 | 30.5 | 4.4 | 1.5 | 22.1 | 2.5 | 0.4 | 5.8 |
| *Themeda villosa* | 0.943 | 2.8 | 1.4 | 1 | 5.4 | 0.8 | 0.4 | 0.4 | 46.3 | 0.2 | 32.6 | 8.7 |

Table 6. AUC values of models and percent of contributions of variables by species; in orange, group of variables that complete 90% of contribution; in red, variables with the highest percent of contribution by species; Bio1. Annual mean temperature; Bio2. Mean diurnal range; Bio3. Isothermality; Bio4. Temperature seasonality; Bio5. Max. temperature of warmest month; Bio6. Min. temperature of coldest month; Bio12. Annual precipitation; Bio15. Precipitation seasonality; Bio18. Precipitation of warmest quarter; Bio19. Precipitation of coldest quarter

***Themeda anathera* (Nees ex Steud.) Hack.** (Figure 5).

91.6% of variation of the model is explained by six variables (three of precipitation, two of temperature and altitude; Table 6). The highest contributions are by precipitation of the coldest quarter (24.9%) and altitude (24.7%), and together they account for ~50% of the variation in the model. The third most important variable is precipitation of the warmest quarter (20.3%).

*Themeda anathera* is endemic to the high altitude region of the western Himalaya (Figure 2A), which receives precipitation throughout the year, but most importantly during the coldest season (Appendix 2).

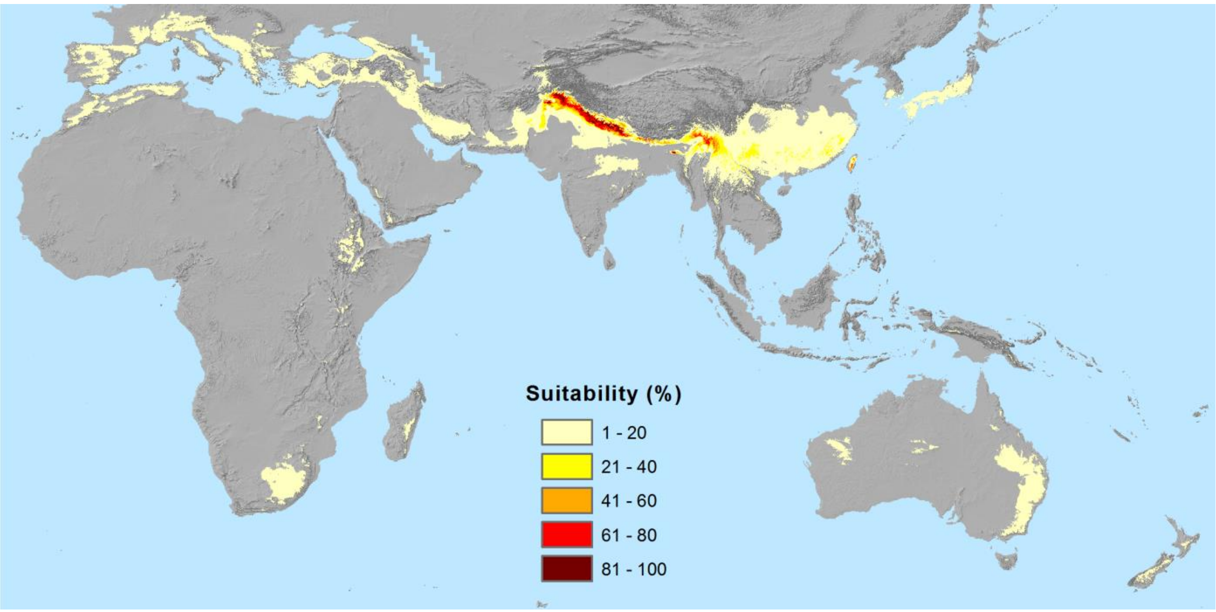

Figure 5. Habitat suitability for *Themeda anathera*.

***Themeda arguens* (L.) Hack.** (Figure 6).

Five variables explain 93.2% of the variation of the model for this species (three related to temperature and one of precipitation, plus altitude; Table 6). The most important is precipitation of the warmest quarter (35.6%), followed by the minimum temperature of the coldest month (17.4%) and altitude (16.5%).

*Themeda arguens* is a widely distributed species found almost exclusively in the tropics of SE Asia and Australia (Figure 3A), which are regions of medium to high precipitation during the warmest season where the minimum temperatures of the coldest month are always above 0°C (Appendix 2). High habitat suitability is predicted for coastal Mozambique, Tanzania and western Madagascar, although the species is not recorded there.

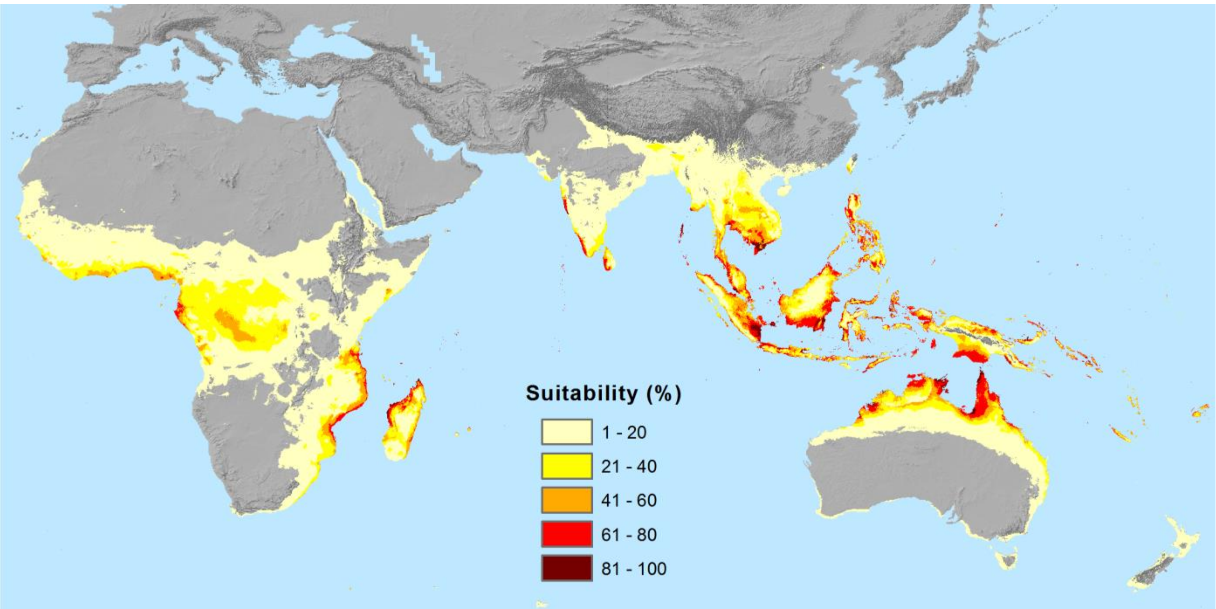

Figure 6. Habitat suitability for *Themeda arguens*.

***Themeda arundinacea* (Roxb.) A.Camus** (Figure 7).

Four variables explain more than 90% of the variation of the model (three variables related to precipitation and one of temperature; Table 6). Mean annual precipitation explains 48.3% of the habitat suitability, followed by the precipitation of the warmest quarter (15.2%) and coldest quarter (12.9%).

The distribution of *T. arundinacea* comprises tropical SE Asia and subtropical India (Figure 3B) and within this region, the species prefers areas with high amounts of annual precipitation, especially during the warm season, within SE Asia and eastern India (Appendix 2).

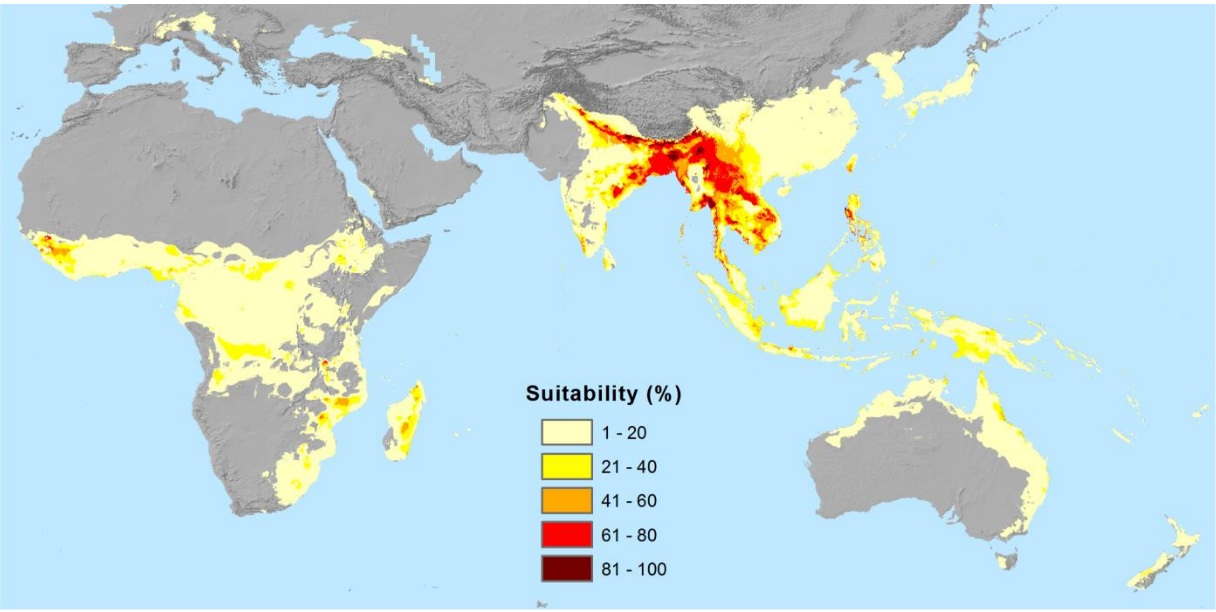

Figure 7. Habitat suitability for *Themeda arundinacea*.

***Themeda avenacea* (F.Muell.) T.Durand & B.D.Jacks.** (Figure 8).

The 90.7% of the habitat suitability model is explained by six variables (three temperature, two precipitation and altitude; Table 6). The most important variable explaining the variation of the model is isothermality (24.6%). However, temperature seasonality and precipitation of the coldest quarter show values similar to isothermality (above 20%).

*Themeda avenacea* is found in the tropical and subtropical areas of Australia (Figure 2A). These areas are characterized by medium changes in daily and annual temperature and low precipitation during the coldest season (Appendix 2).

