AUTECOLOGY AND CONTROL OF *Tithonia diversifolia* (Hemsl.) A. Gray IN SOME SELECTED STATES OF NIGERIA

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CERTIFICATION

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DEDICATION

To my twin sister, Diana C. OBIAKARA

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"A thankful heart is not only the greatest virtue, but the parent of all the other virtues".

- Cicero (63 B C).

Firstly, I am grateful to the everlasting One, the Creator of the ends of the earth, the One whose understanding no one can fathom andwhoseday-by-day merciesI have livedby all through theseyears.

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ABSTRACT

Since its introduction in Nigeria in the 1970s, *Tithonia diversifolia* (*Td*),an invasive species has posed increasing threats to crop production and native species diversity. However, the autecology of *Td* which plays a key role in providing information for its control is yet to be fully understood. This study thereforeinvestigated some autecological and reproductive traits of *Td* in Nigeria.

Principal Component Analysis-env was used tocompare the ecological niche of *Td* between its native range (Mexico) and its introduced range (Nigeria). The current and future geographical distributions of *Td* were modelled using Maximum Entropy principles. Impacts of *Td* were assessed on seed bank species diversity and soil physico-chemical properties using space-for-time substitution approach. Two Lowland Forests (LF), two Derived Savannas (DS) and one Jos Plateau Forest-grassland Mosaic sites were investigated. Nitrogen, Phosphorus and Potassium concentrations in soil and plant parts were determined using standard procedures in soil with highest *Td*. Mode of pollination, fecundity, germination and dormancy were assessed while seed bank behaviour and biomass were modelled in DS. Control of *Td* using paraquat dichloride, manual weeding and controlled agricultural burning were investigated using standard procedures. Data were analysed using descriptive statistics and Analysis of Variance (ANOVA) at $\alpha_{0.05}$.

Tithonia diversifolia occupies a different niche in Nigeria compared to Mexico (Schoener's D=0.01, E=0.99). Maximum entropy models revealed that DS is most suitable for *Td* establishment. *Tithonia diversifolia* exerted no significant impact on seed bank diversity of invaded habitats. However, it significantly altered soil pH, cation exchange capacity, total N, inorganic PO_4, organic C, available P, Fe, Zn and Cu. The leaves had significantly high levels of N, P and K compared to other plant parts. Reproductive allocation of nutrients in DS revealed that N ranged from 5.88-17.40%, P, 8.60-31.65% and K,7.73-22.53%. *Tithonia diversifolia* is facultatively xenogamous with 93% fruit set in open-pollinated capitula and a high pollen-ovule ratio (4,167±76). It produced 49±3 capitula/plant, corresponding to 454-8124 achenes/plant. Achenes of *Td* were permeable but showed morphological dormancy with low germinability (8.67%). Mechanical scarification and Gibberellic acid increased germinability by 40 and 65%, respectively. *Tithonia diversifolia*formed a transient seed bank (<6 months) with 2811±201 achenes/m^2. Seed bank density was best fit with exponential decay model ($\text{density} = 1712e^{-0.49\text{time}} + 24$), with an initial density of 1736 achenes/m^2 at the rate of 0.49 achenes/week. Biomass of *Td* one month after emergence was 2.36±0.38 g/m^2. This increased by 91% after two months. Biomass of *Td* followed a logistic model,$\text{biomass} = 179.7/(1 + 855.4e^{-2.25\text{time}})$. Mature *Td* biomass was 179.56±22.54 g/m^2, with the largest proportion (67%) allocated to shoots. Paraquat dichloride application was most efficient in controlling *Td* with over 80% seedling mortality and 50% reduction in plant height.

The prolific seed production and rapid vegetative growth of *Tithonia diversifolia* are responsible for its aggressive invasiveness. This species can be controlled using agricultural burning and systemic herbicide.

Keywords: Seed dormancy, Ecological niche, Invasive species, Seed bank, Systemic herbicide

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CHAPTER 1
INTRODUCTION

1. 1Background of the study

According to the International Union for the Conservation of Nature (IUCN), analien species is an organism that has been introduced outof their nativehabitat by human agency, either intentionally or accidentally (IUCN, 2000). From this definition, it appears clearly that the number of alien species in the world depends directly on the trend and intensity of human activities. Indeed, among the factors that determine the distribution of alien invasive species,global trade and transports (Van Kleunen *et al.,* 2015; Chapman *et al.,* 2017) as well as agriculture and horticulture (Cullen *et al.*, 2011)have been identified asthe most important.

In one of thelatest meta-analyses, Van Kleunen *et al.* (2015) presented for the first time a global estimate of alien exotic plants. According to their findings, introduced plants make up close to 4% of the extant globalflora. Obviously, this estimateshould be much higherconsidering the unprecedented global exchanges recorded in the last 50 years and the fact that these workers had no data for about 17% of Earth's terrestrial ecosystems. However, this study underscored the pressing need for an in-depth understanding of the spread of invasive plant species and called for robust management strategies againstbiological invasions.Therefore, alien invasive species constitute one of the most significantdrivers of global change with severe ecological and economic consequences. Worryingly, it has been predicted that biological invasions will be recurrent in the future given the increasing levels of connectivity among ecologically different regions of the world(Elton, 2000).

*Tithonia diversifolia,*also known as Mexican sunfloweris a fast-growing annual plantof the Asteraceae family witha woody root system. This species isindigenous to a number of countries in Central America, namelyCosta Rica, Mexico andHonduras(CABI, 2017).*T. diversifolia* has beenrecorded in more than 70 countries around the

world and has become a major invasive plant species in tropicaland subtropical regions (La Duke, 1982).

In Nigeria, *T. diversifolia* was accidentally imported from Israel with maize seeds in the late 1970s (Chukwuka *et al.,* 2007a). This species has spread rapidly and is already abundant in several ecological regions. The preferred habitats of *T. diversifolia* in Nigeria include roadsides, riverbanks and abandoned farmlands where it readily forms large and impenetrable clumps (Appendix 1). This speciesis adapted to high light intensities and temperatures but does not withstand water stress (Chukwuka *et al.,* 2007b; Wen, 2015).

Tithonia diversifolia reproduces sexually with an individual producing thousands of achenes (Muoghalu, 2008), which makes it difficult to control. It has been shown to have allelopathic potentials (Otusanya and Ilori, 2012). Although this species plays an important role in Africa given its medicinal and ethnopharmacological attributes (Ajao and Moteetee, 2017), it is renowned for its adverse effects on the growth of important crops (Tongma *et al*., 1997).

Tithonia diversifolia has attracted considerable research interest in most locations where it has been introduced. A query on the Web of Science database (https://www.webofknowledge.com) in October 2017 using "*Tithonia diversifolia*" as search terms returned 344 articles published between 1980 and October 2017 and amounting to 4,495 citations. In other words, the number of published studies on *T. diversifolia* has increased rapidly in recent years (Appendix 2).

1. 2 Research problem

Since its introduction in Nigeria in the late 1970s, *T. diversifolia* has spread andsuccessfully colonized anextensive range of habitats, especially agricultural lands and road verges. Given that many invasive species cause unwanted changes in introduced habitats, the rapid spread of *T. diversifolia* in Nigeria cannot be without ecological consequences.Moreover, there is little information available on this species, including its current geographical distribution, potential impacts on plant diversity and soil properties as well as traits that may promote its invasiveness. In order to evaluate the potential ecological risks posed by *T. diversifolia* in Nigerian ecosystems, it is of interest to evaluate the degree of its geographical distribution, clarify its biology and community-level impacts (Vilà *et al*., 2011; Pyšek *et al*., 2012).

1. 3Justification

With increasing global trade and movements, many plant species are being introduced into new ecosystems. Species introductions coupled with increasing habitat disturbance by humans are efficient factors that favour high rates of dispersal and establishment of exotic plants. As a result, many non-indigenous plants have become invasivethereby causing severe biodiversity and economic losses.

Most developing countries are endowed with highly diverse natural habitats. Unfortunately, they are ill prepared to tackle biological invasions given the high rate of species introduction globally. Low levels of development and public awareness are among the factors that militate against a better understandingof threats posed by biological invasionsin developing countries. Although much of the information available at the beginning of a new invasion may have little relevance because it usually comes from a different ecological region, a number of predictive approaches have been established aside the conventional study methods to anticipating biological invasions. These approaches are yet to be fully applied in the developing world to predict and monitor potentially invasible habitats. In addition, more measuresare needed including education of the public on the dangers of exotic species and implementation of preventive methods against further species introduction.

1. 4 Objectives

In this work, someecological and biological aspects of *Tithonia diversifolia*(Hemsl.) A. Graywere investigated in Nigeria in order to understand its invasiveness. Specifically, the objectives were as follows:

1. To model the potentialdistribution of *Tithonia diversifolia*, its leaf area andgrowth.
2. To comparethe realized niche of *Tithonia diversifolia* in Nigeriawith that of its native range.
3. To assess the impacts of *Tithonia diversifolia* infestation on the seed bank diversity and soil physico-chemical properties of invaded habitats.
4. To examine therole of reproductive and vegetative traits of *Tithonia diversifolia*in its invasiveness.
5. To investigate the effects of control measures on invasiveness of*Tithonia diversifolia*.

CHAPTER 2
LITERATURE REVIEW

2. 1 Biological Invasions: Causes and Consequences

Biological invasions are the process through which plants, animals and other organismsdisperseand establish outside of their native habitats after crossing natural barriers, mainly through human agency (Richardson *et al.*, 2000). Different types of barriers have been identified during the process of biological invasions including geographical, abiotic and biotic barriers (Figure 2.1). Therefore, a species is considered invasive when it successfully goes through all the following stages in succession: 1) introduction, that is the intentional or accidental propagation of a species due to anthropogenic activities; 2) colonization during which the newly introduced species is able to reproduce itself and generate a colony that is self-perpetuating and 3) naturalization, at this stage, the species forms self-sustaining populations, spreads over a considerable area and becomes a componentof the native vegetation (Richardson *et al.*, 2000). Because various terms have been used ininvasion ecology, Richardson *et al.*(2000)proposed a somewhat standardized terminology to reduce confusions in this field(Table 2.1).

Invasive species negatively affect human society both directly and indirectly. First, they can directly affect human health or well-being (Pyšek and Richardson, 2010). For example, *Ambrosia artemisifolia* is indigenous to North America but significantly increased the rate of allergy in France since its introduction (Laaidi *et al.*, 2003).Secondly, invasive species can also affect human productivity. For example, among terrestrial invasive species, *Chromolaena odorata* now dominates millions of hectares of arable lands in tropical and subtropical regions, as a noxious weed (Zachariades*et al.,* 2009).

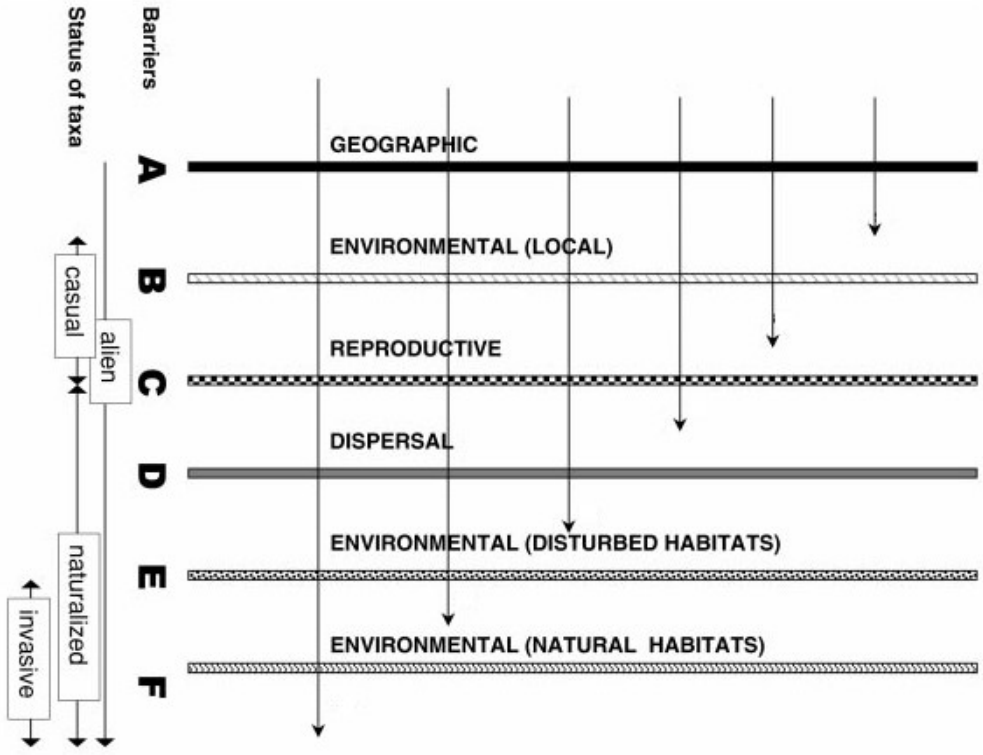

Figure 2.1. The main barriers that can impede the spread of invasive plants

Introduced plant species that overcomethese barriers are considered invasive (Source: Richardson *et al*., 2000).

Table 2.1. Terms used in plant invasion ecology

Term(s)	Definition
Alien plants	Plantsthat have been accidentally or intentionally introduced in new areas by human agency (synonyms: non-native plants, non-indigenous plants, introduced plants,exotic plants).
Casual alien plants	Non-nativeplants that cangrow and reproduce seldom but are unable to establish self-perpetuating populations. Such plants must relyon multiple introductions to persist (synonyms: adventive, transient plants).
Naturalized plants	Alien plantsthat reproduce constantlyand produce self-sustaining populations, that is without human agency.
Invasive plants	Naturalized plantsthat produce large populations and spread widely from entry points (rate of spread: morethan 100 m in less than50 years for plants relying on seed production).
Weeds	Plants (not necessarily non-native) growing where they are not desired.They usually pose environmental and/or economic problems (synonyms: environmental weeds, plant pests).
Transformers	A subdivision of invasive plantsthatcan irreversibly modifyecosystem processes and functioning.

Table adapted from Richardson *et al.*(2000)

Similarly, in aquatic ecosystems,*Eichhornia crassipes* continues to pose serious socio-economic challenges globally (Villamagna and Murphy, 2010). In general, invasive plants have significantadverseeffects on ecosystemdiversity, processes andfunctioning. Many reviews and meta-analyses have shown that biological invasions consistently lead to local biodiversity losses (Powell *et al.,* 2011; Vilà *et al*., 2011; Gioria*et al*., 2014), changes in nutrient cycling (Ehrenfeld 2003; Liao *et al.,* 2007) and losses of ecosystem services in invaded habitats (Pejchar *et al.,*2009).

Invasive plants such as *Bromus tectorum, Centaura stoebe* and *Euphorbia esula* have been reported to differently but consistent negative effects on soil properties (Gibbons *et al.,* 2017). These invasive plantsreduced diversity and either increased or decreased soil pH, Potassium, Nitrate, Magnesium and Sulphate concentrations in invaded plots (Gibbons *et al.,*2017). In the same vein, Osunkoya and Perrett (2011) reported thattotal Nitrogen, organic carbon, pHand Calcium were significantly higher in soils in which *Lantanacamara* was established compared to soils where itwas absent. They concluded that this negative influence of this species on soil physic-chemical properties was a strategy to make underlying soils more suitable for its own growth (Osunkoya and Perrett, 2011).

Invasive species can also drastically affect seed banks, where for example, Gioria and Osborne (2009) showed that *Gunnera tinctoria* formed large and persistent seed banks in invaded communities. These studies highlighted the need for more insights in the processes and impacts associated with biological invasions since outcomes depend both on the invader and the type of habitat under consideration among other factors.

2. 2 Ecological impacts of invasive species

Plant invasions have brought about important adverse impacts on habitat diversity and ecosystems processes all over the world (Ehrenfeld, 2010; Vilà *et al*., 2011; Pyšek *et al*., 2012).Therefore,in recent years, research hasbeen extensively carried out to document and understand the impacts of invasive plants on biotic and abiotic components of resident communities. In most instances, invasive plants species reducedthe diversity of invaded communities (Alvarez and Cushman, 2002; Gioria and Osborne, 2010;Hejda *et al*., 2009; Powell *et al*., 2011). In theirinvestigation of the impacts of thirteen invasive plants on several plant communities in the Czech Republic, Hejda *et al.*(2009) reported that 11 of the invaders reduced species diversity

and richness in the invaded plots with some of the plots losing up to 90% of native species. Alvarez and Cushman (2002) showed that invasion by *Delairea odorata* was associated with a 31% and 88% decline in diversity and abundance respectively of native seedlings compared to non-invaded plots. Furthermore, these authors also showed that after two years of removal of the invader 10% increase in native species richnesswas recorded compared to invaded plots thereby demonstrating the suppressive effect of *D. odorata*.

Invasive species can modify soil properties and nutrient cycling (Evans *et al*., 2001; Ehrenfeld *et al*., 2003; Liao *et al*., 2007; Osunkoya and Perrett,2011; Abella *et al*., 2012;Nielsen *et al*., 2014; Muvengwi and Ndagurwa,2015;Ruwanza and Shackleton, 2016). For example, the studies of Osunkoya and Perrett (2011) and that ofRuwanza and Shackleton (2016), in South Africa andAustralia respectively showed that*Lantana camara*invasion increased several soil properties including moisture, pH, Calcium, organic C and total N. In the same vein, Abella *et al.*(2012) reported that soil NO_3-Nand organic Carbonincreased by about twofold in patches invaded by *Pennisetum ciliare*. In general, the ecological impacts of biological invasions on soil properties depend on the invasive species, invasion stage and characteristics of resident communities. For example,*Chromolaena odorata* invasions have been reported to induce inconsistent effects on soil physico-chemical properties ranging from no alterations in Carbon and Nitrogen pools to important increases in the levels of these elements in severe infestations of about a decade old (Wei *et al.,* 2017).

Many current works investigating the impacts of invasive plants on ecosystems are based on the aboveground vegetation, whereas only few works have investigatedmodifications in soil seed banks concerningplant invasions(Gioria *et al.,*2014). This review revealed two important findings: (1) in most cases, species density and richness of seed banks in invaded plots are significantly lower and (2) propagules of invasive plantsare usually the most abundantin invaded area. These authors emphasized on the need for more seed bank-based studies in order to better understand idiosyncratic impacts of plant invasions.

2. 3The role of plant traits in invasiveness

2. 3. 1 Phenotypic plasticity and plant invasiveness

Plants acquire resources from their surroundings and share these among three most important life functions, generally classified as growth, reproduction and defence. These functions tend to be mutually exclusive and as such, within a plant body, resources that are allocated to any one function automatically become unavailable for others (Bazzaz *et al*., 2000). Plants that can optimally adjust resource partitioning under varying conditions usually exhibit enhanced competitivenessthat enables them to thrive in broad range of abiotic conditions (Pyšek and Richardson, 2007).

Adaptive phenotypic plasticity denotesthe ability of a particular genotype to produce dissimilar, functionally appropriate phenotypes under diversehabitats (Sultan, 1995). Baker (1965) was the first to submit thesignificanceof phenotypic plasticity in biological invasions. Therefore, a high level of plasticity mayhelp expand the ecological niche of alien plants and promote competitiveness and invasiveness (Sultan, 2001; Pyšek and Richardson, 2007; Ruprecht *et al.,* 2014). Invasive species generally achieve a wide soil and climatic amplitude. The workof Claridge and Franklin (2002) indicates that the invasive Japanese stilt grass (*Microstegium vimineum*)grown under different light and nutrient levels showed extreme plasticity under these varying conditions. In the same vein, Gupta and Narayan (2012) reported that the spread of the alien weed *Chonopodiummurale* acrosscontrastingenvironmental conditions in tropical India was as a result of its high levels in phenotypic plasticity,reproduction and nutrientacquisition across a range ofnutrient-poor soils.

Ecological investigations with regards to phenotypic plasticity of invasive plants are scant. Chukwuka *et al.* (2007b) demonstrated plasticity in *T. diversifolia* under screen house conditions. These authors showed that this plant accumulates biomass in a linear way with to increasing levels of nutrient, light and water. Just as in Chukwuka *et al.*(2007b), most studies on invasive species are limited to biomass partitioning (Muoghalu, 2008; Qi *et al.,* 2008). In other words, most studies so far have used dry mass as a measure of resource allocation and phenotypic plasticity.

Reproductive Allocation (RA) is the fraction of a plant's total resources dedicated to its reproductive structures. As mentioned above, it has been a tradition to express RA as the fraction of dry weight of fruits (and ancillary structures) to that of the whole

plant at the time of harvest. Biomass-based estimations of RA have been shown to be generally inadequate (Fenner and Thompson, 2005). Moreover, Bazzaz *et al*. (2000) pointed out some considerable difficulties associated with estimating RA using biomass in perennial polycarpic plants as well as inconsistencies arising from the time of harvest and losses (or omission) of deciduous parts. In spite of this, the majority of studies onRA still focus on biomass allocation to the detriment of important nutrients that have been recommended as the suitable "currencies" for measuring RA, especially when their availability strongly limits plant growth (Thompson and Stewart,1981; Chapin, 1989).

Although the primary focus of soil and plant nutrient testing is nutrient management for enhanced crop production, the application of nutrient analysis methods in other areas of plant science has helped understand how resources are allocated to essential plant functions such as growth, reproduction and defence (Obeso, 2002). Presently, fast spectroscopic techniques are emerging whereby the concentrations of nutrients in plant organs can be determined with little sample handling and at relatively low costs (van Maarschalkerweerd and Husted, 2015). With such technological advances, it is expected that studies on plant resources allocation will drastically shift from the much labour-intensive and time-consuming biomass-estimated RA in the nearest future.

Most of the available studies comparing RA across different currencies have demonstrated that the allocation of biomass tends to differ from that of important nutrients. For example, in *Senecio vulgaris,* RA amounted to 12% of biomass while that of nitrogen,potassium and phosphoruswere respectively 21%, 37% and 4%(Fenner and Thompson, 2005). In addition, other studies have identified a correlation among some RA currencies (Hemborg and Karlsson, 1998; Witkowski and Lamont, 1996) thereby shedding more light into the long-standing question of the most adequate currency for quantifying resource allocation to reproduction, otherwise known as the "currency issue" (Abrahamson and Caswell, 1982; Fenner and Thompson, 2005; Méndez and Karlsson, 2007).

With the aim to compare RA in *T. diversifolia*, this study seeks to investigate the lifetime RA of nitrogen, potassium and phosphorus in thisplant(Bazzaz *etal*., 2000).This would help conclude whether or not RA of these nutrients varies under varying conditions, that is, at several heterogeneous sites and assess the role of

plasticity in RA vis-à-vis invasiveness in *T. diversifolia*. Nitrogen, Phosphorus and Potassium were selected because they have been previously reported to limit its growth (Chukwuka *et al*., 2007b). Reproductive allocation of biomass in this species has been studied in Zambian populations (Muoghalu, 2008) and this species was shown to atypicallyinvest much less biomass in its reproduction. Therefore, exploring RA using other currencies in *T. diversifolia* could help understand its role and ability to respond to fluctuating resources in its competitiveness.

2. 3. 2 Breeding systems and plant invasiveness

In its broad sense, the terminology "breeding systems" (or mating systems or sexual systems) refers to any aspect of sex expressions in higher plants which affects the relative genetic composition of future generations. In pollination ecology, knowledge of breeding systems is essential in evaluating how pollination rates and types relate to seed production and subsequent gene flow between plant populations (Dafni, 1992; Hao *et al.,* 2011).

The breeding system can be inferred from thepollen to ovule ratio (P/O)(Cruden, 1977). The Pollen to ovule ratio is the amount of pollensto that of ovules in a flower. This ratio has been widely used as an indicator of the breeding system of angiosperms since the seminal study of Cruden (1977). Lower P/O values correspond to obligate autogamy or uniparental reproduction while higher values are common in obligately xenogamous species, that is, outcrossing species (Table 2.2). Breeding systems are diverse in angiosperms and have been classified based on several biochemical and morphological features including self-incompatibility/self-compatibility, variation in style and stamens length, that is,heterostyly or enantiomorphyas described by Dafni (1992) and summarized in Table 2.3.Several methods have been used to characterize plantbreeding systems (Dafni,1992).

Two effective and complementary methods include the pollinator exclusion and outcrossing rates. Pollinator exclusion as the name implies consist in preventing pollinators from transferring pollen from one flower to another. This method is essentialin pollination studies and reproductive biology (Dafni, 1992;Kearns and Inouye, 1993). It is based on the use of pollen exclusion bags made from materials with varying attributes (Neal and Anderson, 2004). Observation is usually made on

bagged and/or open emasculated flowers (when possible) as well aswith intact flowers and outcrossinglevels which can be determined (Dafni, 1992).

According to Baker's rule (Baker, 1955; Stebins, 1957), plants that are capable of autonomous sexual reproduction have higher chances to establish in novel ranges than those that rely on pollinators. In other words, the capability of a plant to invade new habitats ispromoted by reproductive self-compatibility rather than self-incompatibility. There has been contrasting evidence on the breeding systems of invasive plants species with some studies documenting widespread self-compatibility in invasive species and other suggesting self-incompatibility. This is illustrated in the assessment of Rambuda and Johnson (2004) who reported that 12 out of 17 invasive plants in South Africa were autonomous self-pollinating species. In the same vein, Hao *et al*. (2011) assessed the mating systems of a dozen of invasive plants in China and found that eight of them relied on self-compatibility for their establishment. In contrast, other studies showed that some invasive plants such as *Coreopsis lanceolata* (Hao *et al*., 2011); *Mikania micrantha* (Hong *et al*., 2007), *Bidens pilosa* (Yan *et al*., 2016) were not self-compatible and therefore depend on external agencies for pollination.

2. 3. 3 Reproductive traits and plant invasiveness

From the time biological invasions became a central issue in ecology in the 1980s, the major goal has been to identify species traits that are linked with invasiveness (Pyšek and Richardson, 2007). These authors discussed some of these traits and concluded that most reproductive traits play an essential function in the success of invasive plant species. Therefore, two basic options are available for an alien plant to successfully establish in a new habitat, it must either have adequately high level of plasticity and a wide ecological amplitude or undergo rapid genetic changes to achieve high levels of adaptation (Richardson and Pyšek, 2006). Among the reproductive traits that have been identified as important drivers of plant invasiveness, high fecundity or prolific seed production (Tiebre *et al*., 2012; Batish *et al.,* 2012); seed dormancy and germination behaviour, especially the capacity to germinate under a wide range of environmental conditions (Leal *et al.,* 2013; Javaid and Tanveer, 2014) have been of great importance.

Table 2.2. Pollen to ovule ratio and corresponding breeding

P/O ratio range	Breeding system
2.7 - 5.4	Cleistogamy
18.1 - 39.0	Obligate autogamy
31.9 - 396.0	Facultative autogamy
244.7 - 2588.0	Facultative xenogamy
2108.0 - 195,525.0	Obligate xenogamy

Table adapted from Cruden (1977)

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Table 2.3. Classification of breeding systems of flowering plants

Class	Description
A. Spatial arrangement of male and female organs	
I Individual plants	1. Hermaphrodite: individual plants bearing only bisexual organs
	2. Monoecy: individual plants bearing male and female flowers
	3. Andromonoecy: individual plants bearing bisexual and male flowers
	4 Gynomonoecy: Individual plants bearing bisexual and female flowers
	5 Polygamonoecy: Individual plants bearing bisexual, male and female flowers
II Groups of plants	1. Dioecy: individual plants with either female or male flowers
	2. Androdioecy: individual plants with either bisexual or male flowers
	3. Gynodioecy: individual plants with either bisexual or female flowers
	4. Polygamodioecy (trimonoecy): individual plants with either bisexual, male or female flowers
B. Temporal or spatial isolation of female and male organs within a flower	
I	Protandy: pollens released from anthers before stigmas become receptive
II	Protogyny: stimas become receptive before pollen is released from anthers
III	Herkogamy: female and male organs spatially separated but mature simultaneously
C. Biochemical recognition or rejection and self-incompatibility of alleles	
I.	Self-incompatibility: No fruit set for pollinations from pollen and stigma with similar alleles
II.	Self-compatibility: all pollinations result in fruit set
D. Breeding systems based on variations in the length of style and stamen	
I	1. Distyly: Individual have flowers with a long style and short stamen or vice versa
	2. Tristyly: Individual have either short-, mid- or long-styled flowers in relation to length of stamens
II.	Enantiostyly (Enantiomorphy): Individuals have both flowers with the deflection of style either to the left or right of the flora axis

Table adapted from Dafni (1992).

2. 3. 3. 1 Fecundity and seed production

Two metrics are often used to characterise seed production in invasive species, namely fecundity and seed production (Moravcová *et al.,* 2015). Fecundity also known as plant propagule number, is the mean number of viable seedseach plant can producewhile seed production, also known as population propagule number is the mean number of seeds per square metre(Moravcová *et al.,* 2015).For example, a single individual of *Parthenium hysterosphorus* Lcan produce more than 15,000 seeds that aredispersed by wind and water (Batish *et al.,* 2012).

A high reproductive potential has been shown in many invasive plants including *C. odorata*(L) King and Robinson, which can produce up to 2,000,000 fruits per plant although more than half are not viable (Tripathi *et al.,* 2012). *Mikania micrantha*kunth produces a huge number of seeds, that is 170,000 seeds/m^2 (Kuo *et al*., 2002). *T. diversifolia* has also been recognized as a prolific seeder. Studies carried out in Cote d'Ivoire and China showed that its seed production ranged between 10,296 - 58,520 seed/m^2 (Tiebre *et al.,*2012) and 80,000 - 160,000 seed/m^2 (Wang *et al.,* 2004) respectively. For such a species that relies on high reproductive output, knowledge of its seed ecology is importantfor an understanding of its invasiveness.

2. 3. 3. 2 Allelopathy

Allelopathy includes a range of biochemical interactions whereby the growth of plants is either inhibited or promoted by their neighbours. This interaction has been considered as an important process in plant invasion and led to the formulation of the Novel Weapon Hypothesis, which proposes that some invasive plant speciesare successful as a result of biochemical "weapons" that act as potent allelopathic agents (Callaway and Ridenour, 2004). The incidence of allelopathy in invasive plant taxa is still a subject of debate (Parepa and Bossdorf, 2016), although this phenomenon is usually associated with the world's worst terrestrial invasive plants. For example, the allelopathic impacts of *L. camara* has beendemonstrated through drasticdecreases in seedling recruitment and stunted growth of almost all neighbouring species (Sharma and Raghubanshi, 2011).

Lantana camara contains 14 phenolic compounds that potentially reduce germination,developmentand growth ofseedlings (Khan *et al.,* 2003).A number of aromatic alkaloids have been be extracted from all parts of this plant (Khan *et al*.,

2003). Soil invaded by*Ageratum conyzoides*L has been shown to be rich in non-volatile allelochemicals (Singh *et al*., 2003) which are phytotoxic and suppress the growth of surrounding plants. Similarly, radicle length of cropsgrown in plots previously infested by*A. conyzoides*in wasstunted (Singh *et al*., 2003). The soil in proximity of *Mikania micrantha*plants was shown to inhibit the growth and germination of other species. (Chen *et al*., 2009). They also suggested that allelochemicals from this plant improved nutrient availability, and helpedthis species successfully invade and establish in new habitats. Similarly, Shao *et al.* (2005) extracted and isolated three sesquiterpenoids from *M. micrantha*, namely, deoxymikanolide,dihydromikanolideand 2, 3-epoxy-l-hydroxy-4,9-germacradiene-12,18:15,6 diolide, which strongly inhibit seed germination and seedling growth of crops.

2. 3. 3. 3 Germination

Germination is one of the most studied aspects of invasive plants. Viera *et al.*(2010) showed that seed germination in*Clausena excavata*Burm.fil. was optimal for wide thermal amplitude and both in light and darkness thereby suggesting its high colonization ability of both open and shaded environments.Similarly, Wang *et al*. (2012) reported a two to five-fold higher germination of achenes of*Ageratina adenophora*(Spreng.) King & Robinsonunder light conditions than under dark conditions. However, this did not respond to a variety of dormancy-breaking treatments including low temperature exposure, soaking in KNO_3, salicylic acid and polyethylene glycol, under either light or dark conditions. These authors suggested that this behaviour is an indicator of the fast spread of this weed when its buried seeds are near the soil surface.Seed germination in *Lantana camara*L has been shown to be as low as 4-45%because of dormancy and meiotic instability (Sharma and Raghubanshi, 2012). According to these authors, this strategy mitigates the extremely high rates of seedling survival occurring under field conditions.

As pointed out by Baskin and Baskin (2014), seed dormancy does not simply mean the absence of germination. Two groups of factors are responsible for the absence of germination: first, the absence of favourable environmental conditions, for example, seeds stored in an envelope (that is, absence of moisture) or buried in mud (that is, insufficient light and/or oxygen) and secondly the presence of a trait that precludes itsgermination. The absence of germination due to endogenous characteristics of the

seed was termed organic dormancy (versus imposed for exogenous factors) in the 1970s (Nikolaeva, 1977). Organic dormancy is the class of dormancy that is of primary importance to seed biologists and ecologists (Baskin and Baskin, 2014). Therefore, seed dormancy can be defined as a condition whereby germination is impeded in an intact, viable seed even under adequate conditions of water availability and temperature requirements.

Dormancy is a fitness trait associated with dispersal and persistence of invasive plants (Presotto *et al.,* 2014). Baskin and Baskin (2004) proposed astandard and experimentally useful definition of dormancy: "a dormant seed does not have the capacity to germinate in a specified period of time under any combination of normal physical environmental factors that are otherwise favourable for its germination".

Nikolaeva developed the first comprehensive classification scheme for seed dormancy (Nikolaeva, 1969). This served as the basis for a classification system that includesdormancy types, levels and classes (Baskin and Baskin, 2014). These authors expanded Nikolaeva's hierarchical classification system to include divisions, subdivisions, classes, subclasses, levels and types of dormancy and presented a dichotomous key for seed dormancy (Table2.4). Therefore, five classes of dormancy have been recognized namely,physical dormancy (PY),physiological dormancy (PD), combinational dormancy (PY + PD),morphological dormancy (MD) and morphophysiological (MPD)(Baskin and Baskin, 2014).

Dormancy plays an important ecological function in angiosperms (Fenner and Thompson, 2005; Baskin and Baskin, 2014). It is an evolutionary trait that regulates the timing of germination to increase the chances of seedling survival in certain conditions (Fenner and Thompson, 2005). Germination characteristics, especially dormancy is an essential trait associated with invasiveness. Generally invasive species germinate better, earlier and under a wider range of conditions compared to native species (Pyšek and Richardson, 2007). Baskin and Baskin (2014) emphasized on the need to conduct germination studies in ecologically meaningful manner, that is the avoidance of harsh treatments (e.g. acid scarification) that the seeds cannot encounter naturally. They proposed a series of guidelines for studying germination ecology. Some of the most important guidelines are summarized as follows:

a)Using mature seeds: Seeds are not to be collected until they are mature.

b) Checking for embryo: Some seed are embryoless due to many factors including death of embryo, degeneration of zygote, infertile hybrids, and degeneration of ovule or insect infestation. A simple way to check for the presence of embryo is by observing sectioned seed under a dissecting microscope.

c) Testing for germination using freshly collected seeds: Seeds should be tested preferably within 7 to 10 days after collection because they can experience changes in germination response during a longer storage period.

d) Testing for imbibition of water: This is an important step in germination studies. A common way to test for water imbibition is to place seeds or fruits on a moist substrate at room temperature then weighing them at regular time intervals after blotting them dry. A substantial increase in seed mass suggests that they have a permeable coat. On the other hand, little or no increase at all in seed mass is indicative of seed coat impermeability.

e) Using intact natural dispersal units: The authors recommend testing natural dispersal units without attempting to exclude accompanying anatomical structures, for example hulls on grass caryopses.

f) Replications: In practice, germination testsmust to be replicated to obtain statistical meaningful results. The authors recommend the use of 50 seeds per treatment.

g) Disinfectants and fungicides: Baskin and Baskin (2014) noted that seeds of most plants are naturally designed to resist fungal attacks (although there are exceptions). Therefore, fungalattacks can be minimized by using fully mature seeds. They also noted that fungi can help in selecting for good seeds by attacking inferior or dead seeds. In cases where fungal infection cause a problem, dispersal units can be soaked about 10 minutes in a diluted solution of sodium hypochlorite (for example, 0.5% NaClO) and rinsed in water.

h) Seed storage under natural or simulated environmental conditions: When testing for germination, seeds should also be returned to their collection siteto assess the effect of natural habitat conditions on their germination. This is usually done by bagging seeds and burying them at collection sites and regularly testing germination.

Table 2.4. The expanded hierarchical classification system for seed dormancy

Class	Description
Division I:	Imposed/quiescent/enforced dormancy: seed does not germinate due to lack of favourable abiotic conditions (no subcategories)
Division II:	Organic/innate dormancy: seed does not germinate due to intrinsic properties
Subdivision I:	Exogenous dormancy
Class I:	Physical (no subcategories)
Subdivision II:	Endogenous dormancy
Class II.	Morphological dormancy
Class III:	Physiological dormancy
Subclass I:	Regular (3 levels, Nondeep, intermediate and deep)
Subclass II:	Epicotyl (2 levels: nondeep and deep)
Class IV.	Morphophysiological
Subclass I:	Simple (6 levels: Nondeep, Intermediate, Deep, Nondeep ecpicotyl, Deep epicoty, Deep simple double)
Subclass II:	Complex (3 levels: Nondeep, Intermediate and Deep)
Class V.	Combinational (3 levels: Nondeep, Intermediate and Deep)

Table adapted from Baskin and Baskin (2014)

i) Length of germination test period: Germination tests mustlast long enough to allow seedsample time to germinate. Baskin and Baskin (2014)recommendedthat germination tests should be completed after 4 weeks given that most seeds germinate (if non-dormant) within 10 days or less.

j) Testing for viability of non-germinated seeds: At the end of germination tests, all seeds that fail to germinate should be tested for viability. This is done using a variety of method including the "pressure test" and the "cut test", which entail applying slight pressure with a pair of forceps and cutting the seeds open.

2. 3. 3. 4 Seed bank

Repeated soil sample collections from within invaded experimental areas isa useful approach forassessing seed bank longevity and rates of depletion (Bear *et al.,* 2012).Another common approach consists in burying a known number of seeds in permeable bags in the area from which they were collected, then exhuming the bags at regular intervals and testing for viability (Tamado *et al.,* 2002; Schwienbacher*et al.,* 2015). These repeated trials exclude factors such as seed emigration, immigration ormortality due to predation and ensures that depletion is a result of natural seed mortality or germination (van Mourik*et al.,* 2005).Nonetheless, the seed bag burial method has been shown to be sensitive to the number of buried seeds per bag (van Mourik *et al.,* 2005).

Some studies have examined the role of soil seed banks in relation to the invasive potential of plants and results suggested that invasive species usually have larger and persistent seed banks (Tamado *et al.,* 2002; Wijayabandara *et al*., 2013; Gioria *et al.,* 2014). The study of Meyer (2010) on the seed bank density of *Miconia calvescens* using soil samples collected at different years (1992, 1993 1995 and 2008) showed that there was a rapid drop in the number of seeds germinating between 1993 and 1995 (4,500 to below 1000 seeds/m^2). However, germination was also recorded in 2008, which was 16 years after keeping the seed bank away from inputs thereby indicating that this invasive species relies on a persistent seed bank for its success. *Parthenium hysterosphorus* has been shown to rely on a copious seed banks with seeds that can retain their viability for many years. About 50% of the seed bank of this plant remains viable for at least 2 years (Tamado *etal*., 2002).

2. 4 Ecological niche modelling

2. 4. 1 The ecological niche concept

The concept of niche has been essentialin ecology (Hutchinson,1957; Holt, 2009). The term "niche" was introduced by Joseph Grinell to denote the set of environmental conditions in which a species can live (Grinnell, 1917). This concept was later formalized by Hutchinson (1957) who considered the environmental niche of a species as an "n-dimensional hypervolume", with each of its points corresponding to a condition of the environment allowing an organism to exist *ad infinitum*. Additionally, Hutchinson (1957) pointed out the difference between the fundamental (also referred to as grinellian niche) and the realized niche of a species. Conversely, the fundamentalniche is delimited by the species' physiological tolerance (its capacity to thrive in a given range of environmental conditions) along environmental gradients whereas the realizedniche corresponds to a compartment of the fundamental niche where the speciespossesses a competitiveadvantage. In other words, the realized niche of a species is constrainedin its fundamental niche bycompetition(Figure 2.2). According to the fundamental or grinnellian niche concept (Figure 2.2 A), a species can only occur anywhere environmental conditions are suitable. Hutchinson's realized niche concept (Figure 2.2 B) proposes that a species will be outcompeted and therefore absent in some parts of its fundamental niche.

Indeed, depending on the biological question at hand, different senses of the term "niche" appear in the ecological literature. In line with Peterson *et al.,* (2011), we consider only the niche concepts that are relevant to one of the objectives of this thesis, which is to estimate the areas of distribution of species. Thus, in this we view a niche as the set of ecological conditions required for the survival of a species at a given location, together with this species' impacts on its habitat and other neighbouring species with which it interacts.

2. 4. 2 Ecological Niche Models

Ecological Niche Models (ENMs),commonly known Species Distribution Models (SDMs) are mathematical models used to estimate and map the fundamental (potential) niche, the realized (actual) niche or the climatic niche (when solely based on climatic data) of a species (Franklin, 2009). Two approaches can be used in estimating species distributions. The first approach is based on mechanistic models, which specifically incorporate known species' tolerances to environmental conditions such as the

maximum or minimum temperature at which a species can survive. Mechanistic species distribution models require detailed data on the eco-physiological responses of species to abiotic conditions. However, such data are often not available (Franklin, 2009). The second approach is the correlative approach, which is widely used in species distribution models. Correlative species distribution models are useful when detailed information about species' tolerances to some environmental variables is lacking. It is based on the assumption that the geographical distribution of a species is indicative of its ecological requirements (Guisan and Zimmermann, 2000).

Correlative ecological niche modelling consists of relating a species' field observation to environmental factors through a statistical model in the form of response surfaces that are used to predict the probability of occurrence of that species under given environmental conditions (Guisan and Thuiller, 2005).Ecological niche models can also be projected in space to determine the probability of occurrence, that is, the suitability index or the likelihood of encountering a species in a given area (Guisan and Zimmermann, 2000).

Ideally, the process of building an ENM follows six stages: 1) conceptualization, 2) data acquisition and preparation, 3) model fitting, 4) statistical evaluation, 5) spatial prediction and 6) appraisal of model applicability. These steps and approaches are discussed in details by Guisan and Thuiller (2005) and summarized in Figure 2.3. More details are given for the second step in Table 2.5.

2. 4. 3. Ecological niche modelling (ENM) for studying invasive species

Preventing and monitoring biological invasions is one of the chief applications of ENMs (Thuiller *et al*., 2005; Broennimann and Guisan, 2008; Jiménez-Valverde *et al.,* 2011). As a remarkable example, Suárez-Mota *et al*. (2016) employed ENM projections to determine that populations of *Chromolaena odorata* invading South Africaoriginate from northern Mexico and southern tropical South America. Based on this type of findings, possible quarantine measures can be adopted against invasive species. In the same way, Goncalves *et al.*(2014) compared the native niche of *Lantana camara* in South America, Australia,Africa and India.

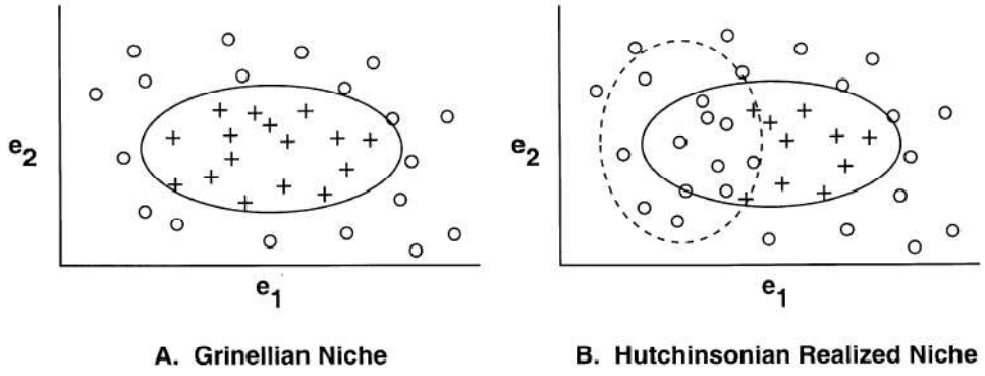

Figure 2.2. Relationship between the niche and the distribution of a species

Here, $e_1,\ e_2,\ e_3 \ldots e_n$ are n independent environmental variables (only e_1 and e_2 are represented). The solid oval depicts the fundamental niche, which isa combination of the$n$ environmental variables ($e_1,\ e_2,\ e_3 \ldots e_n$) in which the species can indefinitely to exist. "+" indicates the occurrence of the species in an area characterized by given values of e_1 and e_2 and "o" indicates its absence(Source: Pulliam,(2000)).