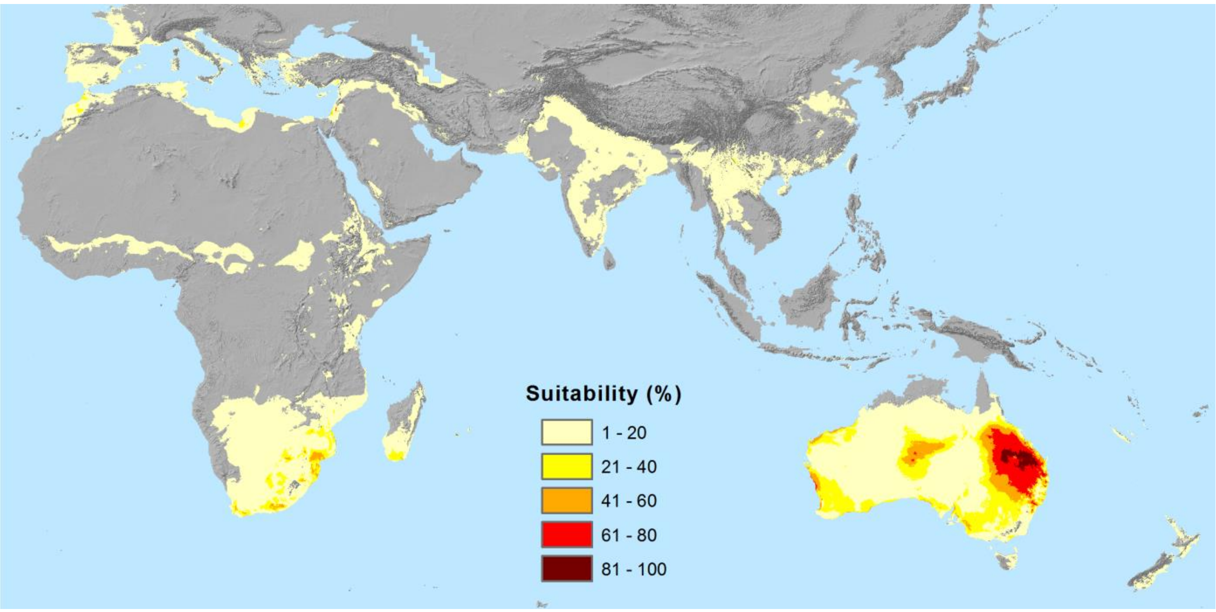

Figure 8. Habitat suitability for *Themeda avenacea*.

***Themeda caudata* (Nees ex Hook. & Arn.) A.Camus** (Figure 9).

Three environmental correlates account for 93.3% of environmental suitability, and all of them are related to precipitation (Table 6). Warm season precipitation is by far the most important variable with 60.2% of variation of the model. The remaining most important variables are mean annual precipitation and precipitation of the coldest quarter, each explain 26.7% and 6.4% of the model respectively.

*Themeda caudata* grows from India to the Pacific Islands (Figure 3C). Within this range it is found in areas with high rainfall during the warm season (Appendix 2).

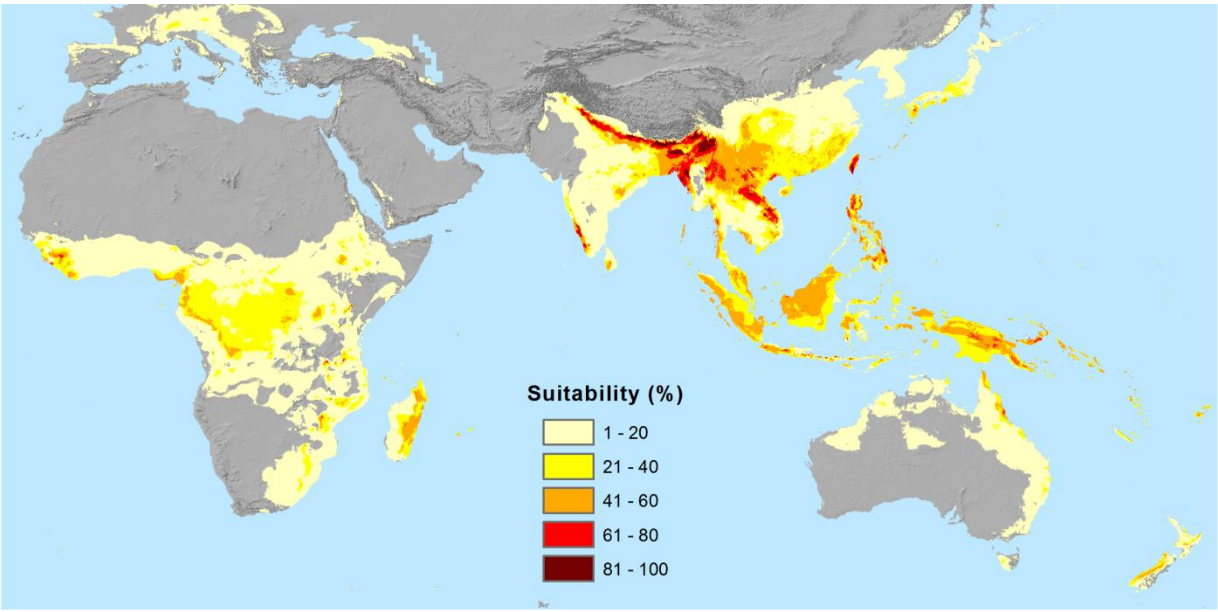

Figure 9. Habitat suitability for *Themeda caudata*.

***Themeda quadrivalvis* (L.) Kuntze** (Figure 10).

The 94.9 % of the variation of the model is explained by seven correlates (four of temperature and three of precipitation; Table 6). In this case, the three most important variables are related to temperature. Mean diurnal range contributes 21.6% of the model fit, while temperature seasonality and isothermality contribute 19% and 17.4%, respectively.

The distribution of *T. quadrivalvis* covers mainly tropical region between Middle East and China (Figure 3D). This range includes areas where the temperature is more or less stable both diurnally and through the year (Appendix 2). High habitat suitability is predicted for areas outside its native range (e.g. New Caledonia), and in some of these it grows as an introduced species (MacKee, 1994).

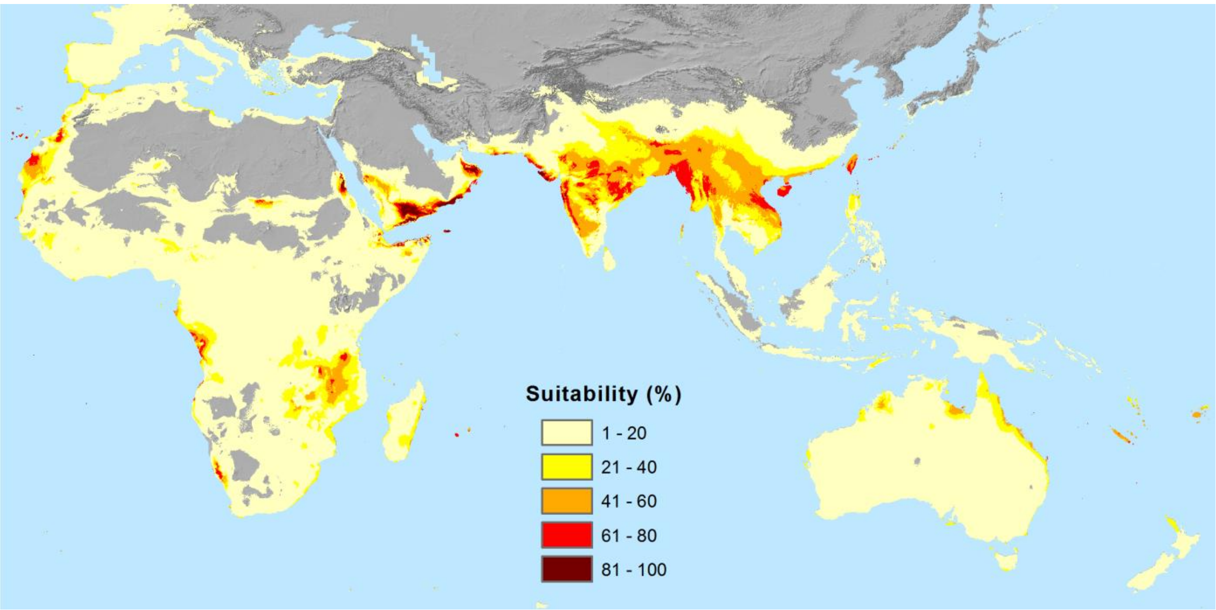

Figure 10. Habitat suitability for *Themeda quadrivalvis*.

***Themeda tremula* (Nees ex Steud.) Hack.** (Figure 11).

Three variables of temperature and two of precipitation explain the 94.9% of the variation of the model (Table 6). The highest value of contribution is from annual precipitation with 30.4% of the variation of the model, followed by isothermality (24%) and precipitation of the coldest quarter (23.8%).

*Themeda tremula* is found in SW India and Sri Lanka (Figure 2B), areas which are characterized by high annual rainfall and high isothermality. High habitat suitability is predicted for areas in SE Asia and the Philippines, although the species is not recorded there (Appendix 2).

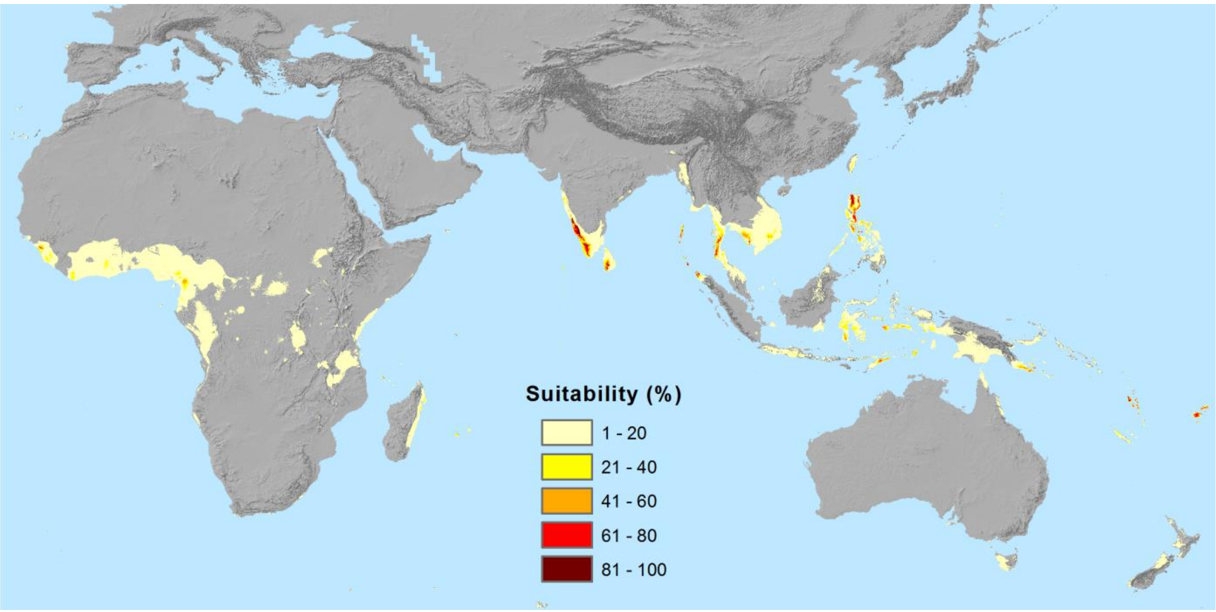

Figure 11. Habitat suitability for *Themeda tremula*.

***Themeda triandra* Forssk.** (Figure 12).

Six variables explain 90.7% of the variation of the model (three variables relating to temperature, two of precipitation and altitude; Table 6). Of these correlates, the most important is temperature seasonality (30.5%), followed by annual precipitation (22.1%) and mean annual temperature (15.2%).

*Themeda triandra* is a cosmopolitan species reaching temperate climatic zones (Figure 3E). From the climatic point of view, the majority of its distribution, which is in the tropics, is characterized by high mean annual temperatures with low temperature seasonally throughout the year (Appendix 2).

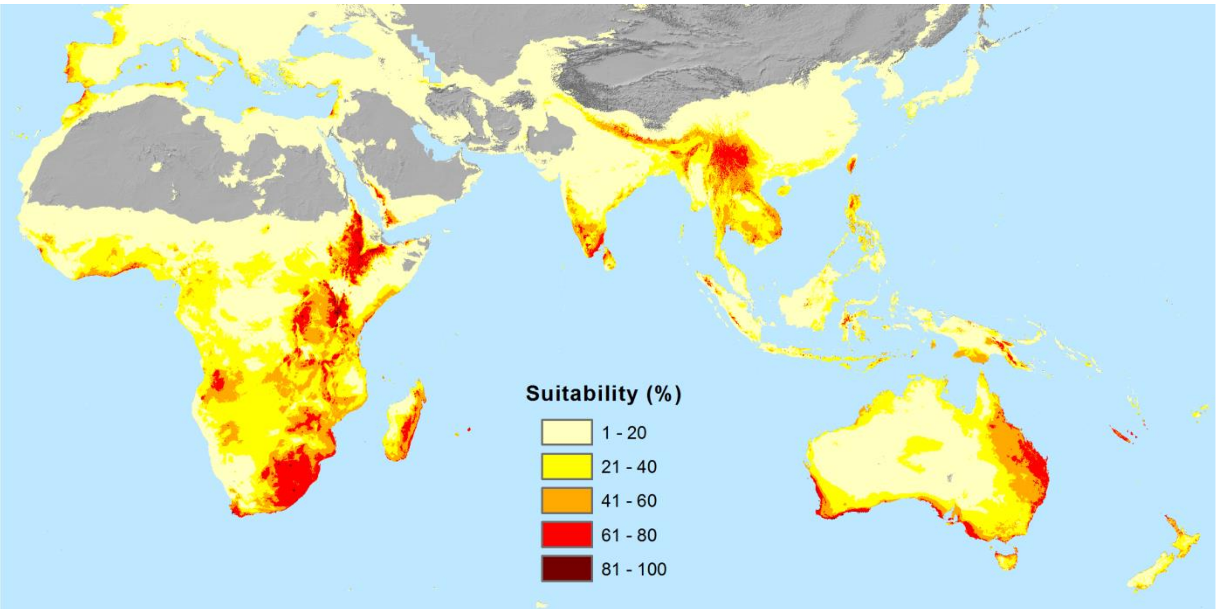

Figure 12. Habitat suitability for *Themeda triandra*.

***Themeda villosa* (Lam.) A.Camus** (Figure 13).

The 93% of variation of this model is explained by four variables (three of which are related to precipitation and only one to temperature; Table 6). The highest contribution to the model is made by annual precipitation (46.3%) while the lowest is attributed to isothermality (5.4%).

*Themeda villosa* grows in tropical and subtropical regions of SE Asia (Figure 3F). Comparing its distribution and annual precipitation it is clear that this species prefers areas with high values of rainfall, concentrated mainly in the warm season (Appendix 2).

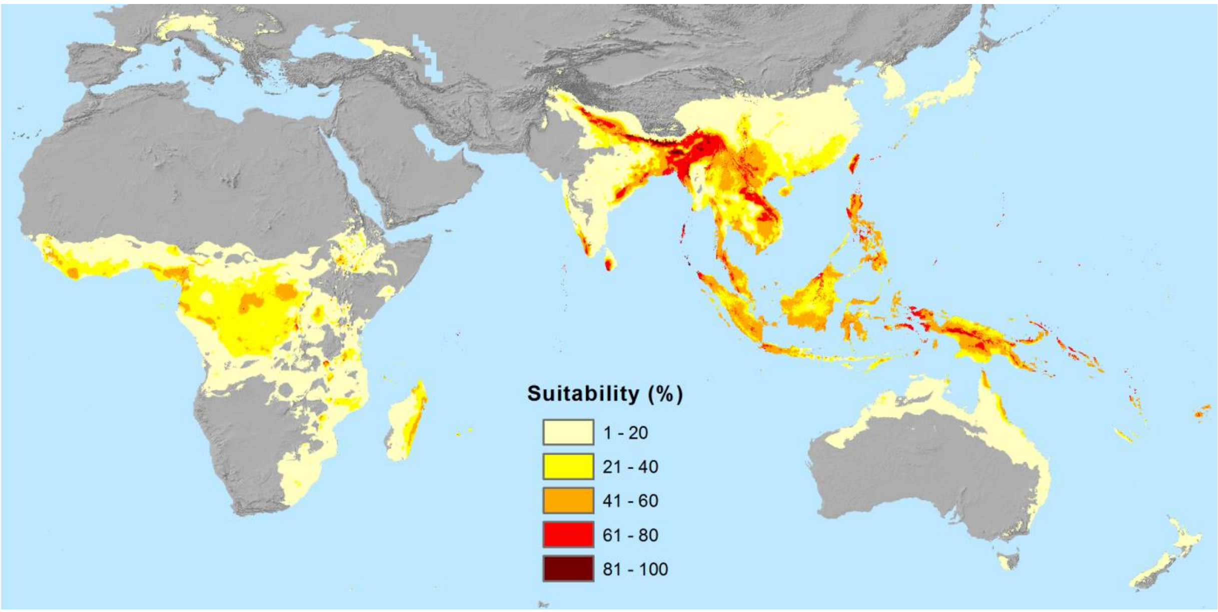

Figure 13. Habitat suitability for *Themeda villosa*.

## 2.4. DISCUSION

*Themeda* comprises one cosmopolitan species, six regionally restricted species and 12 species with narrow distributions. *Themeda triandra* is a widespread cosmopolitan species with the largest range of distribution, extending into the temperate zone in the northern and southern hemispheres. The geographical range covered by *T. triandra* encompasses the distribution of all other species within the genus. Four of the six species with regional distributions are restricted to central and southeast Asia (*T. arguens*, *T. arundinacea*, *T. caudata* and *T. villosa*) and one is endemic to Australia (*T. avenacea*).

The distribution of *T. quadrivalvis* is difficult to determine as its original range has not been established due to multiple records of it being recorded as an invasive and that in past identifications it is often confused with *T. triandra*. Based on my assessment I believe that the original range of this species covers the North Hemisphere only, ranging from the Middle East to China.

Of the 12 species with narrow distributions, six are known from only a few locations (*T. huttonensis*, *T. mooneyi*, *T. novoguinensis*, *T. strigosa*, *T. sabarimalayana* and *T. saxicola*), while the remaining six have been widely collected throughout their distributions (*T. anathera*, *T. cymbaria*, *T. hookeri*, *T. tremula* and *T. trichiata*).

The centre of diversity is located in India with 16 species. The high diversity of this region is determined by the presence of nine of the 12 *Themeda* species with a narrow distribution (*T. anathera*, *T. cymbaria*, *T. hookeri*, *T. huttonensis*, *T. mooneyi*, *T. strigosa*, *T. sabarimalayana*, *T. saxicola* and *T. tremula*).

All niche models show areas of climatic suitability for each species that are bigger than the known ranges of distribution, demonstrating that there are other variables constraining the climatic niches to the real areas of distribution. Four variables appear important for all nine species: isothermality, annual precipitation and precipitation of the warmest and coldest quarter. At least two of these variables are always highly correlated with the distribution of all species.

The most important correlates of the distributions of *T. avenacea, T. quadrivalvis* and *T. triandra* are related to temperature, and these are isothermality, mean diurnal range and temperature seasonality. All these correlates indicate how variable temperature is over a determined period of time. The distributions of these three species are so different it is hard to discern commonalities that underlie the common finding that temperature variables are most influential in determining their distribution. The widespread *T. triandra* is found mostly in tropical regions but also in some subtropical/temperate areas (Figure 3E), such as where *T. avenacea* grows in Australia (Figure 2A). *Themeda quadrivalis* is distributed from Middle East to China and  its range is largely tropical or subtropical (Figure 3D), but some of its Himalayan records are distributed in altitudes close to 2000 m, where  the climate is relatively temperate. Because *T. triandra* and *T. quadrivalvis* respond to similar variables in the same way, they should have similar morphological adaptations to their environments. Perhaps, this is the reason why *T. triandra* and *T. quadrivalvis* are morphologically similar and thus, they are often confused in the herbarium.

The distribution of *Themeda triandra* is an interesting case study, as it is largely tropical but also reaches temperate regions, for example there are some records from China and Australia at 40°N and 42°S. These records presumably provide the model the information to infer that the global distribution is limited by temperature seasonality. It is clear that over the majority of its distribution, which is tropical, *T. triandra* prefers areas where the temperature does not change through the year. The second most important variable in limiting the model of *T. triandra* was annual precipitation. *Themeda triandra* is usually found in areas with 200 to 3000 mm of rainfall per year (sometimes up to 5000 mm). Areas with higher amounts of precipitation may produce a different type of vegetation, allowing the recruitment of woody species, which produce a closed-canopy. *Themeda triandra* is non-viable in this type of environments as it needs high radiation for photosynthesis. The presence of *T. triandra*, as a key grass species in the ground layer of savannas, appears defined by an interaction between temperature seasonality and annual precipitation. During the growing season *T. triandra*, requires high temperatures for performing $C_4$ photosynthesis and it cannot compete with other species growing in areas with high amounts of precipitation.

The distributions of *T. anathera*, *T. arguens*, *T. arundinacea*, *T. caudata*, *T. tremula* and *T. villosa* appear more closely related to variables of precipitation (annual precipitation, precipitation of warmest quarter and precipitation of the coldest quarter). These six species are found in areas with high annual rainfall within tropical and subtropical regions of India and SE Asia. *Themeda arguens*, *T. arundinacea*, *T. caudata* and *T. villosa* can tolerate a dry season (though wet season rainfall must be high), while for *T. anathera* and *T. tremula* require rainfall more evenly distributed throughout the year. *Themera arundinacea*, *T. caudata* and *T. villosa* are characterized as being very tall grasses (up to 6 m; Chapter 1). To reach these heights they require high precipitation.