These authorsshowed that although this species inhabitedportions of its native niche in Australia andAfrica,and as a result may not pose a serious threat in these continents, this was not the case for India where a significant shift in its niche portends negative consequences. Additionally, Ecological Niche Model predictions for *Tecoma stans* revealed that this species is likely to invade areas where it has not yet been observed in Africa, Australia and American (Faleiro *et al*., 2015). This study and many others (e.g.Raimundo*et al.,* 2007; Tererai and Wood, 2014; Wang *et al.,* 2017) therefore can support informed decisions for anticipating and managing plant invasions.

Ecological Niche Models can also be projected in the future to predict the geographical distribution and niche dynamics of invasive species under climate change (Fandohan, *et al*., 2015; Wan *et al.,* 2017; Camenen *et al.,* 2016). For example, Wan *et al.*(2017) used ENMs to predict the distribution of suitable habitatsfor eight representative alien invasive plants in China under climate change. The assessment of the invasibility of *C. odorata* in protected ecosystems in West Africa by Fandohan *et al.* (2015) showed that under the current climate, about 73% of the total lands in these protected areas were highly suitable for this species. This percentage has been predicted to decrease drastically (< 15%) in the future, between 2041 and 2060.

Niche conservatism is one essential assumption that underlies Species Distribution Models. This principle states that the ecological niche of species does not change in space and over time (Wiens *et al.,* 2010). The niche of a species is said to be conserved when it lives in the same environmental conditions in both its introduced and native ranges (Guisan and Thuiller, 2005; Wiens *et al.,* 2010). On the contrary, if these conditions differ, then the species would have shifted its niche.

The prevalence of niche shifts in the course of biological invasions has been a subject of controversy. Some authors argue that niche shifts are widespread for invasive plants (Early and Sax, 2014; Broennimann *et al.*, 2014; Wan *et al.,*2017; Atwater *et al*., 2018) and others support niche conservatism (Petitpierre *et al*., 2012; Dellinger *et al.,* 2016). These divergent results have been partly attributed to several factors including differences in modelling approaches as pointed out by Guisan *et al*. (2014) and individual species traits such as the breeding system (Barrett, 2011).

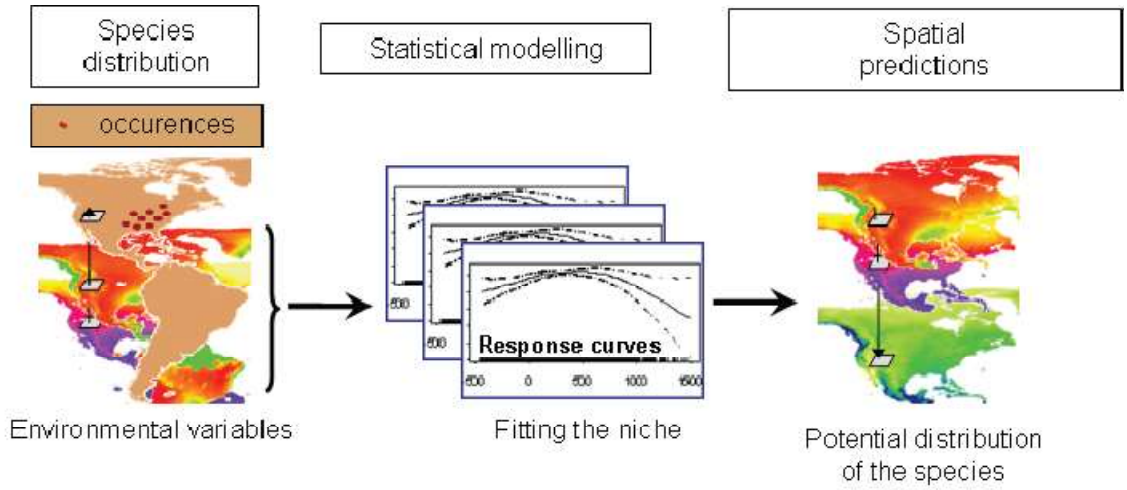

Figure 2.3. Common workflow used in ecological niche modelling

The major steps include acquiringspecies occurrences during surveys, fitting its niche in the environmental space and making predictions from models.(Source: Petitpierre,2013).

Table 2.5. Examples of GIS-based data sources that can be used in ENM

Data type	Data details	Website
Biotic data	Species occurrences (Longitude, Latitude)	GBIF : https://www.gbif.org/ iNaturalist: https://www.inaturalist.org/
Abiotic data	Climate (past, present and future	WorldClim: http://www.worldclim.org/ CHELSA: http://chelsa-climate.org/ https://iridl.ldeo.columbia.edu/
	Soils	SoilGrids: https://soilgrids.org/ FAO: http://www.fao.org/land-water/databases-and-software/en/
	Hydrology	USGS: https://nhd.usgs.gov/
	Topography	USGS: https://earthexplorer.usgs.gov/
	Land use/cover	USGS: https://glovis.usgs.gov/

In one of the most essential reviews on the issue of niche shift/conservatism, after re-examining many studies supporting niche shifts in invasive species, Peterson (2011) showed that the conclusions of these studies resulted from methodological artefacts. In addition, this author pointed out the problem associated with the use of a large number of environmental variables in niche assessments. This problem, which he referred to as "high dimensionality" obscures the results of analyses. In effect, high dimension is common in the literature as seen in the widespread use of the 19 bioclimatic variables offered by databases such as WorldClim (www.worldclim.org). Peterson (2011) rightly argues that if a niche is defined by a very low number of environmental variables (for example a single dimensional such as average annual precipitation) such niche is bound to be conserved. Conversely, a niche characterized by a high number of environmental variables would diverge across space. He therefore advocated for the use of a "correct" number of environmental variable, which he suggested can only be determined indirectly. Peterson (2011) concluded that ecological niches are mainly conserved over moderate to short time periods. In other words, the niche of a species can shift only after between 10,000 to 100,000 years.

There are two major methods to comparing the niches of invasive species in different ranges based on direct observations, that is, the ordination approach or model predictions, that is, ENM approach (Guisan *et al,* 2014). The first approach uses the environmental conditions at locations where a species occurs in its native habitat and compares these conditions with those prevailing in introduced ranges. This comparison has been done mainly using multivariate statistical tests such as Principal Component Analysis, PCA (Petitpierre *et al*., 2012; Broennimann *et al*., 2012) as illustrated in Figure 2.4. The ordination approach has beenfurther improved by computing smoothed densities of species presences in a gridded environmental space in order to circumventbreaks in the niche space resulting from sampling biases(Broennimann *et al*., 2012).

The second approach is based on the predictions of niche models (Peterson,2011) and compares niche overlaps in geographical space. In the ENM, models are built in both the native and exotic ranges of a species and predictions are made by transferring the fitted models into different ranges as illustrated in Figure 2.4 (Fitzpatrick *et al.,* 2007). The outcomes of ordination and ENMs have been examined by Broennimann *et al*. (2012). These authors concluded that ordination quantified niche overlap more

accurately than ENMs. However, Warren *et al.* (2010) have shown that the ENMs are particularly useful to evaluate transferability between ranges.

To benefit from the strengths of both approaches many researchers have resorted to using both complementarily (Goncalves *et al.,* 2014). Ordination is directly based on species occurrences while ecological niche models (ENMs) are based on predicted occurrences. Numbers in squares denote steps for ordination and are 1) reduction of the environmental space using PCA, 2) plotting of occurrences from each habitat in the reduced environmental space, 3) direct niche comparisons based on the plotted occurrences in each range and 4) Determination of niche change indices.

Steps for ENMs (numbers in circles in Figure 2.4) are: 1) calibration of ENMs by associating occurrences with environmental data, 2) ENM projection in geographic space, 3) determination of difference in the geographical projections and 4) determination of niche change indices. Indices of niche change often referred to as niche change metrics can be calculated from both ordination and ENM approaches. The two commonly used niche metrics are niche centroid (*C*) and niche overlap (*O*). The centroid uses Euclidian distance to measure the displacement (in environmental space) of the mean position or centre of the native niche in relation to the invasive niche or vice-versa (Broennimann *et al*., 2007).

Niche overlap estimates the environmental space overlapping between the invaded and native ranges based on Schoener's *D* index (Warren *et al*., 2008). Recently, Guisan *et al*. (2014) further characterized niche changes using a set of new metrics following their COUE scheme (*C* = change, *O* = overlap, *U* = unfilling, *E* = expansion). They defined niche unfilling (*U*) as the fraction of the native niche that is distinct from the exotic niche. In other words, this metric quantifies the set of environmental conditions unique to a species' native range. Niche expansion (*E*) corresponds to the fraction of the invaded niche that does not overlap with the native niche. *E* measures abiotic conditions found in the exotic range but absent in a species' native habitat. Using these metrics, several studies have reported overall niche conservatism for invaders (Goncalves *et al*., 2014).

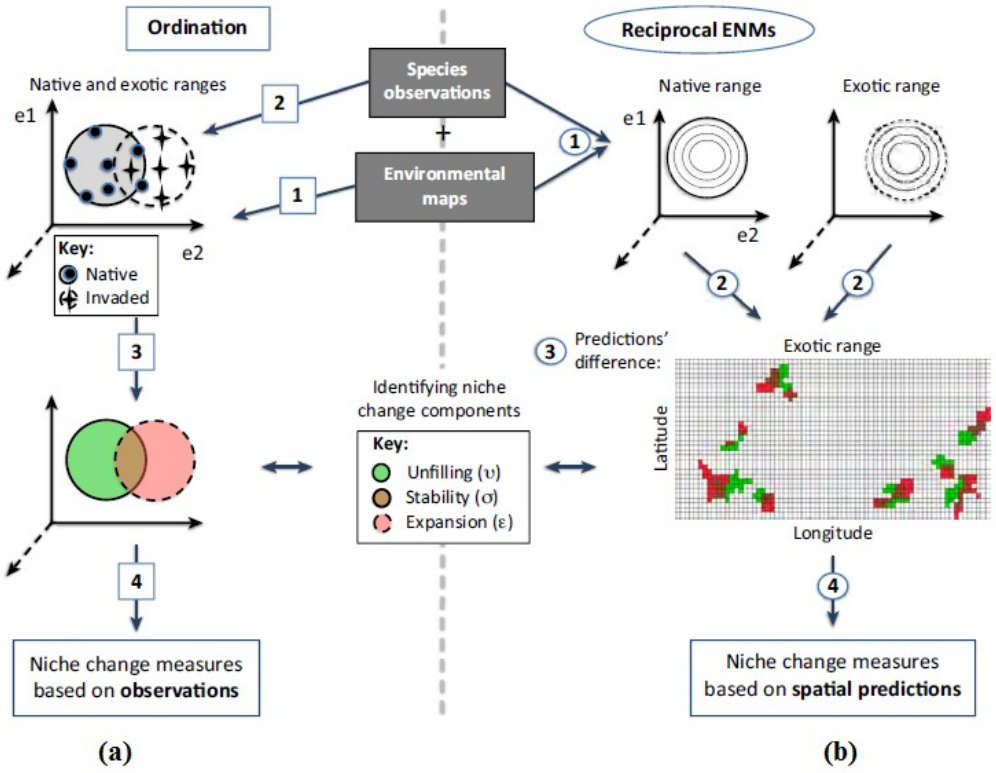

Figure 2.4. The two methods used to evaluate inter-range niche changes

The ordination approach (a) is a multivariate technique used to quantify the environmental conditions at species presence sites. The ENM approach (b) is based on correlative statistical models that are built in species-specific temporal or geographical contexts and transferring in space and time (Source: Guisan *et al.*, 2014).

CHAPTER 3
MATERIALS AND METHODS

3.1 Niche and potential ecological distribution of *T. diversifolia* in Nigeria

3. 1. 1 Determination of occurrence of *T. diversifolia*

The current and future potential geographical distributions of the study speciesand its niche dynamics were assessed in Nigeria using occurrence records from published studies and the Global Biodiversity Information Facility (GBIF). The study workflow is shown in Figure 3.1. Although road surveys were conducted using a design similar to that of Ayeni *et al*., (1997a), these data (Appendix 3) were not included in the analyses of this section. The study ranges considered are shown in Figure 3.2 with the native range of *T. diversifolia* taken as Mexico. This country had the second highest number of presence records (8,868) after Australia on GBIF in May 2018. Using the *rgbif* package (Chamberlain, 2017) in the R language for statistical software, 417 and 7 geo-referenced records of *T. diversifolia* were obtained for Mexico and Nigeria respectively.

All datasets were visually inspected for erroneous, ambiguous and duplicated records. Mexican occurrences for this species showed no dubious records unlike those in Nigeria where duplication was noted. These duplicates were manually removed thereby reducing the effective number of GBIF records for *T. diversifolia* to two in Nigeria. These two records were combined with others sourced from herbarium and published studies between 1979 and 2013 (Table 3.1). To lessen sampling bias and enhance the performance of models (Boria *et al.,* 2014), spatial filtering was done using *spThin* in R (Aiello-Lammens *et al.,* 2015). The thinning distance was set to 1 km and runs were replicated 100 times. This resulted in 311 and 117 records for Mexico and Nigeria respectively.

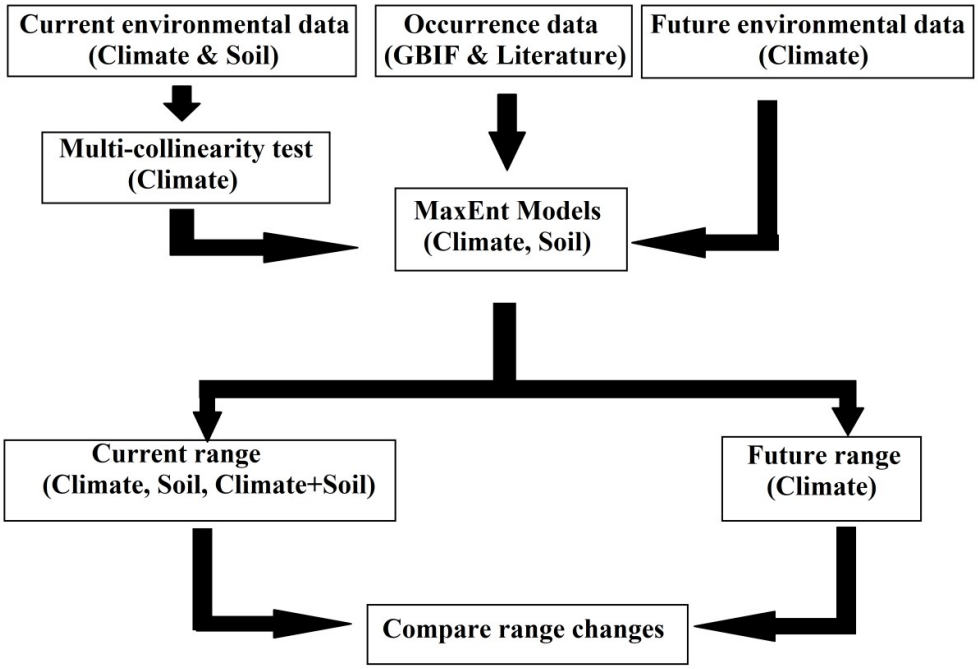

Figure 3.1: Modelling workflow used in this study

Major steps taken to model the niche ecological distribution of *Tithonia diversifolia* in this study. Figure done using Microsoft Paint Windows 8.1.

Figure 3.2. Geographic distribution of *Tithonia diversifolia* in Mexico and Nigeria

All geographical coordinates for *T. diversifolia* in Nigeria (red dots) were pooled from published studies. Native occurrences (green dots) were obtained from the Global Biodiversity Information Facility. Map done using data from Natural Earth Data (https://www.naturalearthdata.com).

Table 3.1. Published occurrence records for *T. diversifolia* in Nigeria (1973-2013)

Source	Count	Location
Ayeni *et al.* (1997a)	147	South western Nigeria
Chukwuka *et al.* (2007a)	19	South western Nigeria
GBIF	2	Mambilla Plateau
Oyewole *et al.* (2008)	1	Babcock University, Shagamu
Owoyele *et al.* (2004)	1	University of Ilorin, Ilorin
Ogundare (2007)	1	Federal University of Technology Akure, Akure
Liasu and Ogunkunle (2007)	1	LAUTECH, Ogbomosho
Fasuyi *et al.* (2010)	1	University of Ado-Ekiti, Ado-Ekiti
Ahmed and Onocha (2013)	1	University of Ibadan Forest Reserve, Ibadan
Oke *et al.* (2009)	2	Ife - Ibadan dual carriageway, Ife
Essiett and Akpan (2013)	1	Ifa Atai, Uyo
University of Ibadan Herbarium	1	University of Ibadan, Ibadan

3. 1. 2 Climate data

Current and future climatic variables for the 1973-2013 and 2041-2060 periods respectively were downloaded from the CHELSA database (Karger *et al*., 2017). This database provides high resolution (1 km) bioclimatic variables similar to those available on WorldClim (http://worldclim.org). These bioclimatic layers capture climate averages, extremes and variability (Table 3.2). They are considered as important drivers of species distributions at the global level (Pearson and Dawson 2003; Elith and Leathwick, 2009). To reduce the adverse effect of collinear variables on model performance, a phenomenon known as collinearity (Braunisch *et al.*, 2013), all variables with a Pearson correlation coefficient, *r* such that - $0.7 < r < 0.7$ were excluded from analyses.

The potential future distribution of *T. diversifolia* in Nigeria was assessed using two predictions of the Coupled Model Intercomparison Project phase 5 (CMIP5), namely the Met Office climate prediction model (HadGEM2-CC : Hadley Global Environment Model 2 - Carbon Cycle) and a Model for Interdisciplinary Research on Climate Change (MIROC-ESM-CHEM). These projections were chosen based on their dissimilarities (Knutti *et al*., 2013) and run under the 8.5 representative concentration pathway (RCP 8.5), which is the most extreme of the four climate scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) in its Fifth Assessment Report (AR5) (Stocker, 2014).These choices allowed for the evaluation of pessimistic or worst case predictions, that is, the largest possible impact that climate change would have on the distribution of *T. diversifolia* species in Nigeria.

3. 1. 3 Soil data

Seven soil physico-chemical properties were downloaded from the SoilGrids database (Hengl *et al*., 2014). This database houses global soil information at 1 km resolution including physico-chemical properties including pH, organic carbon, bulk density, Cation Exchange, sand, silt and clay fractions at six standard depths. Because *T. diversifolia* is a shallow-rooting plant, data at 15 cm depth were used (Table 3.3).

Table 3.2. List of climate data used in this study

Variable	Code	Unit
Annual Mean Temperature	Bio 1	°C/10
Mean Diurnal Range	Bio 2	°C
Isothermality (Bio 2/Bio 7) (× 100)	Bio 3	None
Temperature Seasonality (standard deviation ×100)	Bio 4	°C
Max Temperature of Warmest Month	Bio 5	°C/10
Min Temperature of Coldest Month	Bio 6	°C/10
Temperature Annual Range (Bio 5 - Bio 6)	Bio 7	°C/10
Mean Temperature of Wettest Quarter	Bio 8	°C/10
Mean Temperature of Driest Quarter	Bio 9	°C/10
Mean Temperature of Warmest Quarter	Bio 10	°C/10
Mean Temperature of Coldest Quarter	Bio 11	°C/10
Annual Precipitation	Bio 12	mm/year
Precipitation of Wettest Month	Bio 13	mm/month
Precipitation of Driest Month	Bio 14	mm/month
Precipitation Seasonality (Coefficient of Variation)	Bio 15	None
Precipitation of Wettest Quarter	Bio 16	mm/quarter
Precipitation of Driest Quarter	Bio 17	mm/quarter
Precipitation of Warmest Quarter	Bio 18	mm/quarter
Precipitation of Coldest Quarter	Bio 19	mm/quarter

Data were downloaded from the CHELSA database (CHELSA version 1.2),available from http://chelsa-climate.org/

Table 3.3. List of soil variables used in this study

Abbreviation	Variable name	Unit
BLDFIE	Bulk density (fine earth)	kg/cubic-metre
CLYPPT	Clay content (0-2 micrometre) mass fraction	%
SLTPPT	Silt content (2-50 micrometre) mass fraction	%
SNDPPT	Sand content (50-2000 micrometre) mass fraction	%
CECSOL	Cation exchange capacity	cmol/kg
ORCDRC	Soil organic carbon content (fine earth fraction)	g/kg
PHIHOX	Soil pH × 10 in H_2O	No unit

Variables were downloaded from the ISRIC World Soil Information database (SoilGrids version 0.5.1). Available from soil https://soilgrids.org/

3. 1. 4 Niche analysis

The direct, PCA-env approach of Broennimann *et al*. (2012) and Petitpierre *et al*. (2012) was used in analysing the ecological niche of *T. diversifolia* in relation to the uncorrelated variables selected among those listed in Table 3.2 and soil physico-chemical properties at 15 cm depth (Table 3.3). Briefly, this method consisted in summating the environmental space made up of these fourteen variables on the major axes of a Principal Component Analysis. The resulting environmental space was divided into a grid with 200 × 200 cells. Occurrences of the study species in each cell were smoothed using a kernel density function.

Densities of available environments were calculated using 10,000 randomly generated points in each range. Schoener's *D* index (Warren *et al*., 2008) was used to quantify niche overlap of *T. diversifolia* between Mexico and Nigeria. This indexranges between 0 (in absence of niche overlap) and 1 (when two niches completely overlap). Tests of niche equivalency and similarity were carried out by comparing the degree of Mexican and Nigerian niche overlap (*D*) to that obtained from a null distribution of 100 overlap values(Warren *et al*., 2008). These statistical tests were used to draw conclusions about niche equivalency and similarity based on occurrences of *T. diversifolia* in the study ranges (Broennimann *et al*., 2012).

The test for niche equivalency assessed if the native and invaded niches of *T. diversifolia* are identical/equivalent solely based on the occurrences of this species in both ranges. In other words, the Nigerian and Mexican niches of *T. diversifolia* would be non-equivalent or distinct if our observed overlap, *D* is significantly lower ($p < 0.05$) than that obtained from random niches. The test for niche similarity was used to further extend analyses from the species geographical locations to other surrounding habitats. All such habitats are referred to as background space. Thus, the considered niches would be similar if the observed overlap, *D* is significantly lower ($p < 0.05$) than would be expected by chance.

The framework proposed by Guisan *et al.*(2014) was followed to determine additional niche dynamics indices, namely 1) *niche unfilling* (*U*), which represents the fraction of *T. diversifolia*'s ecological niche that is occupied by this species exclusively in Mexico; 2) *niche expansion* (*E*), the part of this species niche in Nigeria that does not overlap with its indigenous niche and 3) *niche stability* (*S*), the ecological niche filled

by *T. diversifolia* both in Nigeria and Mexico. These analyses were done with the *ecospat* package (Di Cola *et al*. 2017).

3. 1. 5 Reciprocal distribution modelling

The Reciprocal Distribution Modelling approach of Fitzpatrick *et al*. (2007) was used to assess the potential geographical spread of *T. diversifolia* in Nigeria. First, models were calibrated in Mexico using environmental and occurrence data from this range (these models will be subsequently referred to as the Mexican Climate Model, MCM and Mexican Edaphic Model, MEM) and projected onto Nigeria (hereafter, reciprocal Nigerian Climate Model, rNCM and reciprocal Nigerian Edaphic Model, rNEM). Secondly, models were calibrated using occurrence data from Nigeria (Nigerian Climate Model, NCM and Nigerian Edaphic Model, NEM) and projected onto Mexico (reciprocal Mexican Climate Model, rMCM and reciprocal Mexican Edaphic Model, rMEM).

Additionally, each model was also projected in its original calibration area, that is, the model built in Nigeria was projected back to Nigeria while that of Mexico was also projected onto Mexico. Finally, the extent of dissimilarity between the observed and projected models, that is built in a Nigeria and projected onto Mexico and vice-versa was assessed. To further explore the spread of *T. diversifolia* in Nigeria, climatic and edaphic reciprocal models were merged using the maximum predicted value. These models will be hereafter referred to as merged Nigerian Climatic Model and merged Nigerian Edaphic Model, mNCM and mNEM respectively.

The potential geographical ranges of *T. diversifolia* in Nigeria and in Mexico based on current climate (1973 - 2013), future climate (2041 - 2060) and soil data were generated using the Maximum Entropy modelling algorithm (MaxEnt) version 3.4.1 (Phillips *et al.,* 2006). MaxEnt is a widely used method with a track record in modelling species' ranges using presence only data (Elith *et al*., 2006; Yackulic *et al*., 2013). However, running MaxEnt's at its defaults settings can lead to unrealistic and misleading predictions (Merow *et al*., 2013).

To select optimum values for the two parameters which have profound impacts on model performance, that is, the regularization parameter and feature classes (Merrow *et al*., 2013), the *ENMeval* package (Muscarella *et al*., 2014) was used to calibrate a set of models with all possible regularization parameter and feature classes combinations.

Forty-eight MaxEnt models were calibrated based on 10,000 random background points in Mexico and Nigeria respectively. The complementary log-log (cloglog) MaxEnt output was used to determine habitat suitability based on current and future climates and soil data following the recommendation of Phillips *et al*. (2017).

3. 1. 6 Statistical evaluation

To carry out spatially independent model performance tests, the "block" method was executed in the *ENMeval* package to divide data into 4 spatially distinct calibration and evaluation datasets as recommended by Radosavljevic and Anderson (2014). The best models were chosenon the basis ofthe Akaike Information Criterion corrected for small sample sizes (ΔAICc =0) (Warren and Seifert, 2011). In addition, modelperformance was measured using the Boyce index (Boyce *et al*., 2002)based on default parameters in*ecospat*version 3.0 (Di Cola *et al*., 2017).This index ranges from -1 to + 1 withnegative values suggestinga poor model, whereas positive values and those near zero intimate a good and a random model respectively (Hirzel *et al*., 2006). Thisindex was calculated in two ways: using occurrence records in the same range where models were calibratedto examinemodel interpolationand using model projection and occurrence recordsfrom reciprocal ranges to determine model extrapolation.The Boyce index was also reported for the merged predictions of reciprocal models of *T. diversifolia* in Nigeria.The R code used in subsections 3.1.1, 3.1.2, 3.1.4, 3.1.5 and 3.1.6 is provided in Appendix 4.

3.2 Seed bank and Soil properties of sites infested by *T. diversifolia*

3.2. 1 Site selection and data collection

To capture the wide range of environmental conditions in which *T. diversifolia* grows, sites were selected across three major ecological region of Nigeria (Figure 3.3, Table 3.4)and the time-for-space substitution approach of Thomaz *et al.*(2012).The following criteria were used to identify suitable sites as recommended by Global Invader Impact Network (GIIN, Barney *et al*., 2015):

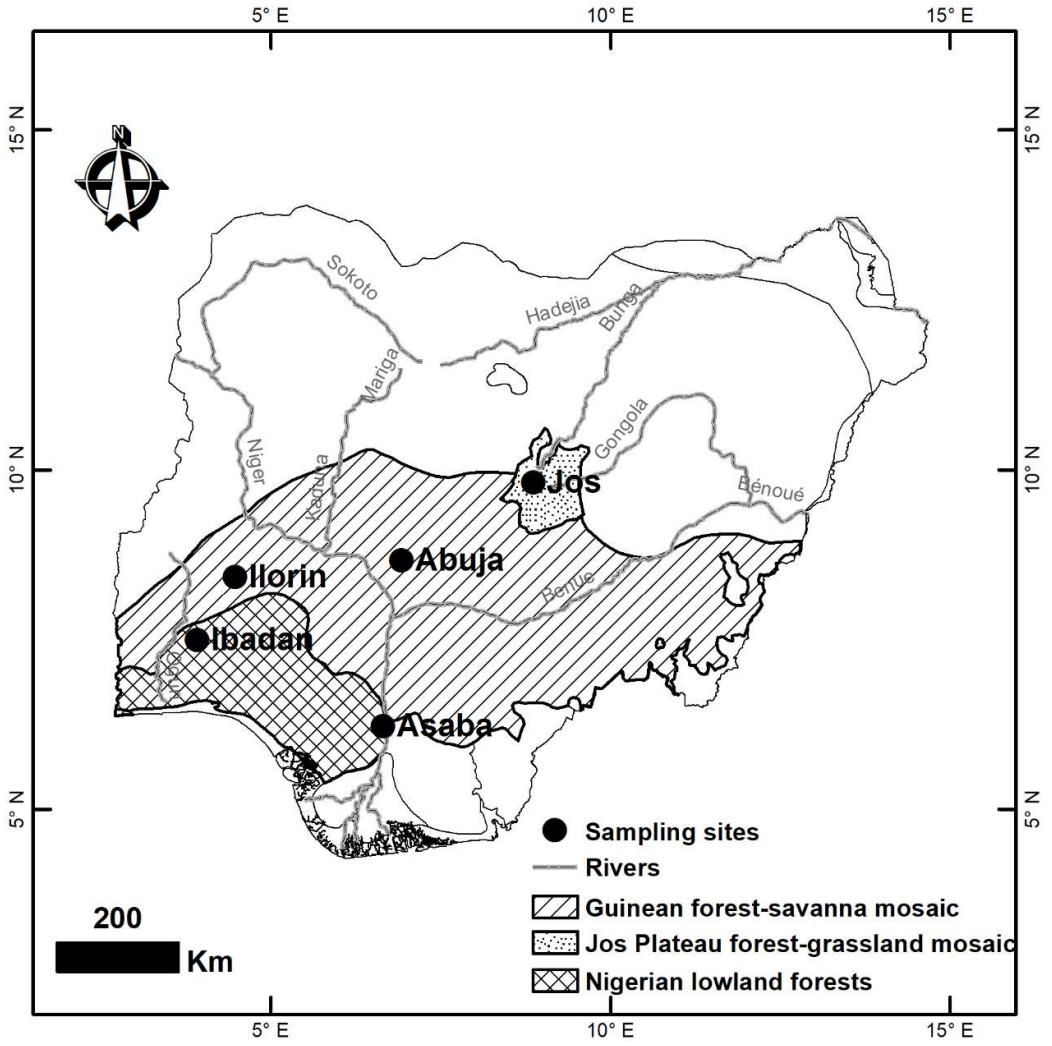

Figure 3.3. Map of Nigeria with the location of sampling sites

Study sites were selected within the three major ecological zones in Nigeria where *T. diversifolia* has been reported including the Lowland Forest, Guinean forest-savanna mosaic and Jos Plateau forest grassland mosaic. Map done using the Terrestrial Ecoregions of the World data available from the World Wildlife Fund (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world).

Table 3.4. Details study sites used to assess effects of *Tithonia diversifolia* on soils

Location	Status	Longitude E	Latitude N	Elevation	Patch size (m^2)
Ilorin	Invaded	4° 28' 41.196"	8° 24' 4.842"	337	1,967
	Non-invaded	4° 28' 40.296"	8° 24' 50.292"	337	-
Asaba	Invaded	6° 38' 55.788"	6° 13' 3.612"	110	2,034
	Non-invaded	6° 38' 55.212"	6° 13' 0.318"	118	-
Jos	Invaded	8° 51' 56.088"	9° 48' 31.356"	1243	1,478
	Non-invaded	8° 51' 51.876"	9° 48' 32.364"	1237	-
Abuja	Invaded	6° 55'2.37"	8° 39' 37.548"	137	1,383
	Non-invaded	6°55' 22.332"	8 ° 39' 34.812"	133	-
Ibadan	Invaded	3° 54' 48.312"	7° 29' 2.526"	209	2,343
	Non-invaded	3° 54' 48.312"	7° 29' 2.526"	205	-

1. All study sites locations were selected along major highways, far from settlements in order to minimize human impacts.
2. All invaded sites were dominated by*T. diversifolia.*
3. Uninvaded or control sites were close to invaded sites and similar to them in terms of slope, aspect and land-use.
4. Sites dominatedby other observed invasive species (such as*C. odorata, Hyptis suaveolens*(L.) Poit.) were avoided in order to reduce their synergistic or antagonistic effects on the site's soil properties.
5. All control, non-invaded plotscontaining very few individuals of *T. diversifolia* (< 10) were selected as thiswas an indication that they were invasible but the study species had not yet spread there (Thomaz *et al*., 2012).
6. To avoid differences in invaded and non-invaded plots due to seasonal vegetation dynamics, sampling and data collection were completed within three weeks at peak community productivity in August 2017.

3. 2. 2 Experimental design and data collection

The geographical coordinates (Table 3.4) of each study location were recorded from a point near the centre using a Garmin eTrex 10 GPS receiver. The size of the invaded site was estimated by walking the perimeter with the GPS receiver. Four 2 m × 2 m quadrats were randomly located within each invaded and uninvaded area for subsequent data collection (Figure 3.4).

3. 2. 2. 1 Seed bank assay

To determine the type of seed bank of *T. diversifolia,* according to the classification of Thompson *et al*. (1997) and the effects of this species on belowground diversity, soil samples were collected in August 2017 at the end of the rainy season. The seed bank was sampled in each invaded and uninvaded area per site, within the four quadrats ensuring an inter-quadrat distance of at least 10 m. Quadrats were randomly laid out to obtain a representative sample from each invaded and non-invaded area (Figure 3.4). Five soil cores (5 cm diametre, 5 cm depth) were sampled from within each quadrat. These samples were taken near the edges and the centre of each quadrat to account for the spatial variation commonly observed in soil seed banks. Thus, a total of 18,997 cm^3 of soil was obtained at each site. Soil cores were 5 cm deep because this layer usually contains the highest percentage of seeds (Guo *et al*., 1998; Holmes, 2002).

All samples were air dried to reduce their weight for two days before being transported for further analysis. The standard seedling emergence method (Price *et al*., 2010) was used to determine the seed bank density and composition in the screenhouse of the Department of Botany, University of Ibadan (Plate 3.1) Briefly, soil samples were transferred into perforatedplastic containers (5 cm depth × 12 cm width × 17 cm length) and randomly stratified according to site in the screenhouse. Containers with river sand were randomly arranged among the samples as control checks for seed contamination. All containers were watered fortnightly, emerging seedlings were inventoried once a week, identified to the specific level and removed from containers. Seedlings not readily identifiable were transplanted into separate containers and left to grow up until identification could be made. The position of containers was randomly changed every two weeks to expose them equally to possiblevariations in light intensity and temperature within the screenhouse.

Species were identified using weed identification manual (Akobundu *et al*., 2016) and herbarium specimens of the University of Ibadan Herbarium.Seedling emergence ceased 19 weeks after the beginning of the experiment. To ensure that all seeds had germinated, soil samples were left to dry for one week, moistened, stirred and observed for two more weeks. However, this treatment did not lead in further seed germination and the experiment was terminated.

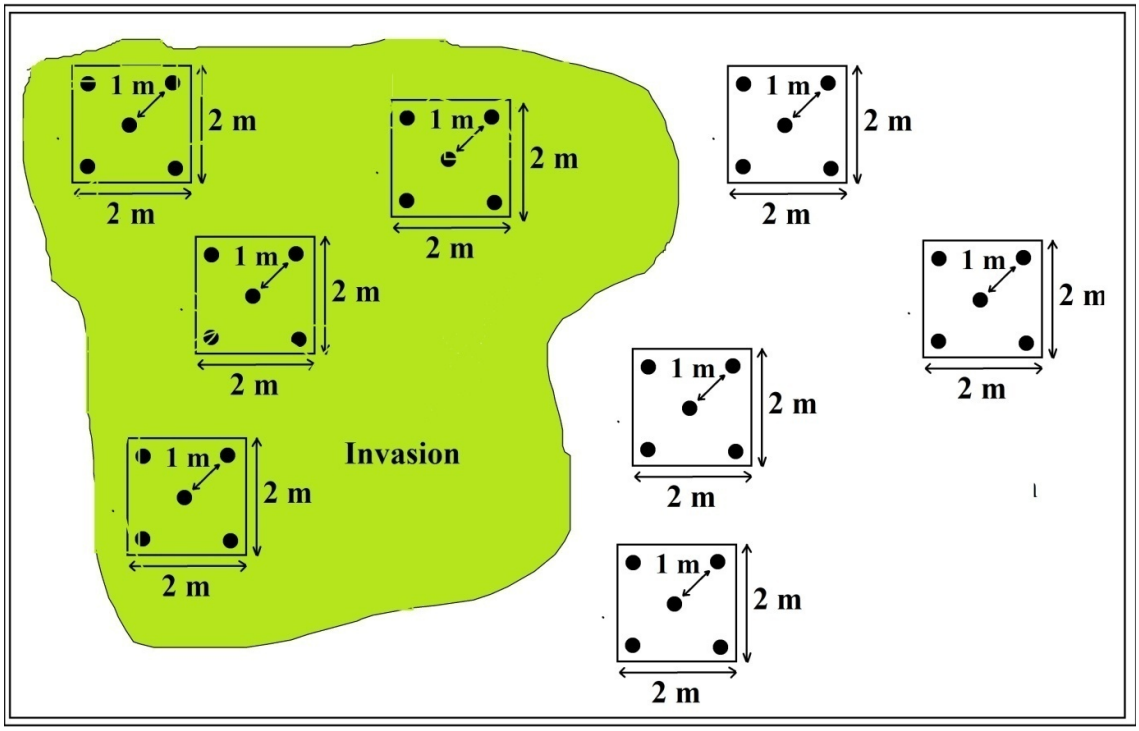

Figure 3.4. Schematic representation of the study design for assessment of seed banks

Quadrats were randomly laid withinthe invaded (green area) and non-invaded area at each study site(Adapted from Barney *et al.,* 2015). Figure done using Microsoft Paint.

Plate 3.1. Seedling emergence technique for seed bank quantification

Seedlings were left to emerge from soil samples kept humid in an open screenhouse. Photo taken at the Department of Botany, unheated screenhouse, University of Ibadan in November 2017.

3. 2. 2. 2 Soil properties

Soil samples meant for physico-chemical analyses were collected following the same design used for seed bank sampling but at a depth of 15 cm. A composite sample was made by manually homogenizing soil from each plot. All samples were air-dried and passed through a 2 mm sieve. The sand, silt and clay fractions of soil samples were determined using the hygrometer method.

To determine organic C and total N contents, a subsample of 10 g was ground and passed through a 0.5 mm sieve. Organic Carbon was determined using the modified Walkley Black method. One gram of soil was transferred to a clean and dry 250 ml conical flask. Blank and carbon standards were made by pipetting 2 ml of working standards 0, 2.5, 5.0, 7.5, 10.0 and 12.5 mg of organic carbon/ml. Ten millilitres of 1 N $K_2Cr_2O_7$ solution was added to each flask followed by 20 ml of concentrated H_2SO_4 and mixed vigorously for one minute under a fume hood. The mixture was allowed to stand for 30 minutes, then 100 ml of distilled water was added and the solution was filtered using Whatman paper No. 2. The absorbance of the filtrate was determined colometrically with the blank set 100 %.

Total Nitrogen was extracted using the Kjeldahl approach and analyzed with a Technicon's AutoAnalyzer II (Tecnicon Instruments Corporation, New York, USA). In this procedure, samples were prepared by transferring 2 g of soil into a 250 ml digestion tube and adding one tablet to 20 ml of the digestion mixture. The samples were placed in a complete Tecator Digestor system and allowed to digest for 3 hours at 370^{o}. After cooling, they were diluted to 250 ml with distilled water, shaken and the resulting clear liquid was poured into the AutoAnalyzer II sample cups.

Nitrate (NO_3-N), Nitrite (NO_2-N) and ammonium (NH_4-N) were extracted using a 2 N KCl solution and determined with the AutoAnalyzer II. Available Phosphorus was extracted using the Bray-1 method and quantified with the Autoanalyzer. In this procedure, 30 ml of Bray-1 extraction solution was added to 5 g of soil samples in extraction cups. The mixture was stirred for 5 minutes using a mechanical stirrer, then allowed to stand for 2 minutes and immediately filtered into another set of extraction cups which were loaded in the AutoAnalyzer.

The pH was measured using a pH meter standardized with buffer solution of pH 4.0 and 7.0. This was done by dissolving 10 g of soil in 10 ml of distilled water. The

mixture was then allowed to stand for 15 minutes, stirred for 2 minutes and left to stand for 10 minutes. Electrical Conductivity (EC) was measured using a saturated soil paste. The soil paste was prepared by adding distilled water to 100 g of soil in a beaker and stirring continuously and allowing the mixture to stand for two hours. The mixture was filtered and 0.1% $NaPO_3$ solution was added to it. Conductivity was measured using a calibrated conductivity meter.

Exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, Mn^{2+}) and effective Cation Exchange Capacity (CEC) were determined using a Flame Photometer and an Atomic Absorption Spectrophotometer. The sample preparation procedure was as follows: 30 ml of 1 N ammonium acetate solution (NH_4OAc, pH= 7) was added to 5 g of soil in extraction cups. The mixture was stirred for 15 minutes on a mechanical stirrer, allowed to stand for 15 minutes and filtered with Whatman paper No. 42. The filtrate was diluted to a ratio of 1:25 using ammonium acetate and the spectrophotometer was used to determine Ca^{2+}, Mg^{2+} and Mn^{2+} while the flame photometer was used for K^{+} and Na^{+}. Effective CEC (me/100g) was determined by summing up the concentrations of exchangeable ions and micronutrients (Mn, Fe, Zn and Cu). The samples were digested with a mixture of perchloric acid ($HClO_4$) and Nitric Acid (HNO_3) and determined using a spectrophotometer. Digestion was carried out for 2 hours at 150^{o} by adding 5 ml of the digestion mix to 0.5 g of soil sample All analyses were carried out in triplicate according to automated and semi-methods for soil and plant analysis (International Institute of Tropical Agriculture, IITA, 1982).

3.2.3Data analysis

Statistical analyses were performed in R. Shannon-Wiener diversity index (*H'*) and species richness (S) were computed using the *vegan* package (Oksanen *et al.*, 2013). Data were square root-transformed where necessary to improve homogeneity of variances and the effect of invasion by *T. diversifolia* on seed bank diversity (*H'* and S) was assessed using analysis of variance. To evaluate the effect of invasion on seed bank structure and composition, we used a Permutational Analysis of Variance (PERMANOVA). This a semiparametric alternative to multivariate analysis of variance that is based on a chosen geometric distance rather than group averages (Anderson, 2001). PERMANOVA is a robust statistical tool with a proven effectiveness in evaluating the effects of plant invasions on soil seed banks at different geographical locations (Gioria and Osborne, 2010).

The invasion status (invaded and non-invaded) and site (Abuja, Asaba, Ibadan, Ilorin and Jos) were taken as fixed and random effects respectively. PERMANOVA was carried out with the *vegan* package. Because of its sensitivity to within-group differences in species composition, homogeneity of multivariate dispersion (PERMDISP) in species composition at each sampling sites was tested prior to PERMANOVA using the function *betadisper*in *vegan*. Significance was assessed using the *permutest* function.Similarity percentage analysis (SIMPER) was used to determine the species responsible for compositional difference between invaded and non-invaded seed banks (Clarke, 1993).

Nonmetric Multidimensional Scaling (NMDS) was carried out to visualise the variation in the species composition of seed banks according to invasion status and site. NMDS and PERMANOVA were based on Bray-Curtis distance. The number of permutations was set to 9999 in all analyses and *p*-values below 0.05 were considered significant.

3.3Variation of N, P, K and reproductive Allocation in *T.diversifolia*

3. 3. 1 Study area

Thirteen sites were randomly chosen across the three ecological zones in South West Nigeria where *T. diversifolia* is abundant(Table 3.5, Figure3.5). All sites were located near major highways and far from settlements in order to minimize human interference.

3. 3. 2 Sample collection and analysis

Five individual plants were randomly harvested at each site before seed dispersal, separated into vegetative (roots, shoots and leaves) and reproductive parts (capitula), bulked and air-dried. Five soil samples were also randomly collected at the surface (0–15 cm depth) from each study site. Soil samples were bulked, air-dried and sifted using a 2 mm sieve.