It is interesting to observe that variables of temperature and precipitation vary in importance for different species within the same genus. Previous studies have argued whether temperature or precipitation are the key factors limiting the distribution of $C_4$ grasses. This study demonstrates that within one $C_4$ genus, both factors are critical, but their relative importance depends upon the species. The results highlight a geographic scale issue in considering this problem of the control of distribution of $C_4$ grasses. At a global scale, exemplified by the case of *T. triandra*, temperature seasonality is critical, but within the tropics, for $C_4$ grasses with more restricted distributions, rainfall seasonality is an important control, as these species are essentially not exposed to as much temperature influence.

# CHAPTER 3. FUNCTIONAL TRAITS IN THEMEDA

## 3.1. INTRODUCTION

Functional traits are measurable features (morphological, physiological or phenological), that affect the growth, reproduction and survival of an organism (Violle *et al.*, 2007). Different individuals of the same species can cope with a range of environmental conditions through the variation of their functional traits (Schlichting, 1989). Thus, trait variation is the physical expression of the how organisms perform their life processes under different environmental conditions.

Determining the relationships between plant form and environments has been one of the central goals of functional ecology (Ackerly *et al.*, 2002). Therefore, trait-based approaches have attracted increasing interest in the last two decades (Cornelissen *et al.*, 2003; Violle *et al.*, 2007; Pérez-Harguindeguy *et al.*, 2013).

Functional traits can be used to answer different questions (Violle *et al.*, 2007), depending whether they have been measured within or among species. Much of the research about functional traits has focused on differences among species (Mitchell & Bakker, 2014). The study of the trait variation among organism enables ecologists to identify functional groups (Schmidt *et al.*, 2011; Zwarg *et al.*, 2012), relate the distribution of these groups to environmental conditions (Thuiller *et al.*, 2004; Leps *et al.*, 2011; Schellberg & da S. Pontes, 2012; Cayssials & Rodríguez, 2013; Schmidt *et al.*, 2013) and to make predictions about community structure (Lavorel & Garnier, 2002; McGill *et al.*, 2006). From this type of study, there is growing evidence that variation in plant traits is associated with many important ecological processes and services at the scale of ecosystems, landscapes or biomes (see Lavorel & Garnier, 2002; Díaz *et al.*, 2007 for a comprehensive summary).

On the other hand, the number of studies at intraspecific level is smaller in comparison to publications at interspecific level, mainly because a useful trait in community ecology may not be useful at species level (Mitchell & Bakker, 2014). This is the result of a trait having high variation at community level, but low variation when measured within species. One way to counteract this effect is through the study of species that are widely distributed (Nicola *et al.*, 2014). These species inhabit a number of environments, resulting in more variation in functional traits. In this sense, trait variation within species is of special interest since it may provide the opportunity to observe divergence and speciation (Mascó *et al.* 2004; Chalcoff *et al.* 2008).

The best traits to measure are those relevant to specific research questions. The selection of these traits depends on the ecological characteristics of the study species, the geographic scale of the study and practical considerations (Pérez-Harguindeguy *et al.*, 2013). For these reasons, plant functional ecologists have generated a refined list of traits that are robust indicators of plants ecological strategies (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013). Some of these traits are well known and relatively easy to quantify, and therefore widely used.

Plant height is a quantitative trait (Schellberg & da S. Pontes, 2012), and has been associated with competitive vigour and whole plant fecundity (Cornelissen *et al.*, 2003). The amount of light available is a key environmental factor, which affects the shape and function of plants through photosynthesis (Cayssials & Rodríguez, 2013), hence, being taller than neighbours is a competitive advantage (Westoby *et al.*, 2002; Moles *et al.*, 2009). At the same time, such competition involves a trade-off between photosynthetic gains and the energetic cost of supporting leaves and lifting water (Givnish, 1982). Other studies have related plant height to climatic conditions such as precipitation, where short stature represents an adaptation to arid conditions (Coughenour, 1985; Milchunas *et al.*, 1988). The relationship between altitude and plant height is an inverse correlation, meaning that increases in altitude are often associated with decreases in plant height (Kappelle *et al.*, 1995; Wilcke *et al.*, 2008).

Leaf traits play an important role in carbon assimilation, water relations and energy balance (Ackerly *et al.*, 2002), and several studies have related the variation of these traits with climate, geology, altitude and latitude (Parkhurst & Loucks, 1972; Givnish, 1987; Cornelissen, 1999; Westoby *et al.*, 2002; Milla & Reich, 2007; Niklas *et al.*, 2007; Poorter & Rozendaal, 2008 ; Royer *et al.*, 2008). In warm and sun-exposed environments, a reduction in leaf area or leaf width is considered an advantageous adaptation, because it reduces the boundary layer, helping to maintain favourable leaf temperatures and higher photosynthetic water-use efficiency (Parkhurst & Loucks 1972; Givnish & Vermeij 1976). In other environments, reductions of leaf size (or leaf area) can be interpreted as a response to conditions of stress (light, water or nutrient; Givnish, 1988; Cunningham *et al.*, 1999; Fonseca *et al.*, 2000).

In this chapter I want to answer two simple questions using the functional trait approach. The first question is whether the widely distributed, *T. triandra*, is more variable in its functional traits in comparison to its congeneric species, and the second aims to determine what kind of relationship exists between the variation experienced by the functional traits of *T. triandra* and environmental factors that limit their distribution.

## 3.2. MATERIALS AND METHODS

### 3.2.1. Definition and measurement of plant functional traits

Data of functional traits were obtained from herbarium specimens from the Royal Botanic Garden Edinburgh and the Royal Botanic Gardens, Kew.

The definitions of functional traits selected in this study followed Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013). These concepts were adjusted considering the use of herbarium specimens and the taxonomy of *Themeda*. Here I present the background gathered during the process and the final definition of the functional traits studied.

*Plant height*

According to Pérez-Harguindeguy *et al.* (2013: 175), plant height is the “shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) on a plant and the ground level”. This definition makes clear that the height of the inflorescence is not to be considered in the measurement of this functional trait. Nevertheless, it also states that the objective is to have a measure of the height of the foliage (photosynthetic tissues). In this respect, *Themeda* species possess a complex inflorescence, which comprises a collection of branches and leaf-like structures (spathes), which participate in the process of photosynthesis. Therefore, in this study I defined plant height as the shortest distance between the roots and the upper spathe of the herbarium specimens. This functional trait was impossible to measure in many herbarium specimens that comprise only the inflorescence.

### *Leaf traits*

When the measurements are taken in the field, Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013) recommend the selection of leaves in terminal and sun-exposed shoots, prioritising the youngest and fully expanded leaves, which are presumably more photosynthetically active. At the same time, they recommend avoiding leaves with signals of pathogen or herbivore attack. In species with simple leaves, as in grasses, only the lamina is considered for measurement of leaf traits, and structures such as the leaf sheath are excluded.

I had to adapt these protocols to work with herbarium specimens. Specimens with symptoms of diseases (e.g. fungus) or without suitable leaves (e.g. broken or rolled leaves) were not used. In other specimens, I identified leaves likely to be more photosynthetically active from the middle zone of the culm. These were the leaves which were new and fully expanded at the time of collection. Incomplete specimens (plants without roots or inflorescence) were also not considered, as the middle zone of a plant can be only established by seeing the whole plant.

In selected specimens, the following traits were measured:

A) *Leaf width*

Maximum diameter of a leaf blade.

B) *Leaf length*

Distance from the collar to the tip of the leaf blade. Leaf length does not represent a functional trait, but it was measured in order to calculate the leaf area.

In this study, leaf area was calculated using the data of length and width. In grasses, the shape of the leaves is simple and it can be approached by the area of a rectangle (length x width).

Data of plant height, leaf length and leaf width were measured using a flexible tape, ruler and a tape measure. The measurements of functional traits were recorded in the database created in

Chapter 2. Values of plant height and leaf length were recorded in centimetres (cm) and leaf width in millimetres (mm). Leaf area was calculated in square centimetres ($cm^2$).

Initially, the intention was to use data of plant height from herbarium sheet labels in the analysis. However, a simple correlation test between the data on the labels and data measured from herbarium specimens showed a low correlation (Figure 14). As a result, I decided not to use the label data because is not entirely representative of plant height.

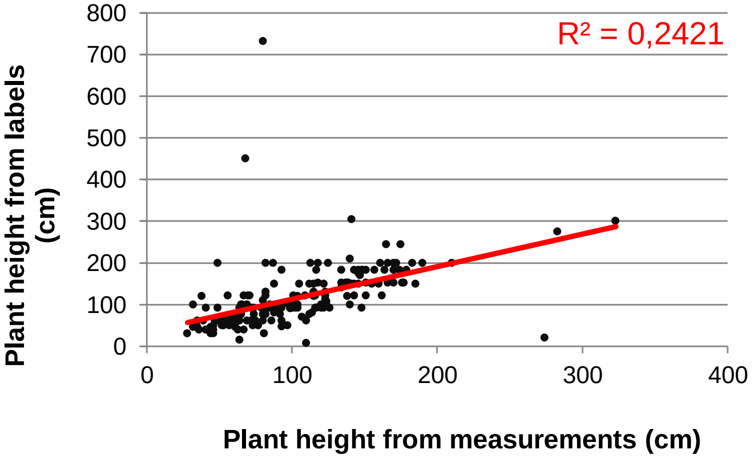

Figure 14. Correlation between plant height from labels and measurements

### 3.2.1. Analysis of plant functional trait

Only species with more than 20 measurements were selected for the interspecific analysis. The comparison of functional traits between species was addressed by graphs.

Intraspecific analysis was carried out only for *T. triandra*, which is the only species with enough samples to assess variability throughout its distribution range. For this species I created two maps showing the distribution of plant height and leaf area. These maps were created in ArcGis v.9.3 and using the cells of 4° x 4° latitude and longitude.

The relationship between values of functional traits and environmental variables was investigated through tests of correlations for *T. triandra*. The variables selected for this analysis were mean annual temperature, mean annual rainfall, temperature seasonality and annual precipitation, which were shown to be the most highly correlated with the distribution of *T. triandra* in Chapter 2. Where necessary, because variables were not normally distributed, these were log-transformed. Linear model comparison was used including all combinations of variables, so in each case 16 linear models were compared using the Aikake Information Criterion (AIC).