Table 3.5. Geographic coordinates of sampling sites for nutrient analysis

Location	Code	Longitude E	Latitude N	Altitude (m)
Fiditi	FID	3^0 54' 22.6"	7^0 40' 59.9"	277
Ajibode	AJI	3^0 54' 12.0"	7^0 27' 49.8"	199
Ekanmejè	EKA	5^0 06" 06.8"	8^0 01' 36.6"	540
Ikere	IKE	5^0 13' 57.3"	7^0 26' 18.6"	399
Gbongan	GBO	4^0 22' 16.7"	7^0 28' 09.9"	215
Odeda	ODE	3^0 32' 00.9"	7^0 14' 24.9"	162
Ifo	IFO	3^0 11' 32.5"	6^0 50' 06.5"	95
Shagamu	SHA	3^0 34' 22.4"	6^0 52' 29.3"	86
Omotosho	OMO	4^0 33' 11.7"	6^0 43' 37.4"	107
Ofosi	OFO	5^0 08' 55.4"	6^0 45' 06.6"	50
Epe	EPE	3^0 56' 98.8"	06^0 35' 22.8"	25
Badore	BAD	3^0 12' 39.7"	06^0 31' 28.3"	13
Okoafon	OKO	3^0 02' 16.2"	06^0 28' 58.9"	10

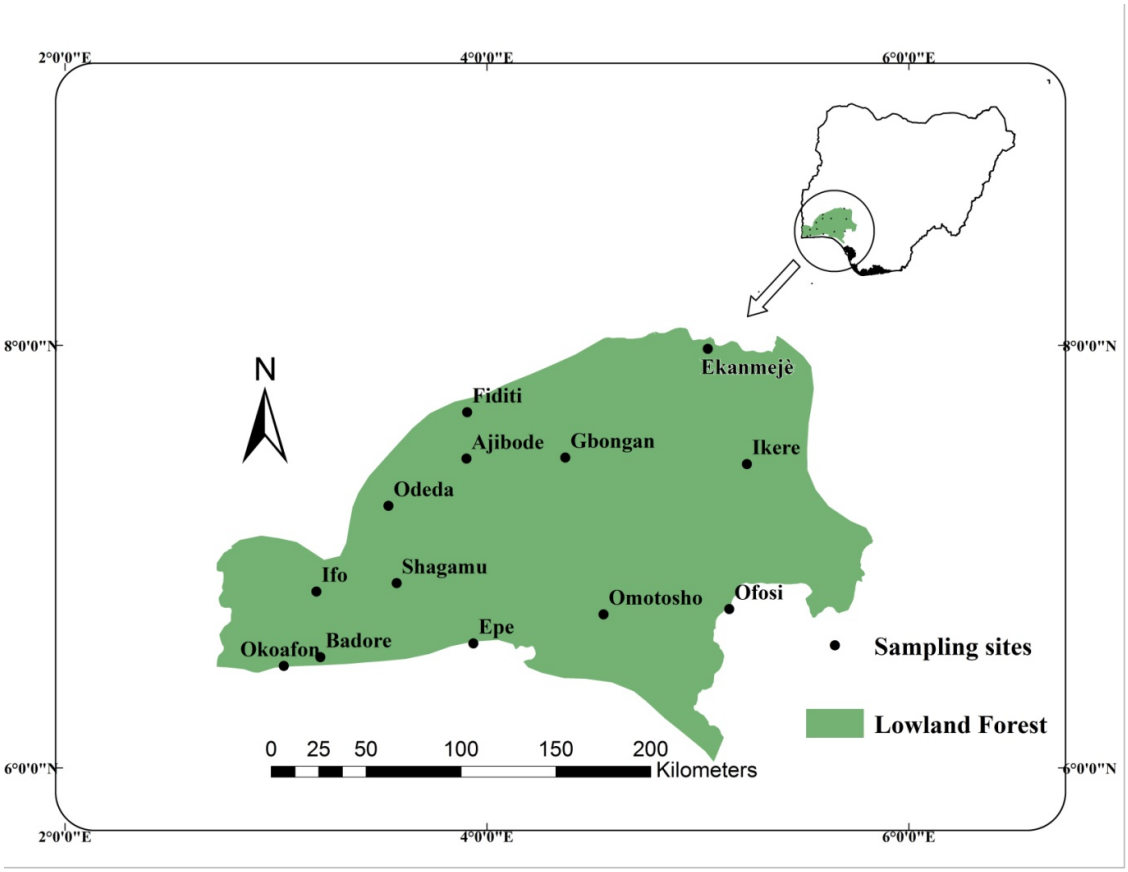

Figure 3.5. Map of South-western Nigeria with the location of sampling sites

All sampling sites were randomly located in the Derived savanna coastal forest within the south-western region of Nigeria.

Total nitrogen was determined in soil and plant samples using a Technicon Autoanalyzer (AAII). Potassium was determined with an atomic absorption spectrophotometer. Available phosphorus was extracted and quantified using the Bray-1 method while total phosphorus in plant tissues was digested with a mixture of Nitric, Percholoric and hydrochloric acids and determined using the Autoanalyzer. All analyses were done in duplicates according to the IITA Automated and Semi-automated Methods for Soil and Plant Analysis manual (IITA, 1982).

3. 3. 3 Data analysis

Differences in nutrient levels in soil and plant parts were assessed across all sites using Analysis of Variance and a Tukey HSD test was performed to separate significant means. Relationships between soil nutrient status and plant nutrients were assessed using simple linear regression. Lifetime Reproductive Allocation of N, P and K (RA_N, RA_P and RA_K respectively) at each site was computed using the formula of Bazzaz *et al.* (2000) as follows:

$$RA_X = \frac{F_X}{R_X + S_X + L_X + F_X} \times 100$$

Where R_X, S_X, L_X and F_X represent the amount of element X in roots, shoots, leaves and flowers respectively.

Difference in reproductive allocation of N, P and K were assessed using Analysis of Variance. The relationships between soil Nitrogen, Phosphorus and Potassium and their corresponding reproductive allocation were assessed by means of linear regression. All analyses were done in GraphPad Prism version 7.00.

3.4Some aspects of the reproductive biology and ecology of *T. diversifolia*

3.4.1 Study site

The breeding system, germination and some aspects of the floral biology of *T. diversifolia* were investigated on the field between September and December 2017. Two populations of the study species were identified within the University of Ibadan Campus (3° 53' 56" N; 7° 27' 42", 202 m above sea level). The first population was located at the Botany Research Farm while the second was at the outskirts of Ajibode village. *Tithonia diversifolia* was found growing luxuriantly at these two sites under natural conditions. The plot at the research farm appeared to have been cropped with cassava and left to fallow for at least one year. Plants at the Ajibode site were also

growing undisturbed on a rock outcrop. The following aspects were specifically studied: 1) the pollen/ovule ratio per floret, 2) autogamous pollination, 3) floral phenology, 4) seed production and 5) germination.

3.4. 2Pollen to Ovule ratio and pollination mode in *T. diversifolia*

The pollen to ovule ratio of *T. diversifolia* was determinedand the breeding systemof the species was inferredfollowing the classification of Cruden (1977).Before anthesis, ten capitula were randomly, each from one plant along a transect, with at least five metres between each plant.Capitula were taken to the Palynology Laboratory of the Department of Archaeology and Anthropology, University of Ibadan, Ibadan. Three florets were usedto estimate pollen productivity as described by Dafni (1992). Using a forceps, a floret was carefully excised from a capitulum and placed into a 1.5 ml eppendorf tube containing a mixture of 0.7 ml glycerine + 0.1 ml of 0.5 % methylene blue solution + 0.2 ml of liquid detergent. The floret was thoroughly crushed in the tube using a fine glass rod. The suspension was vortexed for 5 minute and three subsamples each of 1 µl were transferred onto a glass slide and pollen count wasdone using alight microscope. The putative breeding system of *T. diversifolia* was determined as described in Cruden (1977).

To assess the extent of dependence of *T. diversifolia* on pollinating agents for achene production, autogamy or autonomous self-pollination was assessed using pollinator exclusion bags (Dafni 1992). Capitula on an individual plant were tagged and randomly assigned to bagging and open pollination (control). Depending on availability, 3 to 7 capitula were used for the bagging treatment. All capitulawere at the bud stage and the pollinator exclusion bag was made of a fine, transparent polyester material (0.1 mm × 0.1 mm mesh) as shown on Plate 3.2. On the same plant, three to four capitula were tagged and served as control.It was not feasible to emasculate florets to assess cross- and self-pollination because of their small size (6 - 9 mm long) and the large number of florets per capitulum (63 –82). The effect of bagging on achene viability was determined before seed dispersal, about 4 months after the beginningof the experiments by assessing the number of viable and non-viable achenes in both treatments. Viability was inferred using the pressure test (Price *et al*., 2010). Therefore, an achene was considered nonviable if its walls collapsed under light pressure applied using a pair of tweezers.

3. 4. 3 Floral phenology and reproductive output of *T. diversifolia*

At each site, five branches were tagged on ten randomly selected stands of *T. diversifolia* and the timing from visible bud appearance (discrete, green capitulum enclosed in involucral bracts) at the branch apex to pre-anthesis (capitulum open exposing yellow disk floret buds), from pre-anthesis to anthesis (disk florets releasing pollen), from anthesis to floret withering stage and from floret withering stage to achene dispersal was noted every other day as described by Dafni (1992). At peak flowering (in November), 60 individuals were randomly harvested and the number of capitula was recorded for each of them. Two capitula were randomly harvested from a subset of 50 plants and the diametre was measured using a digital calliper. A subset of 50 mature capitula was taken from each of the collected plants and sectioned transversally near the base using razor blade. A Canon Cybershot W 800 camera was used to capture digital images of each section. The images were saved in JPEG format on a Secure Digital (SD) card and transferred to a computer running Windows 8 with an Intel(R) Pentium (R) CPU 2020M @ 2.40 GHz processor. Florets were counted using ImageJ (Rueden *et al.,* 2017) (Plate 3.3).

A series of germination tests were carried in order to characterize the embryo type and dormancy in *T. diversifolia.* The effect of mechanical scarification and Gibberellic acid (GA_3) on imbibition and germination was assessed four days after collection. The effect of osmotic potential was also assessed on the germination of this species.

Plate 3.2. Bagged capitulum of *T. diversifolia.*

Photo taken on the field site at the University of Ibadan, Ibadan.

3. 4. 4 Germination ecology of *T. diversifolia*

Mature achenes of *T. diversifolia* (Plate 3.4 A) were collected from the two sites in November 2017from randomly selected plants at the two populations described above. Initial germination tests were carried out almost immediately (less than 2 days after collection) in an unheated screenhouse using either germination trays (with fine sand as substrate) or Petri dishes lined with filter paper (in the laboratory). It was noted that achenes that were tested in Petri dishes got covered with fungi after two weeks of sowing and as a result, all test were repeated in the screenhouse using sand as substrate. Germination tests done in an unheated greenhouse have been known to be more ecologically meaningful as its environmental conditions are close to field conditions (Baskin and Baskin, 2014).Unless otherwise specified some germination tests were carried out using Petri dishes in the laboratory; achenes were moistened every other day and considered germinated when the radicle was emerged through the pericarp.

3. 4. 4. 1 Dormancy in fresh achenes of *T. diversifolia*

Previous studies have reported dormancy in this species but the actual dormancy has not been investigated following recently published protocols (Baskin and Baskin, 2014). To find out if freshly mature achenes of *T. diversifolia* were dormant, they were tested for germination for the recommended duration of four weeks (Baskin and Baskin, 2014). Achenes were broadcast on moistened fine sand in germination trays in a screenhouse. Six replicates, each of 50 achenes were used for each population. Achenes were examined after every other day and if germinated, they were counted and removed from trays.

3. 4. 4. 2 Seed type of *T. diversifolia*

Achenes were moistened in a Petri dish at room temperature and retrieved after 12, 24, 48 and 72 hours of imbibition, at which times they individually cut open by making a longitudinal slit in the pericarp with a razor blade. The cotyledons were separated and the tip of the naked achene was carefully longitudinally cut using a razor blade. The embryo was observed under a dissecting microscope (Plate 3.5). At each time, the length of 20 imbibed and non-imbibed achenes were recorded. Seed type was determined following the Martin (1946) key for seed types modified by Baskin and

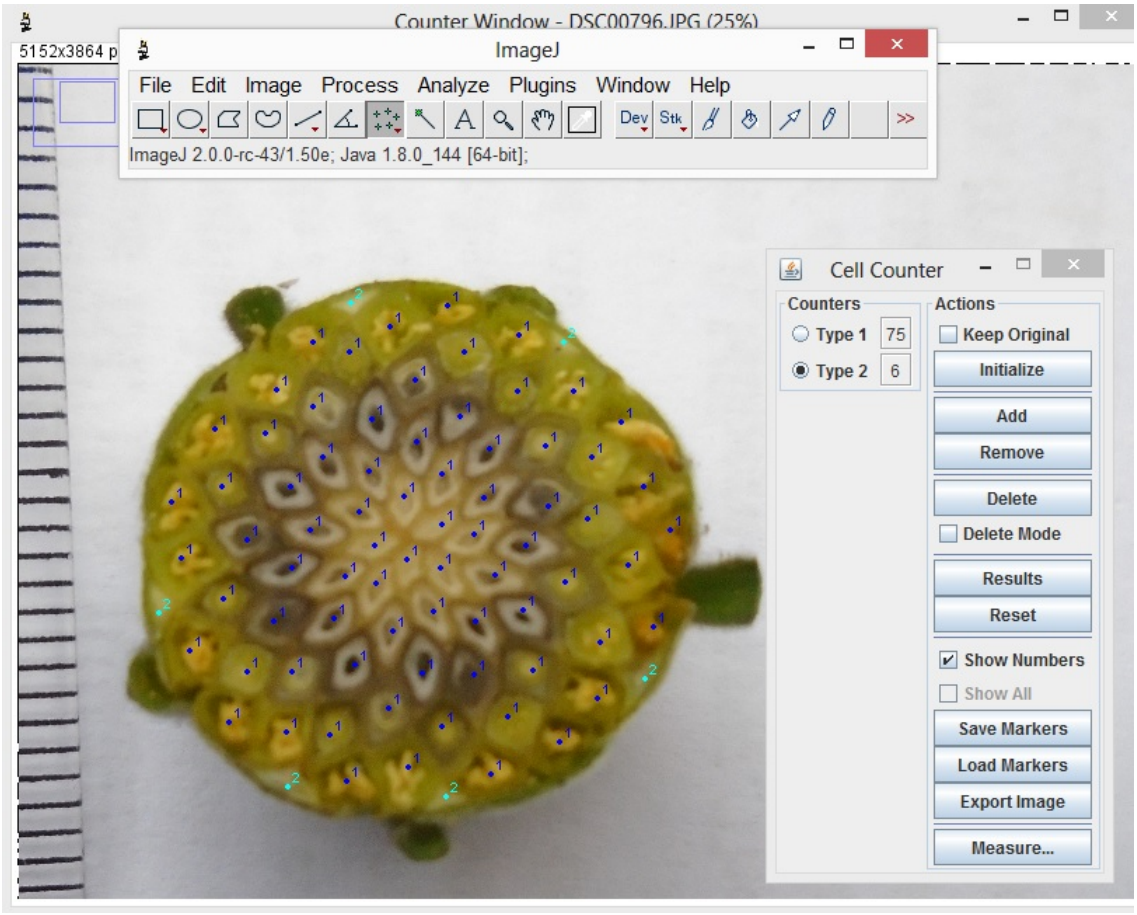

Plate 3.3. Floret counting in ImageJ Graphical User Interface

Manual counting procedure for ray (cyan) and disk florets (blue) of a sectioned capitulum of *T. diversifolia*.

Plate 3.4. Developmental stages of *Tithonia diversifolia*

Mature achenes (a), geminating achene showing radicle (b, c) and a two-day old seedling (d)

Baskin (2014). This was repeated on newly germinated achenes in order to assess whether the embryo is underdeveloped.

3. 4. 4. 3 Effect of osmotic stress on germination of*T. diversifolia*

Freshly achenes of *T. diversifolia* were tested for germination in aqueous solution with varying osmotic potentials (0, -0.5, and -1.0 MPa) prepared by dissolving the required quantity of Polyethylene glycol (PEG 6000) in distilled water. Water potential (in MPa) was calculated following Michel and Kaufmann (1973) as a function of temperature (T =29°) and PEG concentration (C in g of PEG 6000 per kg of H_2O).

$$Water\ Potential = -(1.18 \times 10^{-3})C - (1.18 \times 10^{-5})C^2 + (2.67 \times 10^{-5})CT + (8.39 \times 10^{-8})C^2T$$

Where T = temperature (in ° C) and T = C in g of PEG 6000 (in g/kg of water)

3. 4. 4. 4 Effect of scarification on imbibition of achenes of *T. diversifolia*

The effect of mechanical scarification on water uptake of achenes of *T. diversifolia* was investigated using the approach of Baskin *et al.* (2006). Individual achenes were mechanically scarified by making a slit longitudinally through the pericarp with a razor blade. The initial weight of both scarified and non-scarified (control) achenes was recorded and four replicates each of twenty achenes were placed in 9 mm Petri dishes fitted with filter paper. The dishes were watered for 3 days and all achenes were retrieved after 6, 12, 24, 48 and 72 hours, blotted dry with a towel, reweighed and returned to the dishes. Water uptake was determined as follows:

$$W = m_i - m_d$$

Where m_i and m_d = mass of imbibed and dry achenes respectively.

3. 4. 4. 5 Effect of scarification and GA_3 on germination of*T. diversifolia*

To determine whether or not achenes of this species exhibit dormancy either as a result of an impervious seed coat, that is, physical dormancy *sensu* Baskin and Baskin (2014) or physiological dormancy, germination of achenes was investigated under screenhouse conditions for mechanically scarified and GA_3-treated achenes. Three replicates each of 50 achenes were used for each of the two treatments (1000 ppm GA_3 and

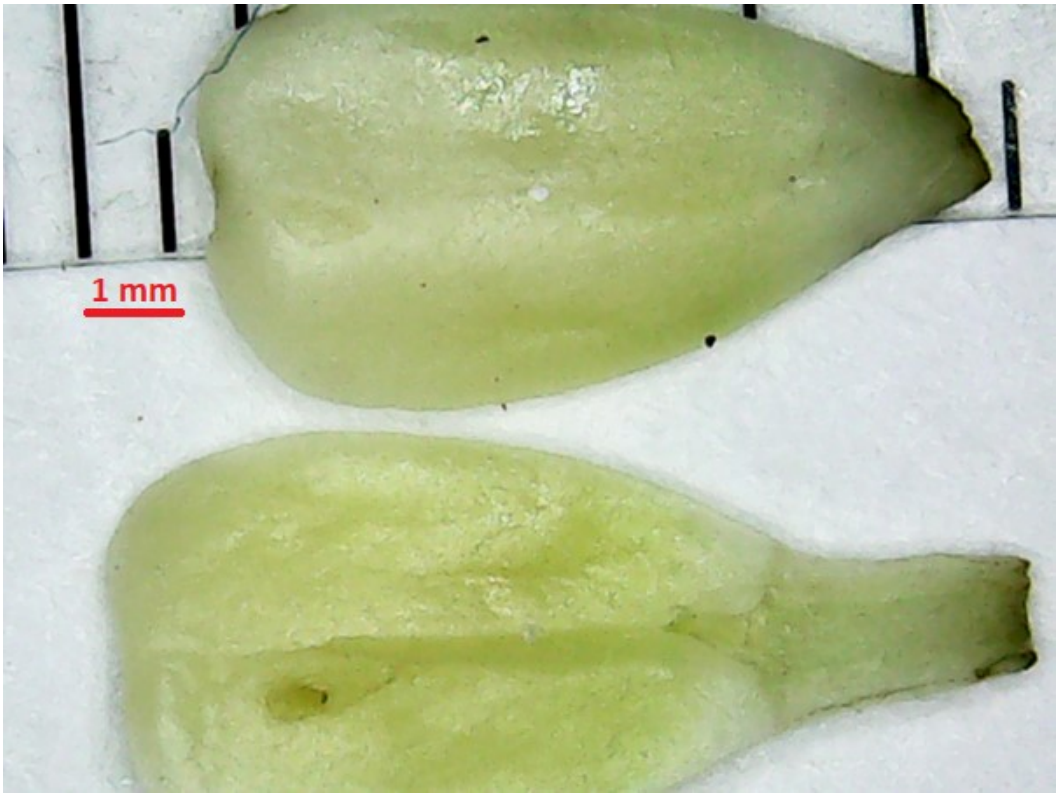

Plate 3.5. Cotyledons of *T. diversifolia* in a newly germinated achene

The embryo is embedded in the lower tip of the achene.

mechanical scarification) and for the control. Perforated trays (17 cm× 12 cm × 5 cm) were half-filled with sand, achenes were broadcast at their surface and moistened. Achenes were watered every other day and germination was scored when the radicle was visible for 14 days (Plate 3.4 C).

3. 4. 4. 6 Temporal patterns in germinability of achenes of *T. diversifolia*

Mature achenes of the study species were collected in November 2017 from each site. Batches of 50 viable achenes each were transferred into fine mesh nylon bags (5 cm × 5 cm). Six points separated by at least 3 metres were randomly located in each plot and three bagswere tethered and buried horizontally at 5 cm depth. Another batch of three (tethered) bags were placed on the soil surface at the original collection site. The burial points were tagged to allow easy retrieval. All bags were left undisturbed at their site of origin. Both buried and surface bags were retrieved randomly at monthly intervals and tested alongside three replicates of 50 achenes stored at room temperature in an envelope. At each retrieval date, non-viable achenes were separated from viable achenes using the pressure test (Price *et al*., 2010). These were then tested for germination alongside the stored achenes.

3. 4. 4. 7 Temporal pattern in seed bank of*T. diversifolia*

Twelve fixed 1 m × 1 m quadrats were randomly established at each site immediately after the first rains, before seedling emergence in March 2018. Four replicate soil cores (5 cm diametre, 5 cm depth) were systematically collected at least 20 cm apart within each fixed quadrat. Samples were collected fortnightly from March to May. The cumulative sampled area per square metre using an auger of diametre 5 cm amounted to 314 cm^2, well above the recommended 250 cm^2 (Forcella 1984). At each time, they were air dried, composited, passed through a 1 mm sieve and all viable seeds were retrieved and counted. This dry sieving technique proved very fast and efficient as the initial soil volume was reduced to about one fifth leaving only gravel (about 5 mm in diameter) after about 5 minutes of sieving (Plate 3.6). Other seeds could be thus recovered including those of *Calopogonium mucunoides*Desv*, Spilanthes costata*Benth*, Centrosema molle* Mart. ex Benth and *Lagera aurita*Benth. ex C.B. Clarke.

Plate 3.6. Direct method of seed bank quantification of *Tithonia. diversifolia*

(a) Soil core extraction with a 5 cm diameter auger, (b) dry sieving using a 1 mm mesh sieve.

3. 4. 4. 8 Data analysis

The number of pollen grain was averaged across all replicates and the total number of pollen grain per floret (N), which is equal to the pollen to ovule ratio was obtained by multiplying the total volume of the solution (1000 µl) by the average number of pollen grain (n):

$$N = 1000 \times n$$

A χ squared test was used to evaluate whether achene viability differed significantly between open-pollinated and bagged capitula. A t-testwas used to assess the difference betweenscarified and control achenes while a one-way ANOVA was used to compare germination in scarified, control and GA_3-treated achenes. Data on temporal variability in germinability and the number of achenes recovered at each sampling date were also analysed using a one-way ANOVA and mean separation was performed using Tukey HSD test. An exponential model wasfit to seed bank data in order to describethe relationship between mean seed bank density (s) as a function of time (t) as follows:

$$s_t = s_0 e^{at}$$

This model was fitusing linear regression on the natural logarithm of mean seed bank density. All analysis were done using GraphPad Prism version 7.

3. 5. Growth and response of *T. diversifolia* to management

3. 5. 1 Study site

This study was carried out at the Research Farm of the Department of Botany, University of Ibadan on an undisturbed plot of a 11 × 16 m where *T. diversifolia* has been dominant and left to grow for at least a year.

3. 5. 2 Experimental setup

Sixteen 1 m × 1 m permanent quadrats were established before field emergence in March 2018. Four treatments were randomly assigned to the quadrats with each treatment replicated four times. All treatments were realized at the peak of farming season, 2-3 weeks after the first rains when germination had just commenced. The treatments were as follows: 1) Control: quadrats left undisturbed during the experiment.This treatment simulated natural field conditions; 2) Fire: stems of senesced *T. diversifolia* were gathered in two randomly selected areas of approximately 4 m^2 and set on fire. The stems burnt readily releasing intense heat in a very short time.This treatment is meant to simulate the impact of a common cultural

practice(senesced vegetation is usually burned to minimize hand weeding before cultivation)on the growth of this species; 3) Manual weeding:Removal of all vegetation in designated quadrats by uprooting manually and 4) Herbicide:Application of Paraquat, a non-selective, herbicide at the recommended rate of 150 ml of herbicide for a knapsack of 16 l (about 9.38×10^{-3} v/v). In all treatments, a buffer zone of about 30 cm was established in order to avoid the edge effect, all vegetation within this zone was manually removed. Treatments are shown on Plate 3.7. The rest of the plot was left undisturbed as much as possible.

3. 5. 3 Data collection

Data were collected on a monthly basis, both non-destructively on 3-10 randomly tagged individuals within each quadrats (Plate 3.7) and destructively on 30 randomly selected individuals within the plot but outside the quadrats. Density was determined by counting all individuals in each quadrat every month. For both destructive and non-destructive measurements, stem diameter at the first internode was taken using digital calliper and plant height from the soil level to the highest apical bud was taken using a ruler to nearest 1 cm. Leaf area for non-destructive samples was estimated from three fully expanded leaves, randomly selected along the stem. Maximum length and width was recorded to nearest 0.5 cm. From July, it became difficult to measure plant height and leaf area as most of the plants were above 2.5 metres in height. Thus these two parameters were discontinued. At each sampling date, destructive sample were obtained by uprooting individuals randomly selected from within the plot. Samples were separated into leaves, shoot and roots, which were washed to remove soil particles. Biomass was determined by drying to constant weight at 100 ° C for three days.

3. 5. 4 Data analysis

The effect of control measures on density, height and stem girth was assessed using a one way Analysis of Variance. Significant means were separated using a Tukey HSD test. For destructive measurements stem girth, plant height, leaf area, root, shoot and leaf biomass were compared at each measurement data using a one way analysis of variance. Multiple regression analysis was used to assess the relationships between

Plate 3.7. Sample plots used for control of *Tithonia diversifolia*

Density and growth parameters of *T. diversifolia* were collected from quadrats in which three treatments were applied including control (a), Paraquat dichloride (b), Fire (c) and manual weeding (d). Dry and slender shoots of *T. diversifolia* from the previous year were used to divide quadrats in smaller sections to ease counting (d).

total biomass, stem girth and height and leaf biomass. Data were analyzed using GraphPad Prism version 7.

3. 6 Leaf area model of *T. diversifolia*

3. 6. 1 Data collection

Healthy, mature and fully expanded leaves of *T. diversifolia* were randomly collected from four populations across the University of Ibadan Campus (Table 3.6). Mature leaves of this species are characterised by 5 lobes as opposed to younger leaves that are either unlobed or possess only 3 lobes (Plate 3.8). One hundred leaf samples were collected from each site and taken to the Department of Botany, University of Ibadan, Ibadan for measurements. Prior to measuring, each leaf was assigned a serial number and flattened on a table.

Leaf length was taken along the midrib from the end of the petiole to the tip of the lamina. Similarly, the breadth was taken between the tips of the two extreme lobes as illustrated in Figure 3.6. All measurements were done using a graduated ruler to the nearest 1 mm and each leaf was photographed Using Canon Rebel Xti camera with a fixed 50 mm lens. Prior to image acquisition, each leaf was flattened on a white cardboard pasted on a flat surface on the ground and portrait photographs were with the camera facing downward, directly above the subject. All leaf photographs were acquired with an object of known size placed near each leaf for scaling. Several trial were done in order to get the correct camera setting and the automatic mode was found adequate as the flash generated eliminated shadows near the leaf edges. This precaution was necessary so as not to introduce bias in area estimations.

Photographs were processed using ImageJ version 2 (Rueden *et al.,* 2017). Leaf area analyses often rely on thresholding the blue channel of the RGB (red, blue, green) images to separate a leaf from its background (Bylesjö*et al.,* 2008). Thresholding was manually done in ImageJ. The length, breadth and area of each leaf were manually extracted from scaled images using the tools available in ImageJ (Plate 3.9) and saved in a spreadsheet alongside the manual values.

Table 3.6. Sampling location details

S/N	Landmark	Population code	Longitude N	Latitude E
1	Department of Botany	UI1	7° 29' 58.23"	3° 45' 23.57"
2	Nnamdi Azikiwe Hall	UI2	7° 28' 03.63"	3° 53' 12.56"
3	UI Research Farm	AJ1	7° 27' 53.33"	3° 53' 49.90"
4	Runsewe Olatunde Hall	AJ2	7° 27" 49.13"	3° 54' 10.16"

Description and geographical coordinates of the four populations from which leaf samples of *T. diversifolia* were collected within the University of Ibadan Campus**.**

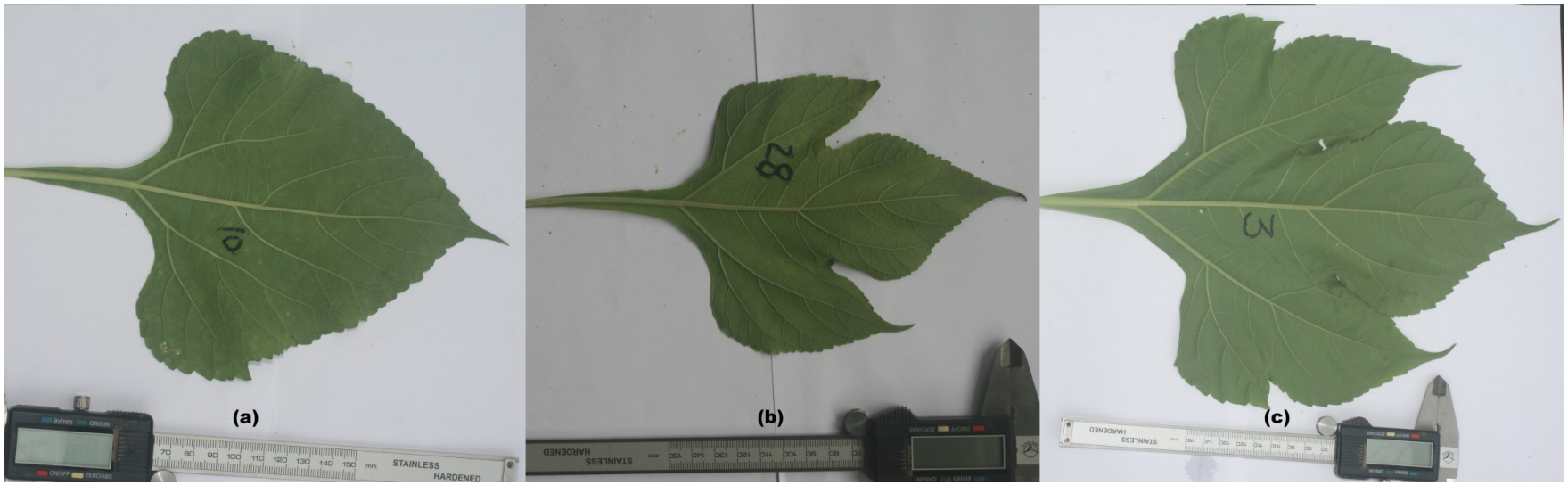

Plate 3.8. Leaves of *T. diversifolia* at different growth stages

Leaves of *Tithonia diversifolia.* (a) Young unlobed leaf, 1-3 weeks after germination, (b) Young 3-lobed leaf, 3-7 weeks after germination, and (c) mature 5-lobed leaf, > 7 weeks after germination.

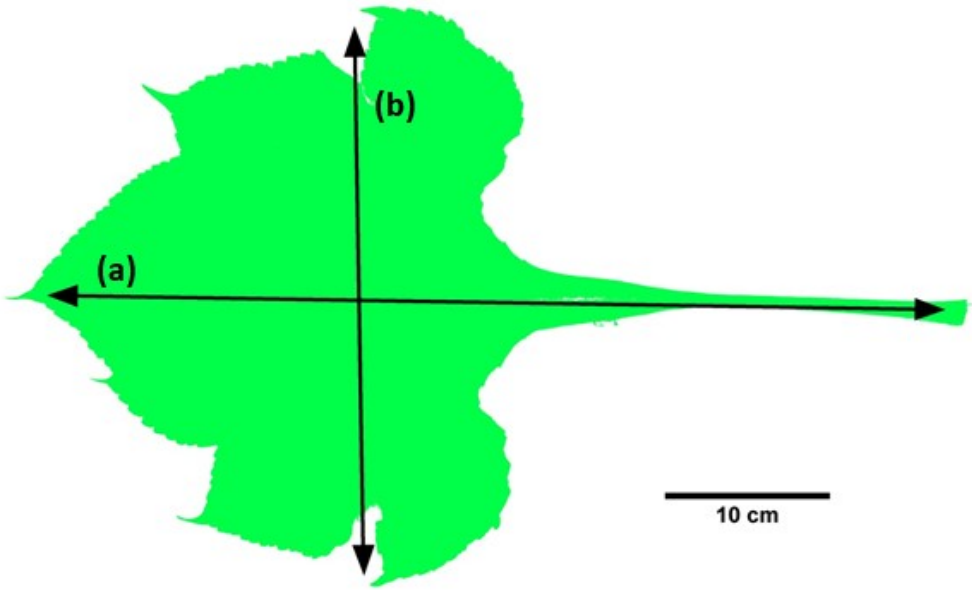

Figure 3.6: Outlines of a mature leaf of *T. diversifolia*

The horizontal (a) and vertical (b) arrows depict the direction of leaf length and breadth measurement respectively. Figure done using ImageJ version 2 .

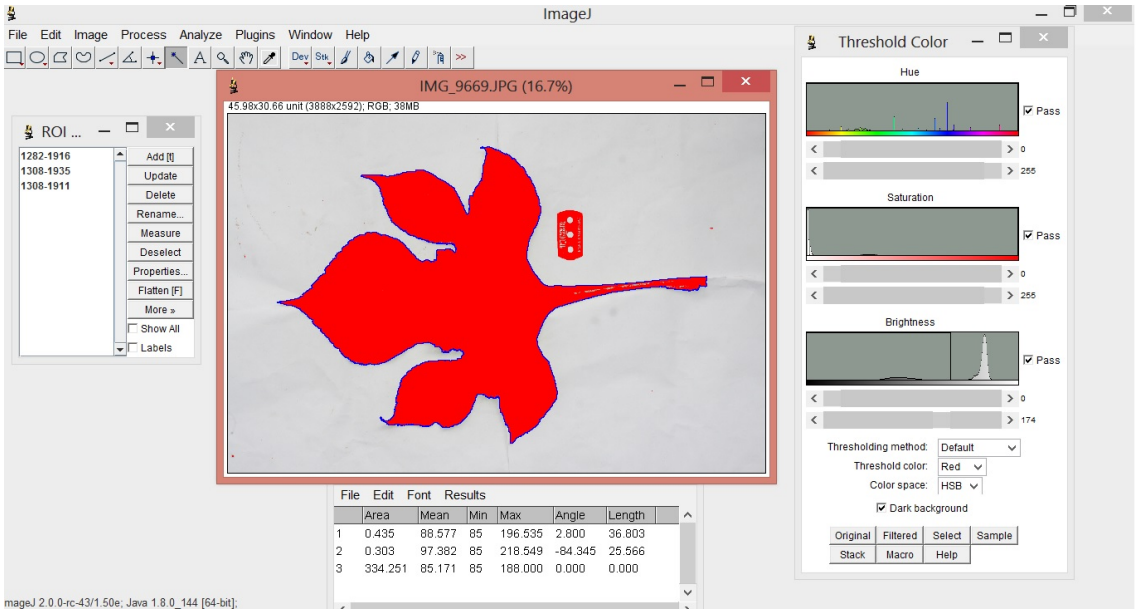

Plate 3.9. ImageJ Graphical User Interface for leaf metric extraction

Thresholded input image (centre), ROI manager (left) where operations are saved, Colour threshold adjustment (right) and result panels (bottom) where leaf metrics are displayed after processing

3. 6. 2. Data Analysis

The variation in manually measured leaf length and breadths was explored graphically and a one-way Analysis of Variance was used to assess site effects on these metrics. Descriptive statistics were computed for both manually and photographically estimated leaf metrics pooled across sites. A paired t-test was carried out to assess the differences between manual and image-derived leaf metric estimates. The relative mean absolute error E, between both methods for each leaf metric was computed as follows:

$$E = 100\left[\frac{1}{n}\sum_{i=1}^{n}\left(\frac{M_{(i)} - I_{(i)}}{I_{(i)}}\right)\right]$$

Where $I_{(i)}$ and $M_{(i)}$ are leaf area metrics derived from image and manual measurements respectively for a leaf *i* and *n* the total number of leaves.

Using image derived leaf metrics, six linear and nonlinear candidate leaf area functions (Table 3.7) were selected based from a previous study (Holguín *et al.,*2019) based on their performance. All models were calibrated using 80% (320 measurements) of the data and validated with the remaining 20%. To compare the ability of the selected model in predicting leaf area, four statistical criteria were used based on the predicted leaf areas (Table 3.). The root mean square error (RMSE) and relative mean absolute error (RMA) are indicators of the accuracy of model estimates; the adjusted determinant coefficient (R^2_{adj}) is a measure of the correlation and goodness-of-fit between observed and estimated data whereas the Akaike's information criterion (AIC) is an index used to choose the best model from a suite of tested models. Generally, low values of RMA, RMSE and AIC with high values of R^2_{Adj} indicate better models. The predictive ability of all models was visually assessed by Pearson correlation analysis between image-derived and manual linear measurements.

Manual and photographic methods of leaf area estimation for *T. diversifolia* were compared using a one way ANOVA. Dunnett's multiple comparison test was used to separatethe means from photographic leaf area (control) with predicted leaf areas from the two best models separately. Manual estimates were derived from the two best model, which was used to predict leaf area from manually measured length and breadth. Analyses were done using R version 3.6.0 and Microsoft Excel.

Table 3.7. Selected linear and nonlinear leaf area models of *T. diversifolia*

S/N	Number of parameters	Equation
1	2	$A = aL + b$
2	2	$A = aB + b$
3	2	$A = aLB + b$
4	3	$A = aL + bB + c$
5	3	$A = aB^2 + bL + c$
6	2	$A = a(LB)^b$

A: Leaf area (cm^2); *L:* leaf length; *B:* leaf breadth; a, b, and c: parameters of the equation.

Table 3.8. Selected leaf area model performance criteria for this study

S/N	Function name	Equation
1	Adjusted determinant coefficient (R^2_{adj})	$R^2_{Adj} = 1 - \frac{\sum_{i=1}^{n}(A_i - \hat{A}_i)^2}{\sum_{i=1}^{n}(A_i - \bar{A}_i)^2} \times \frac{n-1}{n-p-1}$
2	Relative mean absolute error (RMA)	$RMA = \frac{\sum_{i=1}^{n}\left\lvert\frac{A_i - \hat{A}_i}{\hat{A}_i}\right\rvert}{n} \times 100$
3	Root mean square error (RMSE)	$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(A_i - \hat{A}_i)^2}{n-p}}$
4	Akaike's information criterion (AIC)	$AIC = nln(RMSE) + 2p$

$\hat{A}_i$: predicted area; $\bar{A}$: mean observed area; A_i : Observed area; n: number of observations; p: number of model parameters to be estimated; *ln:* natural logarithm.

CHAPTER 4
RESULTS

4.1 Niche and potential distribution of *T. diversifolia* in Nigeria

4.1. 1Niche analysis

Among the 19 bioclimatic variables downloaded from the CHELSA database, seven had a low Pearson correlation coefficient, *r* such that - 0.7 < r < 0.7. These variables are presented in Table 4.1. The lowest positive correlation coefficientwas obtained betweenMean Diurnal Range, Bio 2 and Precipitation of Warmest Quarter, Bio 18 (*r*=0.02). This was followed by 0.07 between Temperature Annual Range,Bio 7 and Precipitation Seasonality Bio 15. The highest value (*r*= 0.62) was between Precipitation of Driest Month, Bio 14 and Precipitation of Coldest Quarter,Bio 19. On the other hand, the weakest negative correlation was obtained between Precipitation Seasonality, Bio 15 and Precipitation of Warmest Quarter, Bio 18 (*r*=-0.09), followed by -0.10, between Bio 2 (Mean Diurnal Range) and Bio 19 (Precipitation of Coldest Quarter). The strongest negative correlation was between Bio 7 (Temperature Annual Range) and Bio 11 (Mean Temperature of Coldest Quarter).

Niche dynamics and niche categories of*T. diversifolia* between Mexico and Nigeria are illustrated inFigure 4.1. Based on the selected environmental variables, there was no overlap in the niches of this species between the two ranges (Schoener's index, D = 0.01) according to the classification scheme of Rödder and Engler (2011). Niche equivalency and similarity tests were not significant (Figure 4.2)implying that the niche of *T. diversifolia* between Mexico and Nigeria is neither equivalent nor similar.In other words this species occupies different environmental conditions at both presence and background locations in these two ranges. The observed overlap and the very high niche expansion index (E = 0.99) indicate that this species shifted its niche in Nigeria.*Tithonia. diversifolia* has not yet to occupied all environmentally suitable habitats inMexico as suggested by the very high unfilling index (U = 0.99)

Table 4.1. Correlation matrix of climatic variables in this study

	Bio 2	Bio 7	Bio 11	Bio 14	Bio 15	Bio 18	Bio 19
Bio 2	1.00						
Bio 7	0.18	1.00					
Bio 11	0.59	-0.52	1.00				
Bio 14	-0.15	-0.36	0.31	1.00			
Bio 15	0.31	0.07	0.10	-0.34	1.00		
Bio 18	0.02	-0.25	0.41	0.57	-0.09	1.00	
Bio 19	-0.10	-0.45	0.41	0.62	-0.16	0.34	1.00

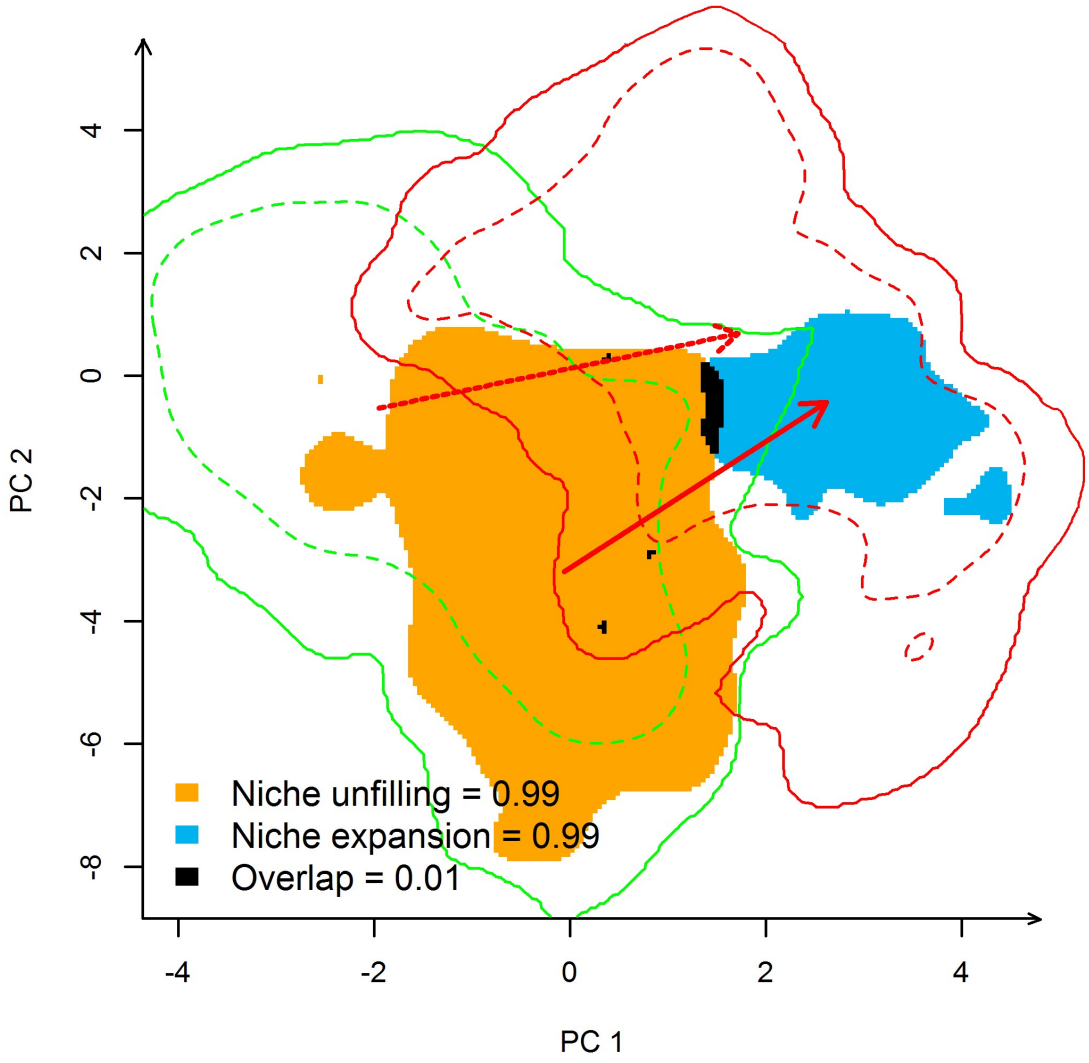

Figure 4.1. Niche dynamics of *T. diversifolia* between Mexico and Nigeria

The green and red lines are limits of the niche in Mexico and Nigeria respectively while the dashed and solid lines represent 100% and 50% of the ecological niche respectively.The dashed arrow shows the direction of the shift of the niche centroid between the Mexican and Nigerian environmental space while the solid arrow (below) links the centroid of the native and exotic distributions of the study species. PC 1 and PC 2 are the first axes of the Principal Component Analysis of the niche of *T. diversifolia* based on bioclimatic variables.