## 3.3. RESULTS

### 3.3.1. Dataset of plant functional traits

I measured functional traits in 828 specimens (41% of the total of specimens examined in this study and recorded in the database). In the database, all 828 specimen records have data of plant height and 371 have data for leaf traits (Table 7).

| **Species** | **Specimens in the database** | **Plant height** | | | **Leaf traits** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **Specimens measured** | **Height (cm)** | | **Specimens measured** | **Length (cm)** | | **Width (mm)** | | **Area ($cm^2$)** | |
| | | | **Min.** | **Max.** | | **Min.** | **Max.** | **Min.** | **Max.** | **Min.** | **Max.** |
| *Themeda anathera* | 79 | 43 | 24 | 122 | 16 | 7 | 38 | 2 | 4 | 1,4 | 15,2 |
| *Themeda arguens* | 135 | 84 | 16 | 175 | 97 | 4,2 | 55 | 2 | 7 | 1,9 | 27,3 |
| *Themeda arundinacea* | 91 | 7 | 141 | 283 | 0 | — | — | — | — | — | — |
| *Themeda avenacea* | 68 | 44 | 70 | 186 | 33 | 20,2 | 52 | 2 | 4 | 4,5 | 14,4 |
| *Themeda caudata* | 65 | 9 | 100 | 187 | 0 | — | — | — | — | — | — |
| *Themeda cymbaria* | 31 | 3 | 136 | 206 | 0 | — | — | — | — | — | — |
| *Themeda helferi* | 5 | 0 | — | — | 0 | — | — | — | — | — | — |
| *Themeda hookeri* | 15 | 12 | 42 | 80 | 15 | 10,2 | 28,1 | 2 | 4 | 2,8 | 8,9 |
| *Themeda huttonensis* | 5 | 0 | — | — | 0 | — | — | — | — | — | — |
| *Themeda mooneyi* | 4 | 2 | | 48 | 4 | 12,6 | 19,1 | 2 | 3 | | 3,4 |
| *Themeda novoguinensis* | 4 | 1 | | 140 | 0 | — | — | — | — | — | — |
| *Themeda quadrivalvis* | 67 | 22 | 35 | 161 | 3 | 15 | 31 | 4 | 5 | 7,5 | 15,5 |
| *Themeda sabarimalayana* | 1 | 0 | — | — | 0 | — | — | — | — | — | — |
| *Themeda saxicola* | 2 | 2 | 35 | 36 | 5 | 6,1 | 9 | 1 | 2 | | 1,2 |
| *Themeda strigosa* | 3 | 1 | | 125 | 1 | | 10,2 | | 2 | | 2 |
| *Themeda tremula* | 54 | 37 | 31 | 204 | 48 | 3,8 | 27 | 2 | 6 | 1,8 | 14,5 |
| *Themeda triandra* | 1,089 | 557 | 19 | 274 | 149 | 5 | 47 | 2 | 8 | 1 | 26,9 |
| *Themeda trichiata* | 2 | 1 | | 195 | 0 | — | — | — | — | — | — |
| *Themeda villosa* | 156 | 3 | 172 | 250 | 0 | — | — | — | — | — | — |

Table 7. Number of specimens in the database and number of functional traits measured by species

### 3.3.2. Interspecific trait variation

The aim of this section is to determine trait variability among *Themeda* species. Six species were suitable (in terms of sufficient numbers of measurements) for plant height comparison, while only four species were suitable for the comparison of leaf traits.

*Plant height*

The comparison among species shows that *T. triandra* has the widest range of variability. In contrast, *T. anathera* and *T. avenacea* show considerable homogeneity in height (Figure 15).

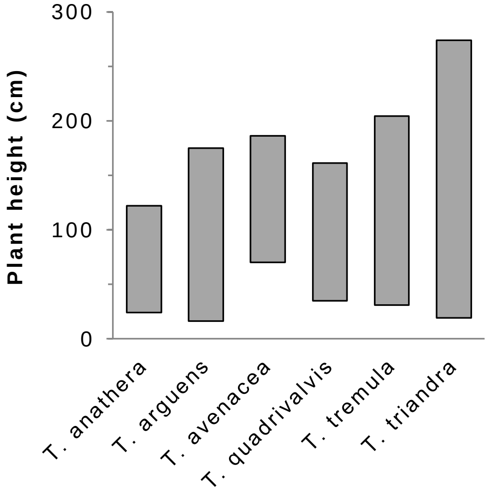

Figure 15. Plant height variation by species

### *Leaf width*

The smallest variability in leaf width is displayed by *T. avenacea* and largest by *T. triandra* (Figure 16).

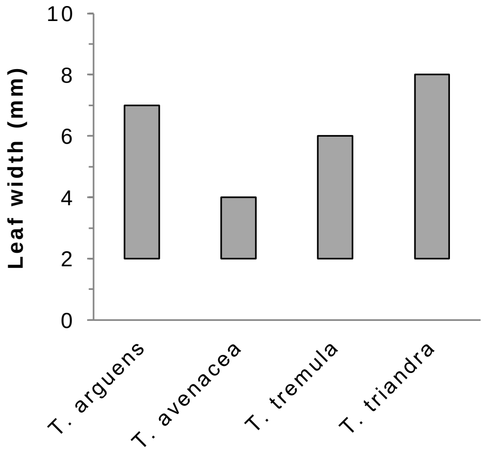

Figure 16. Leaf with variation by species

### *Leaf area*

The biggest range of leaf area is shown by *T. triandra* and *T. arguens*. Again for this trait, *T. avenacea* has the smallest range of variation (Figure 17).

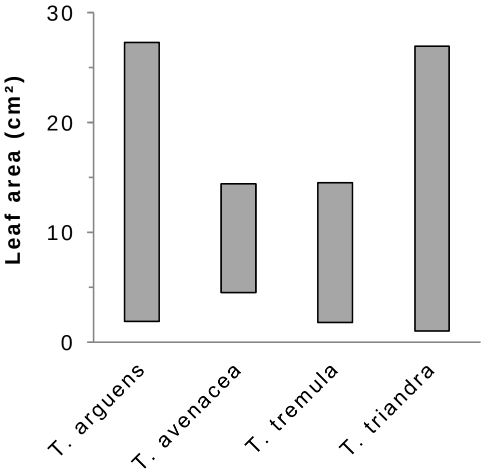

Figure 17. Leaf area variation by species

### 3.3.3. Intraspecific trait variation in *Themeda triandra*

For this analysis I used the data from 557 specimens. All have data for plant height and 149 have data for leaf traits.

The tallest specimens of *T. triandra* are found in tropical Africa and India (Figure 18A), but overall, by visual inspection, a clear pattern in height throughout the area of distribution is hard to discern.

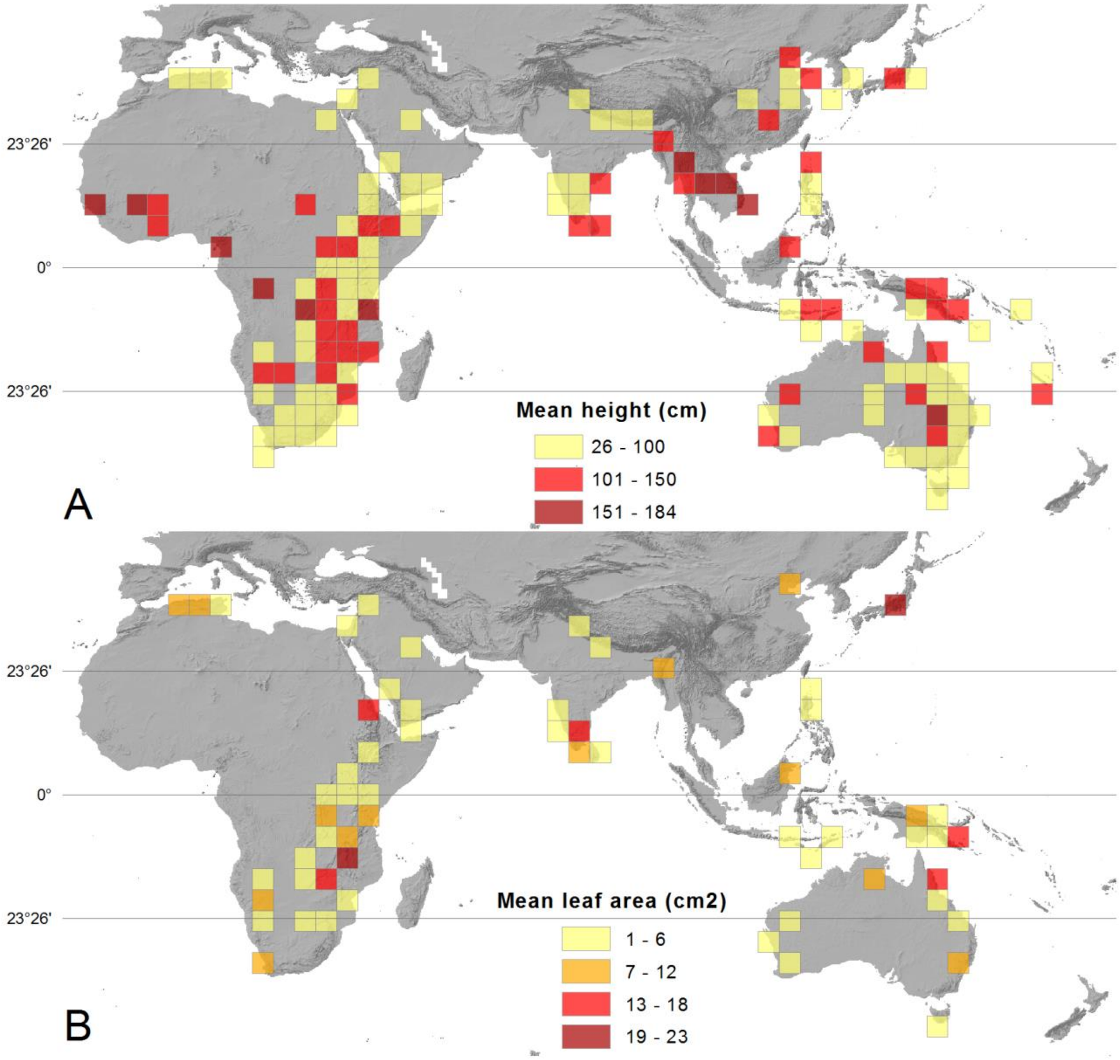

Figure 18. Distribution of functional traits of *Themeda triandra*. A. Mean height; B. Mean leaf area.

There are two cells with the biggest value of leaf area (Figure 18B). One is in the tropical zone of Africa and the other is in Japan, very close to the distributional limit of *T. triandra*. However, as for height, it is difficult to see by visual inspection a clear geographic pattern for the trait of leaf area.

The results of the correlations between plant height and leaf traits variation and environmental variables show the expected directional relationships, though in all cases these are somewhat weak. Mean annual temperature and mean annual precipitation show a positive relationship with height and leaf traits (i.e., taller plants and larger leaves in warmer, wetter environments), while temperature seasonality and altitude have a negative slope (i.e., smaller plants in more seasonal and higher altitude locations) (Figures 19, 20 and 21). A linear model including mean annual temperature, mean annual rainfall and temperature seasonality was the most relevant to explaining variation in height, explaining 21.55% of the variation in the data. For other leaf traits, models were less explanatory, explaining c. 10-19% of variation in the data.