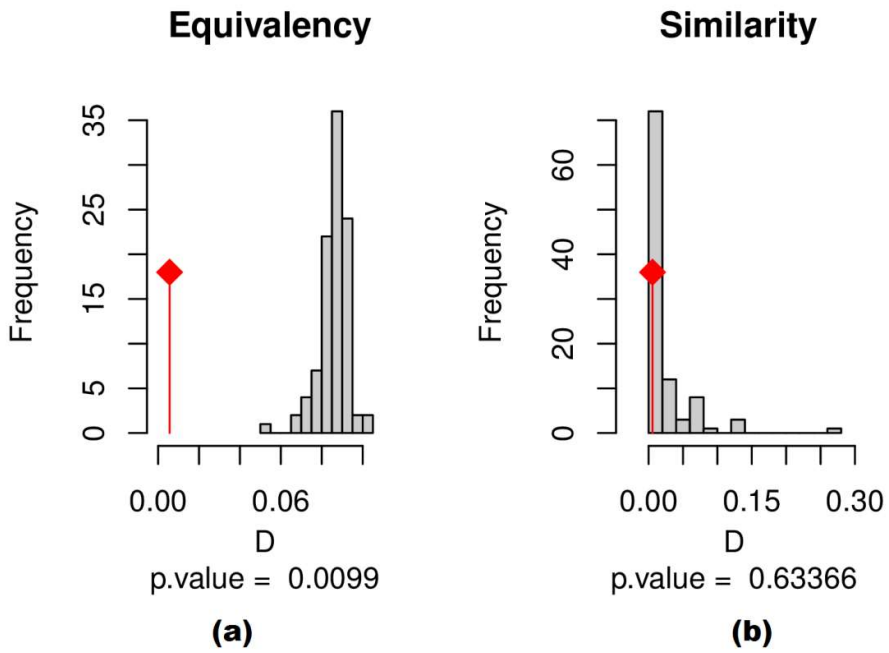

Figure 4.2. Equivalency and similarity tests for the niche of *Tithonia diversifolia*

Observed and simulated overlap values (D) with p-values for equivalency (a) and similaritytests (b). Simulations were based on a null distribution of 100 overlaps.

Figure 4.3 and Table 4.2 show the relationships and contributions of environmental variables in relation to the geographical distributionof the study species in Nigeria and Mexico. The first two Principal Components explained 62.9% of the variance in the set of the fourteen environmental variables used. Mean temperature of the coldest quarter (Bio 11), Bulk density (BLDFIE), sand content (SNDPPT) and Precipitation seasonality (Bio 15) had the highest contribution to the first PCA axes (Table 4.2).

4. 1. 2 Reciprocal distribution model parameters and performance

The evaluation metrics and MaxEnt settings for the best climatic and edaphic models (ΔAICc = 0) are shown in Table 4.3. The best edaphic and climatic models for Mexico and Nigeria were characterized by low regularisation multipliers ($1 \leq RM \leq 2$). Feature classes for Mexican and Nigerian Climatic Models included Linear, Quadratic, Hinge (LQH) and Linear, Quadratic, Hinge, Product (LQHP) respectively. The Mexican Edaphic Model had an additional feature class (LQHP) while the Nigerian Edaphic Model presented only one feature class (Hinge, H).

Both climatic and edaphic models showed a very good predictive power (mean Area under the Curve,AUC > 0.80) (Table 4.3). Predictive performance was also very good as shown by all Boyce indices except for the Reciprocal Mexican Climatic and Edaphic models (rMCM and rMEM respectively). Both Reciprocal Nigerian Climatic and Edaphic Models (rNCM and rNEM) that is, those calibrated in Mexico and projected to Nigeria appeared as robust predictions of suitable habitats for this species in Nigeria with a Boyce index of 0.89 and 0.92 respectively. A more robust prediction was achieved by merging both Nigerian climatic models (NCM and rNCM) based on their maximum predicted values (Boyce index = 0.95) as opposed to merging both edaphic Nigerian models, NEM and rNEM (Boyce index = 0.89). Therefore rNEM is a more accurate representation of the geographic distribution of *T. diversifolia* with respect to soil physico-chemical properties.

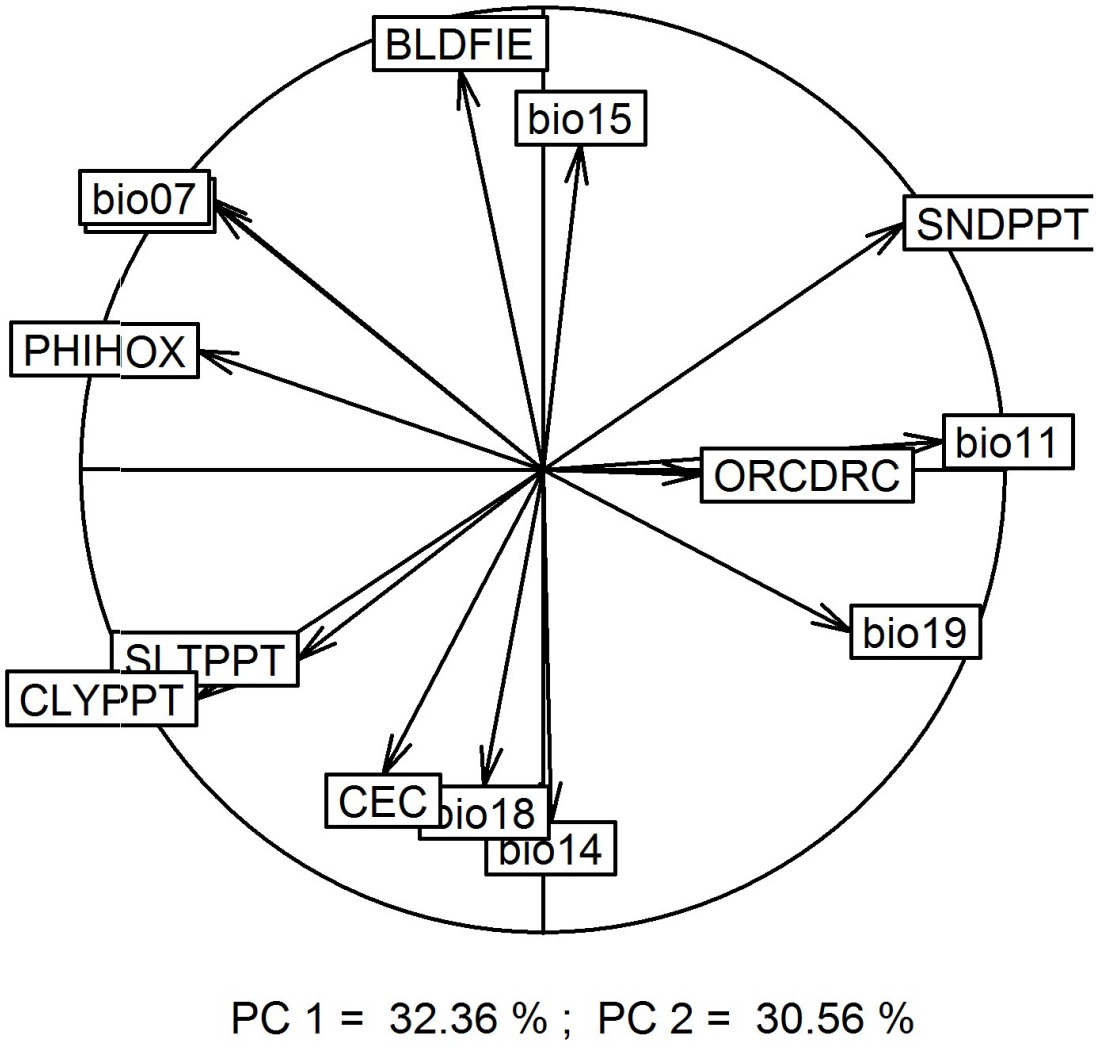

Figure 4.3. Principal Component Analysis for the niche of *Tithonia diversifolia*

This circle shows the relationships among the variables used in modelling the niche of *T. diversifolia.* Each arrow represents a variable. The length of an arrow depicts the strength ofits correlation coefficient. Arrows pointing in the same direction indicate that the corresponding variables increase (or decrease) in tandem. The full description of all variables is shown in Tables 3.2 and 3.4.

Table 4.2. Contributions of variable in PCA analysis for *Tithonia diversifolia*

Variable	Axis 1	Axis 2
Mean Temperature of Coldest Quarter(Bio 11)	0.86	0.06
Sand content (SNDPPT)	0.78	0.53
Precipitation of Coldest Quarter(Bio 19)	0.66	-0.34
Organic Carbon (ORCDRC)	0.34	-0.01
Precipitation Seasonality (Bio 15)	0.08	0.70
Precipitation of Driest Month(Bio 14)	0.01	-0.75
Precipitation of Warmest Quarter(Bio 18)	-0.12	-0.68
Bulk density (BLDFIE)	-0.17	0.86
Cation exchange capacity (CEC)	-0.34	-0.65
Silt content (SLTPPT)	-0.53	-0.40
Mean Diurnal Range (Bio 02)	-0.71	0.57
Temperature Annual Range (Bio 07)	-0.72	0.58
pH (PHIHOX)	-0.74	0.25
Clay content (CLYPPT)	-0.75	-0.49

Table 4.3. Evaluation metrics for models of *Tithonia diversifolia*

Models	Feature Class	RM	Mean AUC	Δ AICc	Boyce index
MCM	LQH	1.0	0.89	0.00	0.98
NCM	LQHP	2.0	0.95	0.00	0.92
rMCM	--	--	--	--	-0.59
rNCM	--	--	--	--	0.89
mNCM	--	--	--	--	0.95
MEM	LQHP	1.5	0.84	0.00	0.99
NEM	H	1	0.92	0.00	0.98
rMEM	--	--	--	--	-0.27
rNEM	--	--	--	--	0.92
mNEM	--	--	--	--	0.89
m(mNCM, rNEM)	--	--	--	--	0.94

MaxEnt settings: RM (regularization multiplier) and feature classes (L = Linear, Q = Quadratic, P = Productand H = Hinge).

4. 1. 3 Ecological distribution of *T. diversifolia*

The current potential ecological distributions of *T. diversifolia* in Mexico and Nigeria based on current derived bioclimatic variables (1973-2013) is shown in Figure 4.4. Unsurprisingly, the highest climatic suitability for *T. diversifolia* as predicted by NCM was constrained to the western part of the derived savanna, which corresponds to South-western Nigeria.

The prediction of MCM showed that only southern Mexico is climatically suitable for *T. diversifolia* (Figure 4.4a). Upon projection to Nigeria, MCM (which is equivalent to rNCM) predicted that the climate of the south-westernderived savanna zone is the most suitable for this species (Figure 4.4b). This model also predicted moderate climatic suitability across the middle belt.Although this prediction closely matches the observed distribution of the study species in Nigeria,merging both rNCM and NCM provided the most likely climatic niche of the focal species. The Boyce index calculated for nNCM confirmed this (Table 4.3). As shown by mNCM, the most suitable climatic zone for *T. diversifolia* stretches throughout the Derived Guinea Savanna, from the southwest to the middle belt of the country (Figure 4.5).

The future potential spread of *T. diversifolia* (2041 - 2060) based on the HadGEM2-CC and MIROC-ESM-CHEM models for RCP 8.5 presented a similar pattern with areas of highest climatic suitability forming a belt that cuts across the Derived Savanna (Figure 4.6). It is worthy to note that these models predicted a wider distribution, which corresponds to an expansion of the range of this species compared to the current models (Figure 4.4).

A visual inspection of edaphic models of *T. diversifolia* (Figure 4.7) shows that they clearly differ from climatic models (Figure 4.4). The MEM predicted that a small extent of Mexican soils, mainly in the southern region of this country can support the growth of the study species. The prediction of NEM agree with that of NCM, with soils of the south-western region of Nigeria being the most suitable for the study species. However, the reciprocalNigerian Edaphic Model (rNEM) showed that *T. diversifolia* can grow under a wider range of soil types throughout the southern and the north central regions. According to the evaluation metrics in Table 4.3, rNEM appears as the best spatial representation of soil physico-chemical variables that play a central

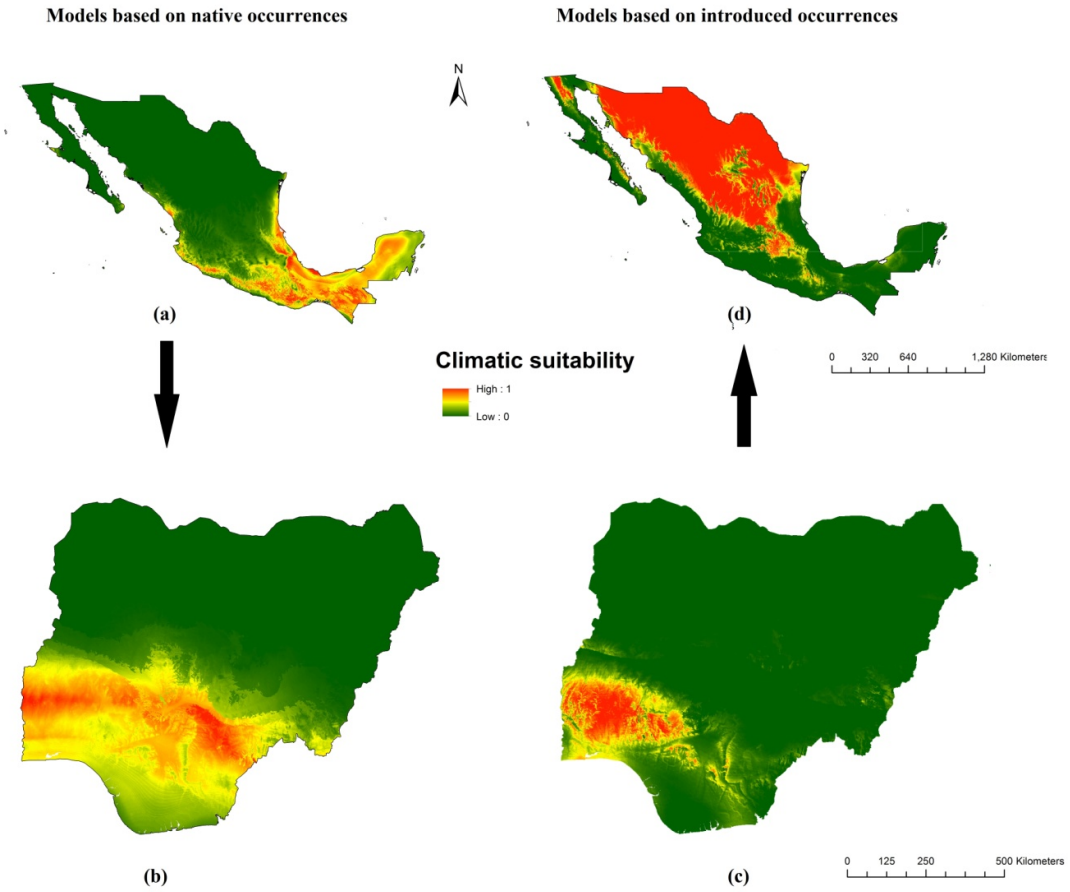

Figure 4.4. Current reciprocal climatic distribution of *Tithonia diversifolia*in Nigeria

Current maps based on (a) Mexican Climatic Model (MCM), (b) reciprocal Nigerian Climatic Model (rNCM)withnative data, (c) Nigerian Climatic Model (NCM) and (d) reciprocal Mexican Climatic Model (rMCM), with introduced records from published studies. Areas of high habitat suitability are depicted in warmer colours.

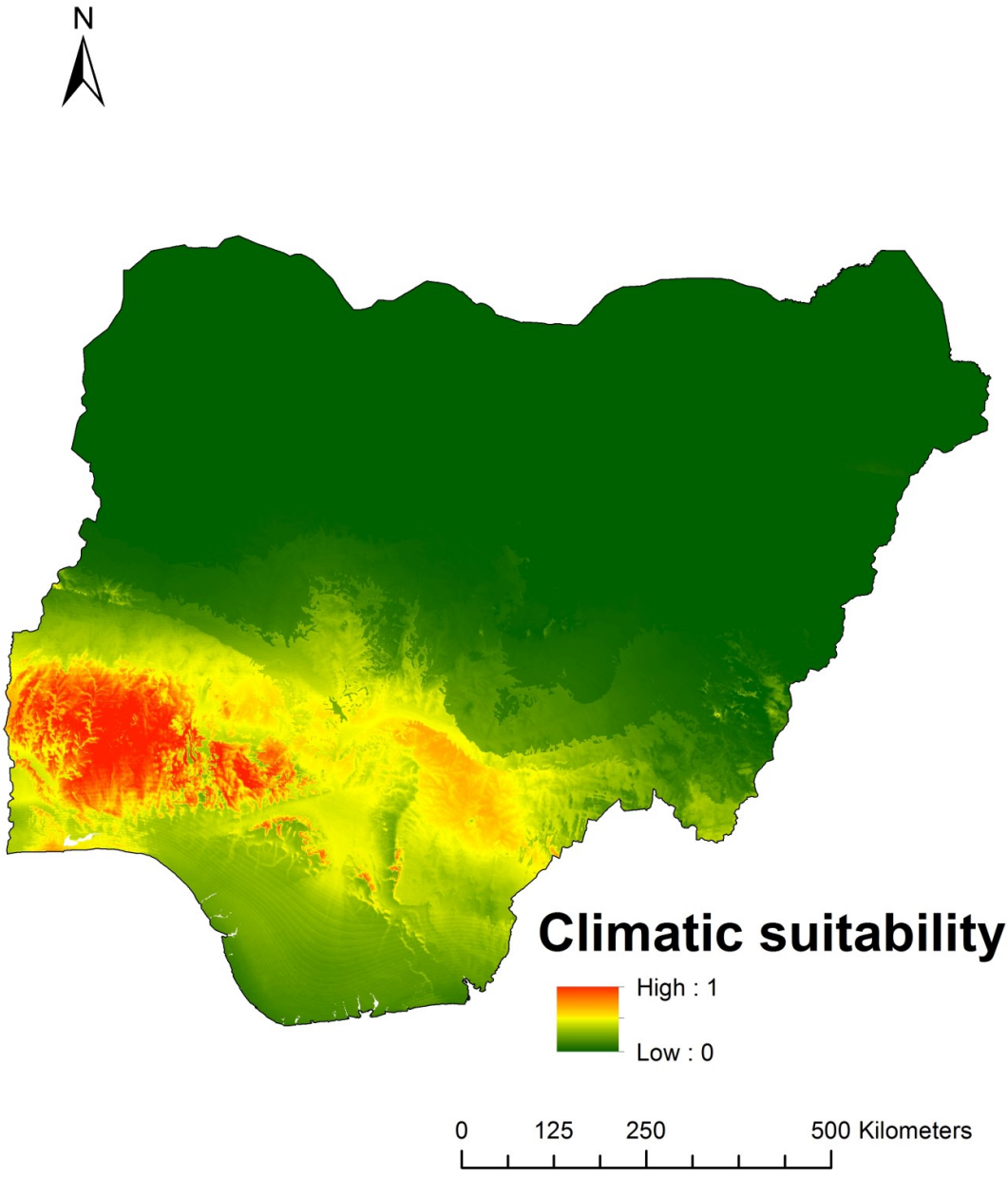

Figure 4.5. Current potential climatic distribution of *Tithonia diversifolia* in Nigeria

Map based on the maximum predicted values from merged reciprocal models.Areas of high habitat suitability are depicted in warmer colours.

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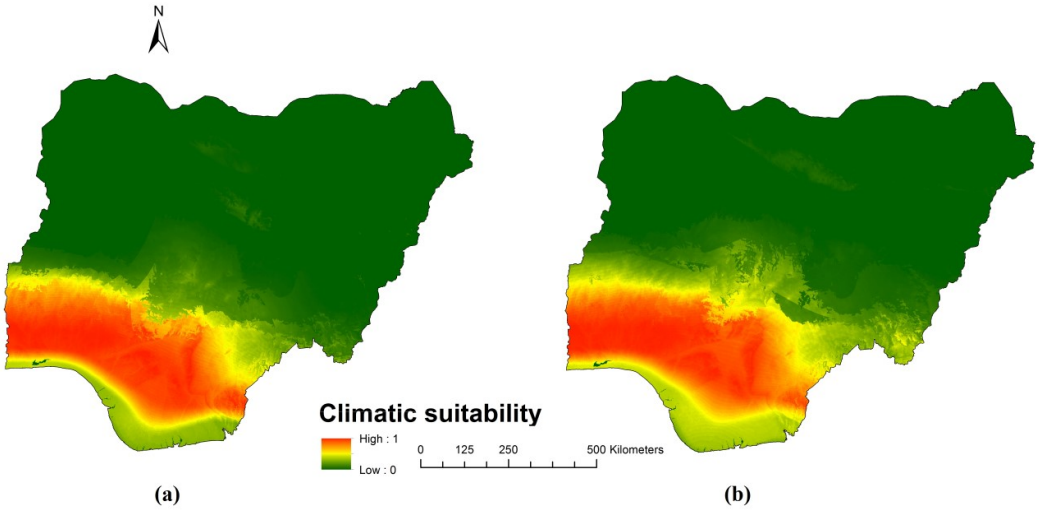

Figure 4.6. Future potential climatic distribution of *Tithonia diversifolia* in Nigeria

Maps arebased on the two selected climate scenarios: (a) HadGEM2-CC, (b) MIROC-ESM-CHEM.Areas of high habitat suitability are depicted in warmer colours.