*Plant height*

The variation of height in *T. triandra* appears to be directly correlated with mean annual temperature more than any other variable (Figure 19). The lowest correlation value was obtained from the analysis between this trait and temperature seasonality.

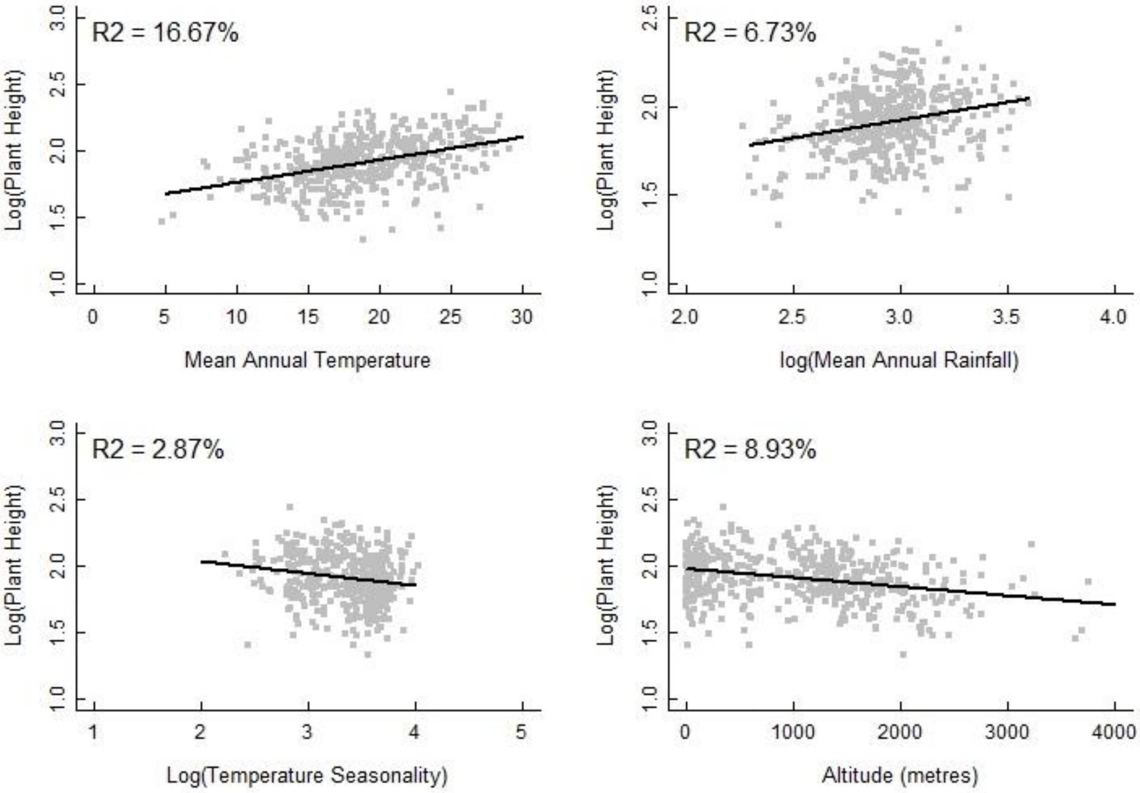

Figure 19. Correlation between plant height and selected environmental variables

*Leaf width*

As in plant height, the variations of this trait appear to be more correlated to mean annual temperature (Figure 20), while altitude has the lowest correlation with leaf width.

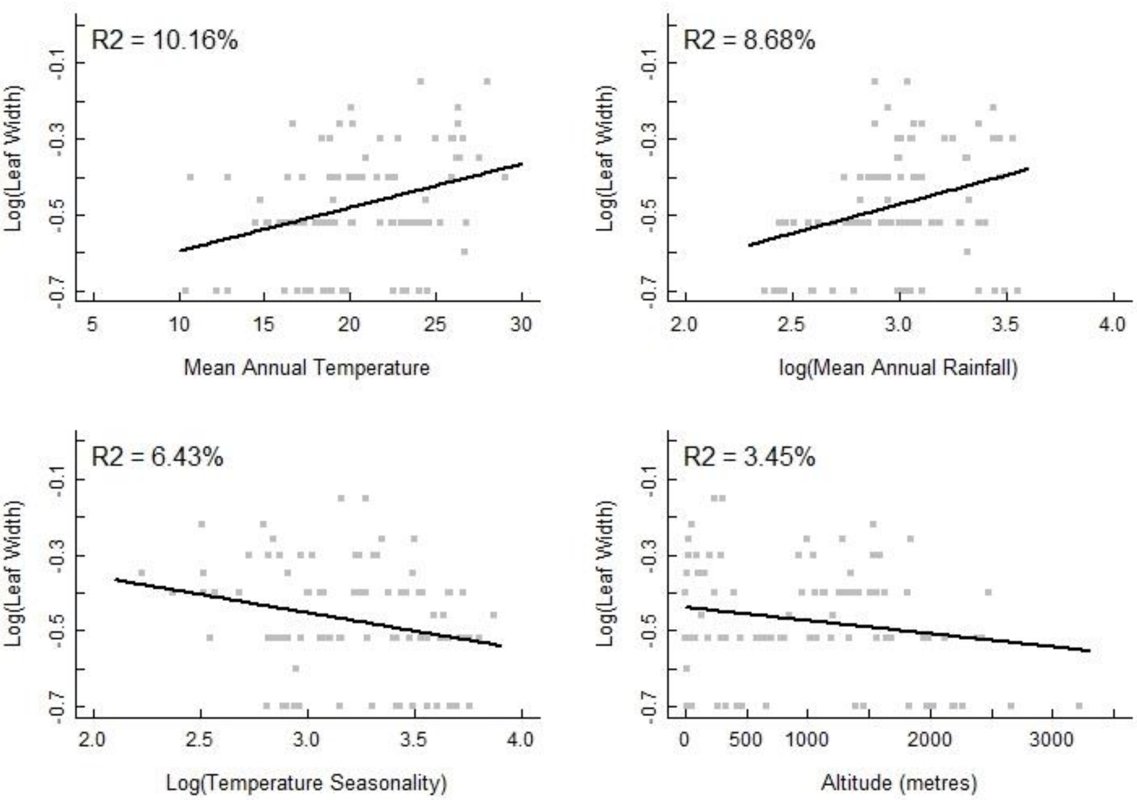

Figure 20. Correlation between leaf width and selected environmental variables

*Leaf area*

Again, the strongest correlation for the trait variation is found with mean annual temperature (Figure 21), but at difference of the result of leaf width, the lowest correlation was found with temperature seasonality.

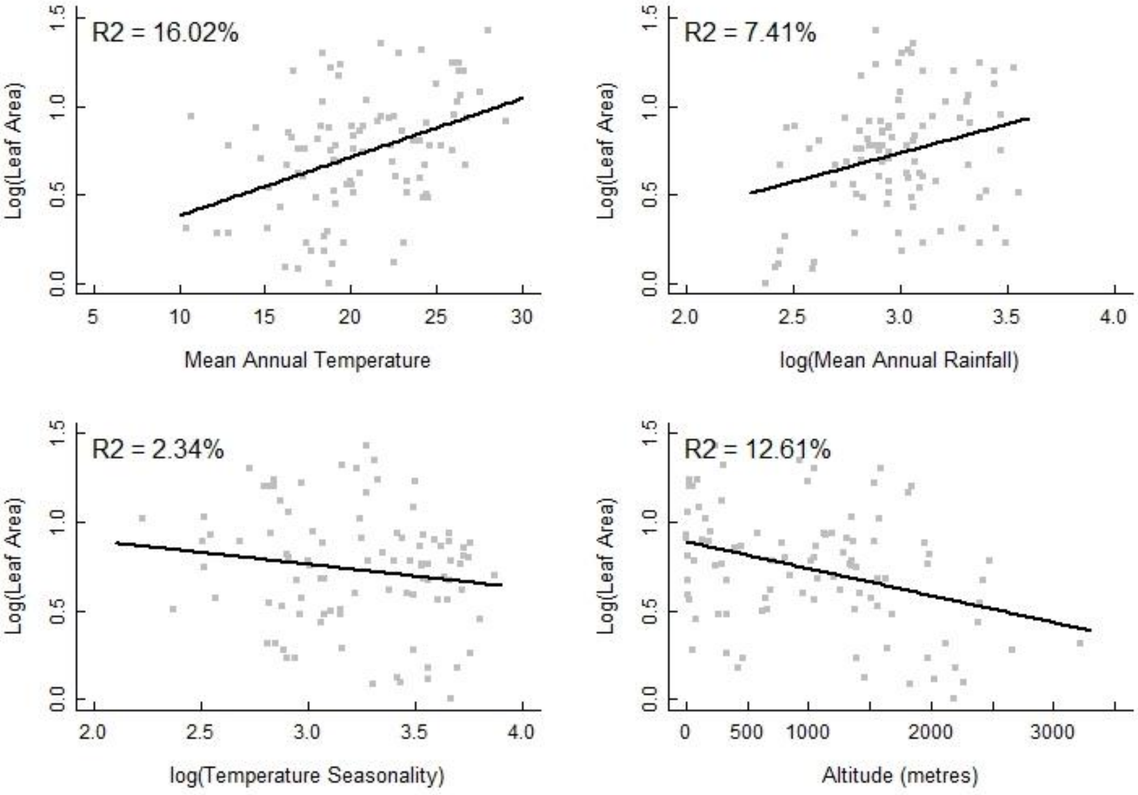

Figure 21. Correlation between leaf area and selected environmental variables

## 2.4. DISCUSSION

The results of interspecific analysis show that *T. triandra* has the widest range of variation for the traits analysed (plant height, leaf width and leaf area). *Themeda arguens*, another widespread species, also shows wide variation in its leaf traits. Interestingly, *T. arguens* and *T. triandra* are morphologically similar and may be closely related.

The trait variation presented by *T. triandra* may be related to its wide distribution. However, the size of the geographical distributions does not explain the levels of trait variation among *Themeda* species. For example, plant height in *T. avenacea* is less variable than in *T. tremula*, but *T. avenacea* covers an area which is several times bigger than that covered by *T. tremula*

(Chapter 2, Figure 2A and 2B). Functional traits vary in relation to the environmental conditions and not simply according to the range of distribution, so this may reflect that *T. tremula* grows in more diverse environments.

The analyses of trait variation in *T. triandra* relative to environmental gradients shows directional relationships with altitude, temperature and rainfall, but these relationships are weak. A linear model including mean annual temperature, mean annual rainfall and temperature seasonality was the most relevant to explaining variation in height, explaining 21.55% of the variation in the data. This actually compares well to a global study of more than 7000 plants species (Moles *et al.*, 2009), which showed that 28% of variation in plant height was explicable by models incorporating 22 environmental variables.

The climate variable showing the weakest relationship with traits is temperature seasonality. This is puzzling in the sense that this was the key correlate of the range limits of *T. triandra* (Chapter 2), so one would expect a correlation with traits of height and leaf traits, which should be key in determining range limits. This interesting result may reflect issues with using data from herbarium specimens, which will be discussed in the next section

### Using herbarium specimens for functional trait analysis: some issues

From the 1,996 specimens examined, only 41% were suitable for measuring functional traits. Most of the specimens were not suitable for plant height measurement because they did not include the whole individual. Regarding leaf traits, most of the specimens were not measured because the leaves were rolled, folded or broken. Suitable specimens for plant height were more abundant than suitable specimens for leaf traits.

The lack of data for a number of species (especially the tallest grasses within the genus) prevented testing some hypotheses about the distribution of plant height. In terms of the specific focus on the widespread species *T. triandra*, I cannot establish with complete certainty whether it is the most variable species within the genus, because a large fraction of species were not included in the analysis. More widely, the taxonomical work carried out in

Chapter 1 suggests that the maximum heights in *Themeda* are found in species in SE Asia. *Themeda arundinacea*, *T. caudata* and *T. idjensis* can be up to 6 m tall and are distributed across SE Asia where there are high amounts of rainfall through the year, but especially during the growing season (warm season). Therefore, the comparison between distribution and environmental variables, such as annual precipitation, could be interesting to study, but was not possible based on herbarium specimens.

A weak relationship between data on herbarium labels of plant height and height measured from the specimens themselves is also an important result from this research. It points to great caution being required in using herbarium label data to measure some key functional traits, and also suggests questions relating to the behaviour of collectors. It is possible that collectors are not accurately recording plant heights in the field notes, or that collectors consistently press small grass plants (perhaps because they fit the plant press better), or more likely, a combination of both of these problems. Whatever the underlying reason, there are consequences for the use of herbarium specimens in measuring trait values that must be considered in future work.

Further issues with herbarium specimen data arise from considering of the perhaps unexpected result of the lack of correlation of traits with climate seasonality, which was shown (Chapter 2) to be the most important determinant of the range limits of *T. triandra*, so might be expected to show a strong correlation. This could reflect issues described above in terms of the accuracy of the measurement of traits, but another possible source of error or noise could reflect that herbarium specimens are collected across multiple time periods, spanning decades or even centuries. A trait such as plant height or leaf size could reflect, in part, the rainfall received in the particular time that it was collected. Finally, variables such as soil properties could influence traits, and these cannot be inferred from herbarium specimens. These issues of the varied time of collection of herbarium specimens over many years needs careful consideration if specimens are to be used in studies of functional traits.

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# APPENDIX 1. TAXONOMIC RESOURCES

## *Themeda* Forssk.

### *Descriptions*

- J. Arnold Arbor. 29: 371 (Reeder, 1948).
- Fl. Java 3: 614 (Backer & Bakhuizen Van Den Brink, 1968).
- Fl. Iraq 9: 552 (Bor, 1968).
- The grasses of Central Australia: 237 (Lazarides, 1970).
- Fl. Taiwan 5: 701 (Hsu, 1978).
- Fl. Pakistan 143: 315 (Cope, 1982).
- Grasses of New South Wales: 263 (Wheeler *et al*., 1982).
- Fl. Tamilnadu Carnatic 2: 1908 (Britto & Matthew, 1983).
- Grasses of Southern Africa: 334 (Russell *et al*., 1991).
- Fl. Ethiopia & Eritrea 7: 353 (Phillips, 1995).
- The grasses and Bamboos of India 1: 228 (Moulik, 1997).
- Fl. Taiwan 5: 583 (Hsu *et al*., 2000).
- Fl. Bhutan 3(2): 817 (Noltie, 2000).
- Gard. Bull. Singapore 57(suppl.): 132 (Duistermaat, 2005).
- Grasses of South Australia: 533 (Jessop *et al*., 2006).
- Fl. China 22: 633 (Schouliang & Phillips, 2006).
- Fl. Arab. Pen. Socotra 5(1): 312 (Cope, 2007).
- GrassBase (Clayton *et al*., 2014).

### ***Themeda anathera* (Nees ex Steud.) Hack.**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 213 (Bor, 1941).
- Fl. Pakistan 143: 316 (Cope, 1982).
- Fl. China 22: 635 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Pakistan 143: 307, fig. 34 (3-4) (Cope, 1982).

### ***Themeda arguens* (L.) Hack.**

*Descriptions*

- J. Arnold Arbor. 29: 371 [as *T. frondosa* (R.Br.) Merr.] (Reeder, 1948).
- Gard. Bull. Singapore 57(suppl.): 134 (Duistermaat, 2005).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Indo-Chine 7(4): 354, fig. 37 (4-5) (Camus & Camus, 1922).
- Gard. Bull. Singapore 57(suppl.): 133, fig. 138 (Duistermaat, 2005).

### ***Themeda arundinacea* (Roxb.) A.Camus**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 205 (Bor, 1941).
- Acta Bot. Neerl. 1: 481 (Jansen, 1952).
- Fl. Bhutan 3(2): 820 [as *T. subsericans* Ridl.] (Noltie, 2000).
- Fl. Bhutan 3(2): 822 (Noltie, 2000).
- Fl. China 22: 637 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Indian Forest Rec., Bot. 2(1): pl. LXII (Bor, 1941).
- Fl. Bhutan 3(2): 821, fig. 60 (g-h) [as *T. subsericans* Ridl.] (Noltie, 2000).
- Fl. Bhutan 3(2): 823, fig. 61 (a) (Noltie, 2000).

### ***Themeda avenacea*** **(F.Muell.) T.Durand & B.D.Jacks.**

*Descriptions*

- A manual of the grasses of New South Wales: 93 [as *Anthistiria avenacea* F.Muell.] (Maiden, 1898).
- The grasses of Central Australia: 240 (Lazarides, 1970).
- Grasses of New South Wales: 263 (Wheeler *et al*., 1982).
- Grasses of South Australia: 533 (Jessop *et al*., 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Grasses of South Australia: 534, fig. 455 (Jessop *et al*., 2006).

### ***Themeda caudata*** **(Nees ex Hook. & Arn.) A.Camus**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 207 (Bor, 1941).
- Acta Bot. Neerl. 1: 482 (Jansen, 1952).
- Fl. Taiwan 5: 703 (Hsu, 1978).
- Fl. Taiwan 5: 585 (Hsu *et al*., 2000).
- Fl. Bhutan 3(2): 824 [as *T. longispatha* (Hack.) Raizada & Jain] (Noltie, 2000).
- Fl. Bhutan 3(2): 824 (Noltie, 2000).
- Fl. China 22: 636 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Bhutan 3(2): 823, fig. 61 (e-f) (Noltie, 2000).
- Fl. Bhutan 3(2): 823, fig. 61 (g) [as *T. longispatha* (Hack.) Raizada & Jain] (Noltie, 2000).
- Fl. China (Illustr.) 22: 888, fig. 888 (1-4) (Schouliang & Phillips, 2006).

### ***Themeda cymbaria*** **Hack.**

*Descriptions*

- Fl. Tamilnadu Carnatic 2: 1908 (Britto & Matthew, 1983).
- Bull. Bot. Surv. India 29(1-4): NA (Sreekumar & Nair, 1987).
- Fl. Palni Hills 3: 1598 (Mathew, 1999).
- Fl. Tamil Nadu: 478 (Kabeer & Nair, 2009).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Illustr. Fl. Palni Hills: 875, fig. 875 (Matthew, 1996).

### ***Themeda gigantea*** **(Cav.) Hack. ex Duthie**

*Descriptions*

- J. Arnold Arbor. 29: 373 (Reeder, 1948).
- Acta Bot. Neerl. 1: 480 (Jansen, 1952).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

***Themeda helferi*** **Hack.**

*Descriptions*

- Fl. China 22: 635 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. China (Illustr.) 22: 885, fig. 885 (Schouliang & Phillips, 2006).

***Themeda hookeri*** **(Griseb.) A.Camus**

*Descriptions*

- Fl. Bhutan 3(2): 820 (Noltie, 2000).
- Fl. China 22: 635 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Bhutan 3(2): 821, fig. 60 (f) (Noltie, 2000).
- Fl. China (Illustr.) 22: 887, fig. 887 [same as Fl. Sichuan. 5: pl. 220] (Schouliang & Phillips, 2006).

***Themeda huttonensis*** **Bor**

*Descriptions*

- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

***Themeda idjensis*** **Jansen**

*Descriptions*

- Acta Bot. Neerl. 1: 482 (Jansen, 1952).
- Fl. Java 3: 615 (Backer & Bakhuizen Van Den Brink, 1968).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

### ***Themeda intermedia*** **(Hack.) Bor**

*Descriptions*

- J. Arnold Arbor. 29: 373 [as *T. gigantea* var. *amboinensis* Hack.] (Reeder, 1948).
- Acta Bot. Neerl. 1: 481 (Jansen, 1952).
- Fl. Bhutan 3(2): 822 (Noltie, 2000).
- Fl. China 22: 636 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Bhutan 3(2): 823, fig. 61 (b) (Noltie, 2000).

### ***Themeda minor*** **L.Liou**

*Descriptions*

- Fl. Xizang. 5: 343 (Liang, 1987; translation by X. Song, MSc Student 2013/14).
- Fl. China 22: 634 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Xizang. 5: 344, fig. 189 (1-3) (Liang, 1987).

**_Themeda mooneyi_ Bor**

*Descriptions*

- Kew Bull. 1951(3): 451 (Bor, 1952).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

**_Themeda novoguineensis_ (Reeder) Jansen**

*Descriptions*

- J. Arnold Arbor. 29: 374 [as *T. gigantea* var. *novoguineensis* Reeder] (Reeder, 1948).
- Acta Bot. Neerl. 1: 483 (Jansen, 1952).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

**_Themeda pseudotremula_ Potdar, Salunkhe & S.R.Yadav**

*Descriptions*

- Kew Bull. 58(1): 243 (Potdar *et al*., 2003).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Kew Bull. 58(1): 244, fig. 1 (Potdar *et al*., 2003).

**_Themeda quadrivalvis_ (L.) Kuntze**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 209 (Bor, 1941).
- Fl. Iraq 9: 554 (Bor, 1968).
- Grasses of New South Wales: 263 (Wheeler *et al*., 1982).
- Fl. Bhutan 3(2): 819 (Noltie, 2000).
- Fl. China 22: 634 (Schouliang & Phillips, 2006).
- Fl. Arab. Pen. Socotra 5(1): 312 (Cope, 2007).
- Fl. Tamil Nadu: 481 (Kabeer & Nair, 2009).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Iraq 9: 553, pl. 213 (Bor, 1968).
- Fl. Iranica 70: tab. 72 (Rechinger, 1970).
- Bull. Bot. Res., Harbin 9(2): 62, fig. 4 [as *T. chinensis* (A.Camus) S.L.Chen & T.D.Zhuang] (Zhuang & Chen, 1989).
- Bull. Bot. Res., Harbin 9(2): 62, fig. 5 [as *T. yuanmounensis* S.L.Chen & T.D.Zhuang] (Zhuang & Chen, 1989).
- Fl. Bhutan 3(2): 821, fig. 60 (e) (Noltie, 2000).

### ***Themeda sabarimalayana* Sreek. & V.J.Nair**

*Descriptions*

- Bull. Bot. Surv. India 29(1-4): 987 (Sreekumar & Nair, 1987).
- Fl. Palni Hills 3: 1599 (Mathew, 1999).
- Fl. Tamil Nadu: 482 (Kabeer & Nair, 2009).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Bull. Bot. Surv. India 29(1-4): 128, fig. A-K (Sreekumar & Nair, 1987).

### ***Themeda saxicola* Bor**

*Descriptions*

- Kew Bull. 1951(3): 452 (Bor, 1952).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

### ***Themeda strigosa* (Ham. ex Hook.f.) A.Camus**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 210 (Bor, 1941).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- None.

### ***Themeda tremula* (Nees ex Steud.) Hack.**

*Descriptions*

- Fl. Palni Hills 3: 1599 (Mathew, 1999).
- Kew Bull. 58(1): NA (Potdar *et al*., 2003).
- Fl. Tamil Nadu: 482 (Kabeer & Nair, 2009).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Suppl. Illustr. Fl. Palni Hills: 1222, fig. 1222 (Matthew, 1998).

***Themeda triandra* Forssk.**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 208 (Bor, 1941).
- J. Arnold Arbor. 29: 372 (Reeder, 1948).
- Fl. Iraq 9: 552 (Bor, 1968).
- The grasses of Central Australia: 238 (Lazarides, 1970).
- Grasses of New South Wales: 263 [as *T. australis* (R.Br.) Stapf] (Wheeler *et al.*, 1982).
- Fl. Tamilnadu Carnatic 2: 1908 (Britto & Matthew, 1983).
- Grasses of South West Africa/Namibia: 262 (Müller, 1984).
- Grasses of Southern Africa: 335 (Russell *et al.*, 1991).
- Fl. Ethiopia & Eritrea 7: 353 (Phillips, 1995).
- Fl. Palni Hills 3: 1600 (Mathew, 1999).
- Fl. Taiwan 5: 585 (Hsu *et al.*, 2000).
- Fl. Bhutan 3(2): 819 [as *T. laxa* (Andersson) A.Camus] (Noltie, 2000).
- Grasses of South Australia: 534 (Jessop *et al.*, 2006).
- Fl. China 22: 634 (Schouliang & Phillips, 2006).
- Fl. Arab. Pen. Socotra 5(1): 313 (Cope, 2007).
- Fl. Tamil Nadu: 479 [as *T. laxa* (Andersson) A.Camus] (Kabeer & Nair, 2009).
- Fl. Tamil Nadu: 483 (Kabeer & Nair, 2009).
- Guide to grasses of Southern Africa: 49 (Van Oudtshoorn, 2012).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- The grasses of Burma, Ceylon, India and Pakistan: 253, fig. 27 (Bor, 1960).
- Les graminées d' Afrique tropicale: 313, fig. 251 (Jacques-Félix, 1962).
- Illustr. Fl. Tamilnadu Carnatic: 943, fig. 943; 944, fig. 944 (Matthew, 1982).
- Fl. Xizang. 5: 344, fig. 189 (4-5) (Liang, 1987).
- Grasses of Southern Africa: 335, fig. 218; 378, pl. 198; 379, pl. 199 (Russell *et al.*, 1991).

- Fl. Ethiopia & Eritrea 7: 355, fig. 145 (Phillips, 1995).
- Fl. Taiwan 5: 586, pl. 247 [as *T. japonica* (Willd.) Tanaka] (Hsu *et al.*, 2000).
- Fl. Bhutan 3(2): 821, fig. 60 (a-d) [as *T. laxa* (Andersson) A.Camus] (Noltie, 2000).
- Grasses of South Australia: 535, fig. 456 (Jessop *et al.*, 2006).
- Fl. China (Illustr.) 22: 884, fig. 884 (Schouliang & Phillips, 2006).
- Fl. Arab. Pen. Socotra 5(1): 311, fig. 63 (C). (Cope, 2007).
- Fl. Tamil Nadu: 480, fig. 86 [as *T. laxa* (Andersson) A.Camus] (Kabeer & Nair, 2009).
- Guide to grasses of Southern Africa: 49 (Van Oudtshoorn, 2012).

### ***Themeda trichiata*** **S.L.Chen & T.D.Zhuang**

*Descriptions*

- Bull. Bot. Res., Harbin 9(2): 58 (Zhuang & Chen, 1989).
- Fl. China 22: 636 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Bull. Bot. Res., Harbin 9(2): 62, fig. 3 (Zhuang & Chen, 1989).
- Fl. China (Illustr.) 22: 888, fig. 888 (6-8) (Schouliang & Phillips, 2006).

### ***Themeda unica*** **S.L.Chen & T.D.Zhuang**

*Descriptions*

- Bull. Bot. Res., Harbin 9(2): 56 (Zhuang & Chen, 1989).
- Fl. China 22: 636 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Bull. Bot. Res., Harbin 9(2): 62, fig. 1 (Zhuang & Chen, 1989).
- Fl. China (Illustr.) 22: 889, fig. 889 (Schouliang & Phillips, 2006).

### ***Themeda villosa* (Lam.) A.Camus**

*Descriptions*

- Indian Forest Rec., Bot. 2(1): 211 (Bor, 1941).
- Acta Bot. Neerl. 1: 482 (Jansen, 1952).
- Fl. Bhutan 3(2): 822 (Noltie, 2000).
- Gard. Bull. Singapore 57(suppl.): 134 (Duistermaat, 2005).
- Fl. China 22: 635 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

- Fl. Xizang. 5: 341, pl. 188 (Liang, 1987).
- Fl. Bhutan 3(2): 823, fig. 61 (c-d) (Noltie, 2000).
- Gard. Bull. Singapore 57(suppl.): 133, fig. 139 (a-b) (Duistermaat, 2005).
- Fl. China (Illustr.) 22: 886, fig. 886 [same as Fl. Xizang. 5: 341, pl. 188] (Schouliang & Phillips, 2006).
- Fl. China (Illustr.) 22: 888, fig. 888 (5) (Schouliang & Phillips, 2006).

### ***Themeda yunnanensis* S.L.Chen & T.D.Zhuang**

*Descriptions*

- Bull. Bot. Res., Harbin 9(2): 58 (Zhuang & Chen, 1989).
- Fl. China 22: 637 (Schouliang & Phillips, 2006).
- GrassBase (Clayton *et al*., 2014).

*Illustrations*

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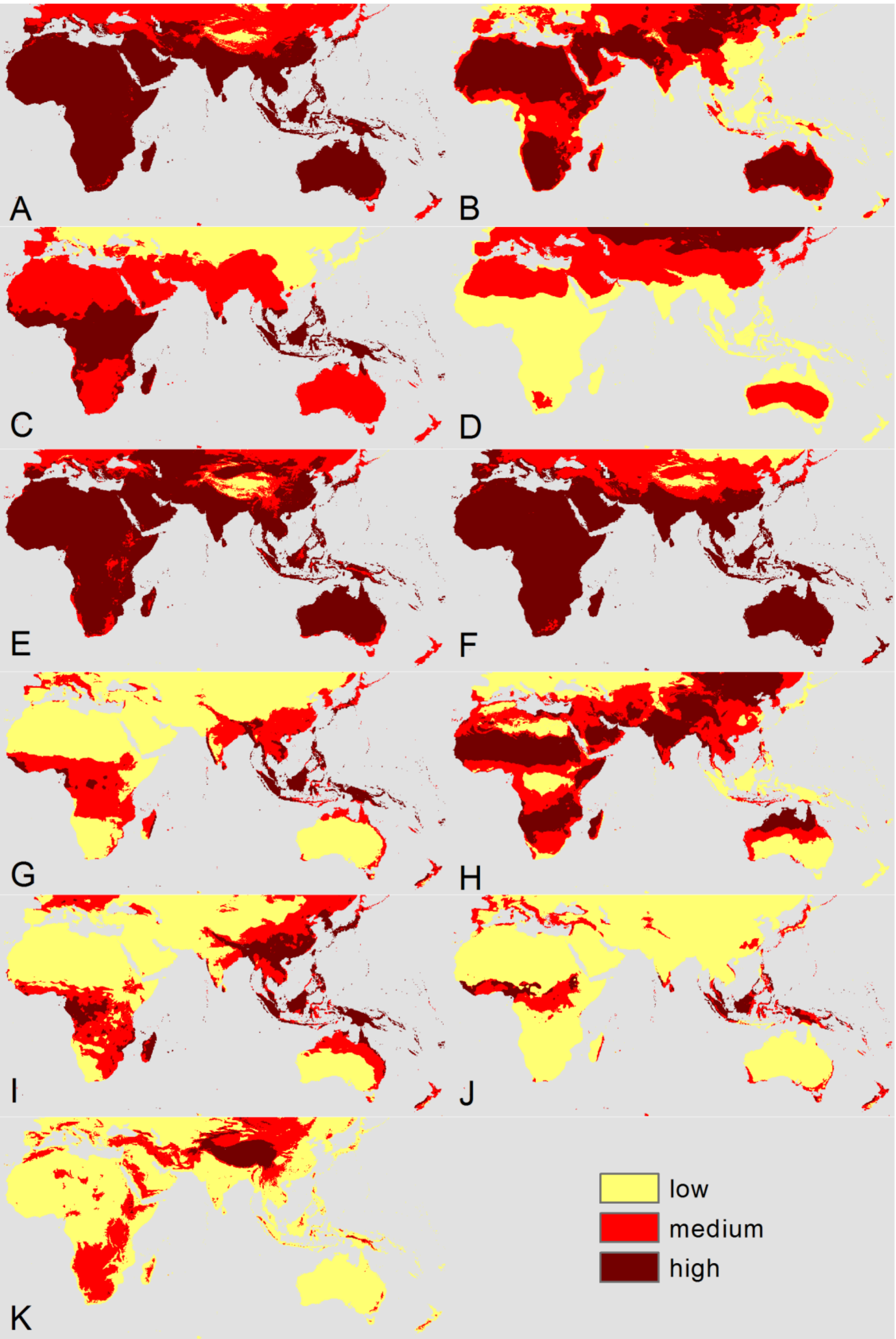
# APPENDIX 2: DISTRIBUTION OF ENVIRONMENTAL CORRELATES



A. Annual mean temperature; B. Mean diurnal range; C. Isothermality; D. Temperature seasonality; E. Max. temperature of warmest month; F. Min. temperature of coldest month; G. Annual precipitation; H. Precipitation seasonality; I. Precipitation of warmest quarter; J. Precipitation of coldest quarter; K. Altitude.