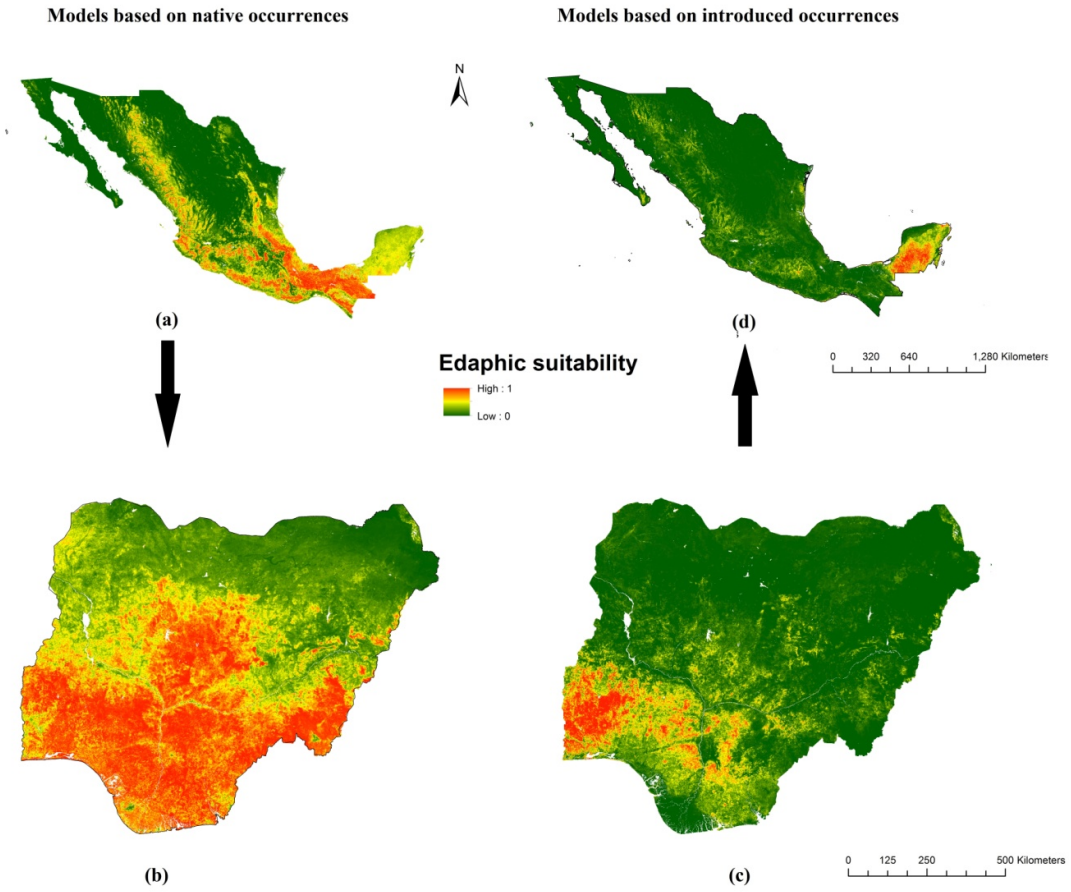

Figure 4.7. Reciprocal distribution models of *Tithonia diversifolia* in Nigeria

Maps arebased on seven soil physico-chemical properties at 15 cm depth. (a) Mexican Edaphic Model (MEM), (b) reciprocal Nigerian Edaphic Model (rNEM), based on native data, (c) Nigerian Edapahic Model (NEM) and (d) reciprocal Mexican Edaphic Model (rMEM), based on introduced records.Areas of high habitat suitability are depicted in warmer colours.

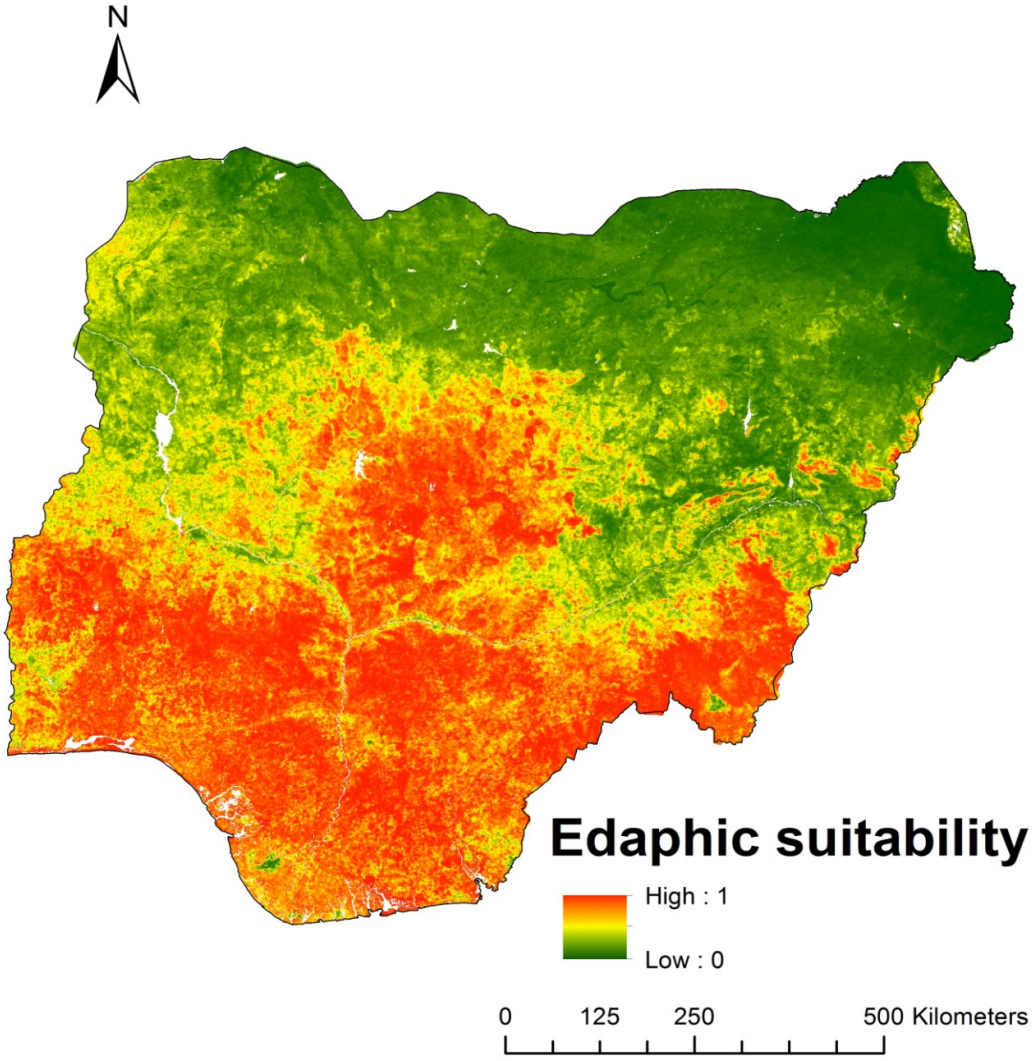

Figure 4.8. Potential distribution of *Tithonia diversifolia* in Nigeria

Map is based soil physico-chemical properties at 15 cm depth.Areas of high habitat suitability are depicted in warmer colours.

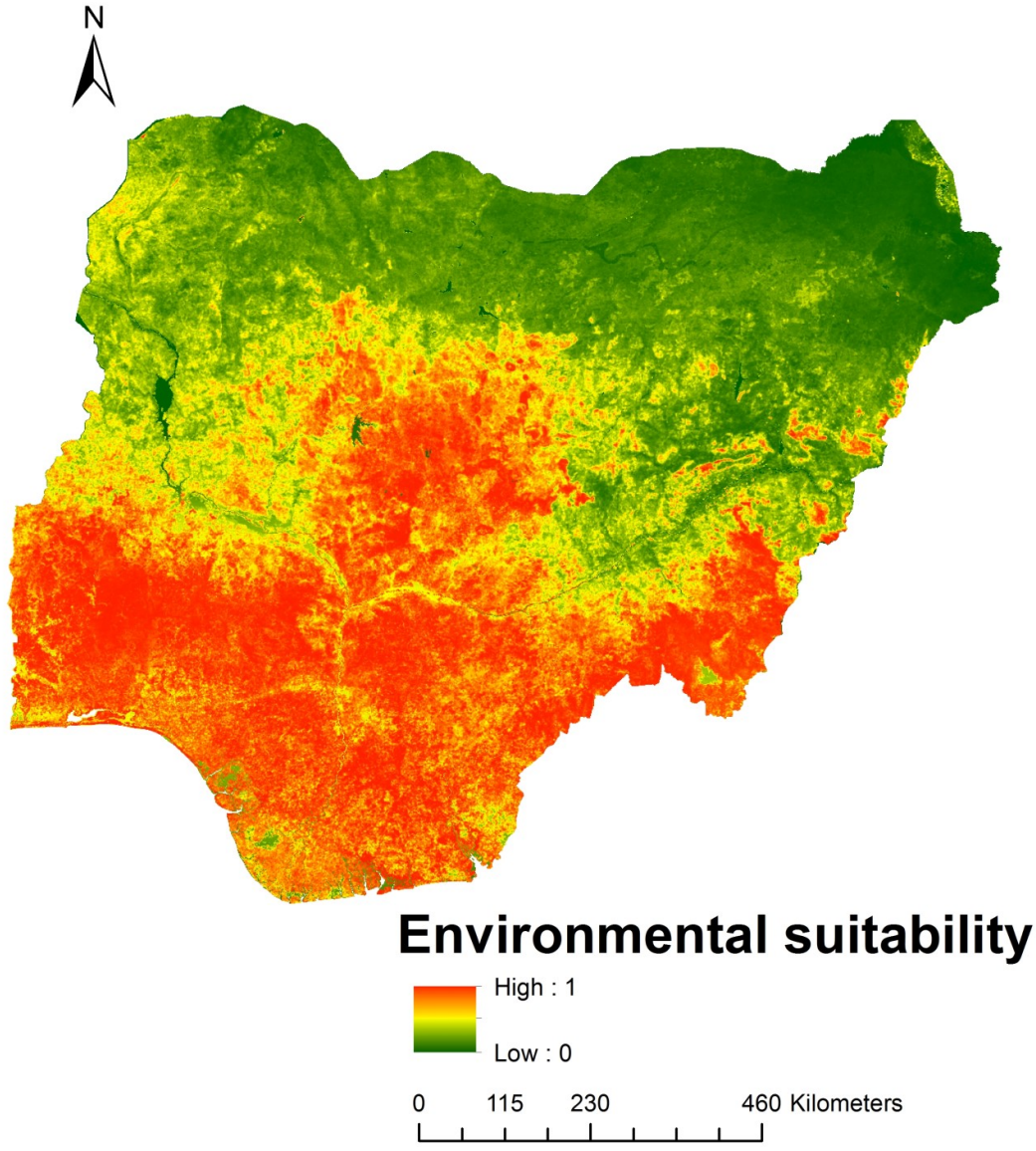

Figure 4.9. Potential ecological distribution of *Tithonia diversifolia* in Nigeria

Map is based on both climatic and edaphic factors. Areas of high habitat suitability are depicted in warmer colours.

role in the spread of the study species in Nigeria (Figure 4.8). Merging rNEM and mNCM (Figure 4.9) produced a wider distribution of this species.These models combined together predicted that most of the southern part of Nigeria is suitable for the study species when both climatic and edaphic factors are considered.

4. 1. 4 Variable importance

The relative contributions of abiotic variables used in the analyzing the ecological niche of *T. diversifolia* in Mexico and Nigeria with MaxEnt are shown in Table 4.4. For MCM, Temperature annual range (BIO 7) had the highest contribution (84 %) indicating that this variable plays a vital role in the distribution of the study species in Mexico. In contrast, for NCM, four bioclimatic variables were identified as the most important, that is, precipitation of driest month (Bio 14), precipitation of coldest quarter (BIO 19), Mean temperature of coldest quarter (Bio 11) and precipitation of warmest quarter (Bio 18). Together, these variables contributed about 95% to this model.

Almost the same set of soil physico-chemical properties had the highest contribution to both MEM and NEM (Table 4.4). However their contribution differed as bulk density, pH and Organic carbon content at 15 cm depth together contributed 92 and 65% to MEN and NEM respectively. NEM differed from MEM with silt content contributing 33.11% in the former and less than 0.5% for the later.

4. 1. 5 Variable responses

Figure 4.10 and Figure 4.11 show the response of each environmental variable used in analysing the spatial distribution of the study species in relation to climatic and edaphic variables respectively. These curves depict model prediction changes in relation to each environmental variable when others is kept constant. Therefore, each curve shows a separate MaxEnt model built solely based on one variable. Values on the Y-axis represent the probability of climatically suitable sites as given by the *cloglog* output of MaxEnt when any other variable is set to its average value.

Table 4.4. Contribution bioclimatic variables in models of *Tithonia diversifolia*

Variable source		Percent contribution	
		Bioclimatic model	
		MCM	NCM
Bioclimatic variables	Mean Diurnal Range (Bio 2)	1.78	0.70
	Temperature Annual Range (Bio 7)	84.90	0.70
	Mean Temperature of Coldest Quarter (Bio 11)	4.39	15.45
	Precipitation of Driest Month (Bio 14)	3.2	50.32
	Precipitation Seasonality (Bio 15)	3.83	2.83
	Precipitation of Warmest Quarter (Bio 18)	0.79	10.87
	Precipitation of Coldest Quarter (Bio 19)	1.10	19.14
		Edaphic models	
		MEM	NEM
Edaphic variables	Bulk density (BLDFIE)	32.05	37.77
	SNDPPT(Sand content)	6.24	1.00
	Silt content (SLTPPT)	0.40	33.11
	Clay content (CLYPPT)	0.13	0.09
	pH (PHIHOX)	29.36	17.26
	Cation exchange Capacity (CECSOL)	0.47	0.23
	Organic carbon (ORCDRC)	31.36	10.54

MCM = Mexican Climatic Model; NCM = Nigerian Climatic Model

MEM = Mexican Edaphic Model; NEM = Nigerian Edaphic Model

In general, climatic suitability of both study ranges for *T. diversifolia* was below 0.5 for each of the seven variables taken individually, except for Bio 7 (in both ranges), Bio 2 and Bio 11 (in the introduced range). In Nigeria, climatic suitability was highest, (= 1) for values of Bio 2 ranging from 14^{o} to 58.53^{o}. Next, between 59.67 ^{o} and 74.93 ^{o}, climatic suitability decreased abruptly from 1 to 0.56. In contrast, for the native range, predicted climatic suitability was 0 for this variable suggesting ithad no effect the study species in Mexico. In Nigeria, for values of Bio 7 between 18^{o}C to 26.5^{o} C predicted climatic suitability for *T. diversifolia* linearly increased from 0 to 1 while in Mexico, this variable followed a bimodal pattern with a maximum suitability of 0.77 and 0.92 at 10.10^{o} and 14.23^{o} respectively. For Bio 11,maximum habitat suitability was recorded between 10.6 ^{o} and 11.6^{o}. Beyond this range, a decrease was noted. In contrast, suitability was 0 for all values of Bio 11 in Mexico. Both in Mexico and Nigeria, predicted suitability in relation to either Bio 14 or Bio 15 was very low (< 0.2). The response curve for Bio 18 was unimodal in the Nigeria with the highest predicted (0.43) at 15.5^{o}. However, for this all possible values of this variable in the native range of *T. diversifolia,* thepredicted suitability was 0. A similar pattern was observed for Bio 19 in both ranges.

Generally, predicted suitability in term of soil properties as shown in Figure 4.11 was below 0.5 for all edaphic variables at 15 cm depth except sand and silt content in the introduced range. Edaphic suitability was highest for sand content values ranging from 17 % to 23% and lowest between 49% and 73%. In the introduced range, silt content showed a unimodal distribution when used individually to model the distribution of this species while keeping other variables at their mean values. Maximum predicted edaphic suitability was 0.68 in the introduced range, which corresponds to a silt content of 14%.

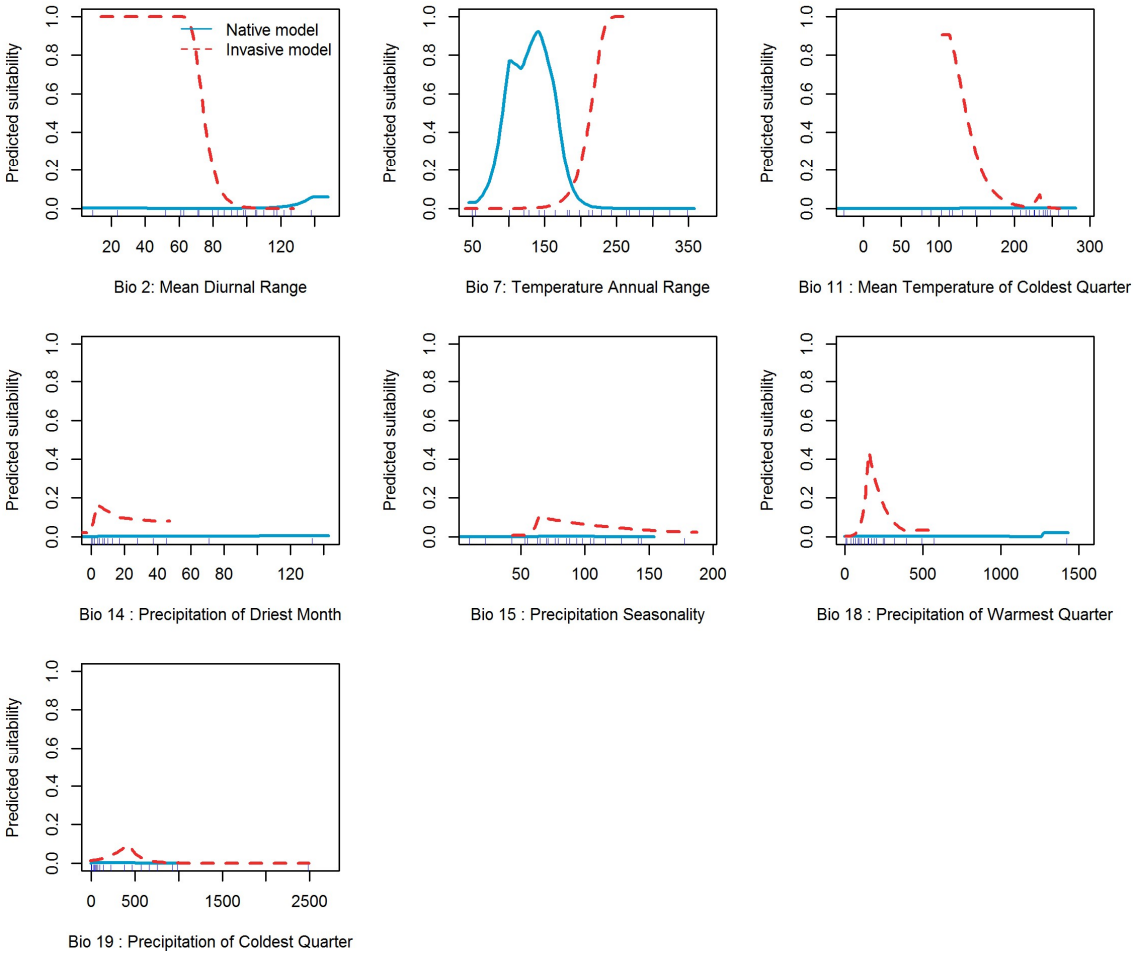

Figure 4.10. Response curves of climatic variables in models of *Tithonia diversifolia*

The red dashed and solid blue lines represent variable response curves in Nigeria and Mexico respectively.

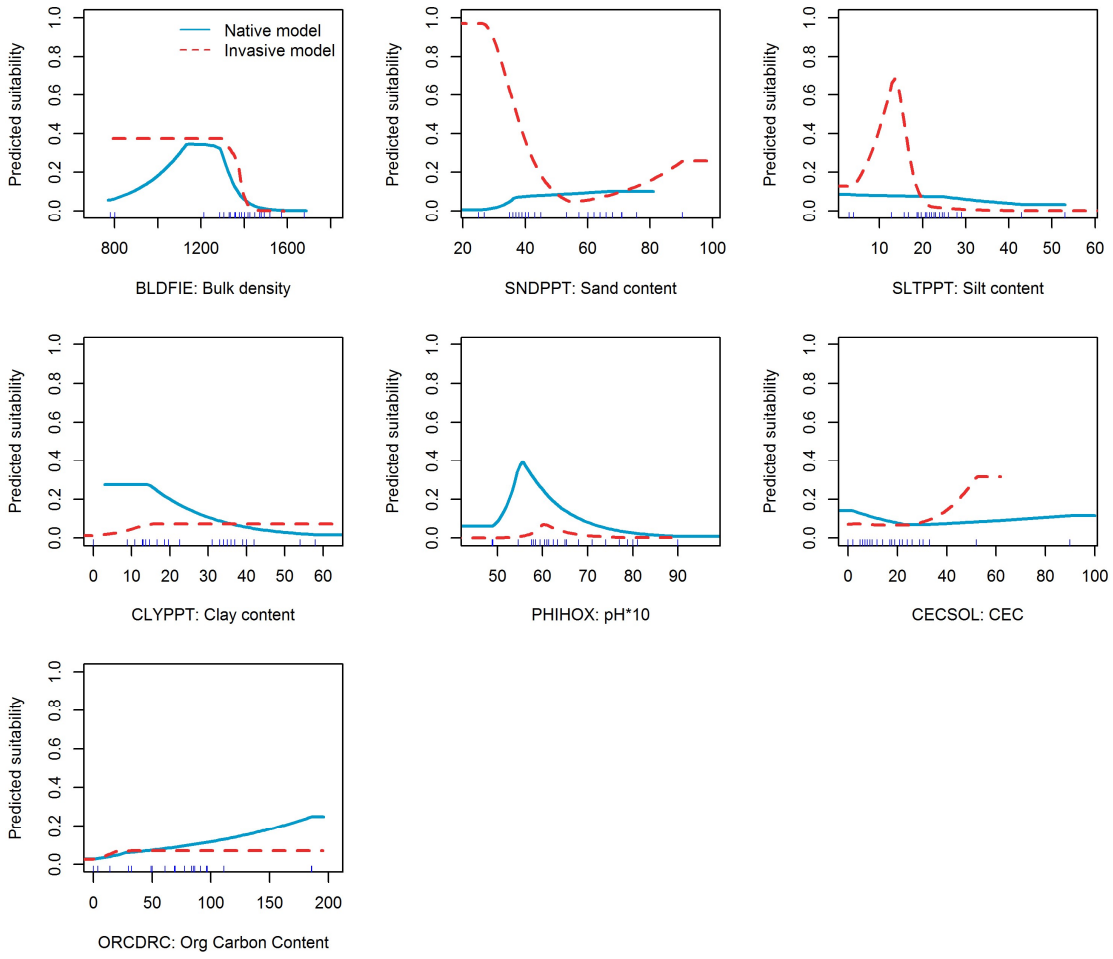

Figure 4.11. Response curves of edaphic variables in models of *Tithonia diversifolia*

The red dashed and solid blue lines represent variable response curves in Nigeria and Mexico respectively.

4. 2 Seed bank and Soil properties of sites infested by *T. diversifolia*

4. 2. 1 Seed bank diversity of sites infested by *T. diversifolia*

A total of 1665 seedlings from 69 species were identified from all soil samples (Appendix 5). The greatest seed bank abundance and diversity were obtained in Ibadan (39.04%) and Ilorin (29.49) while the least was at Abuja (3.18%). The SIMPER analysis revealed the study species had no influence on the seedbank of invaded sites (Table 4.5). Although dominant in the aboveground vegetation at all sites, *T. diversifolia* was not found in the seed bank at Abuja and Jos. The ten most influential species, accounting for 62.12% of all emergents were *Oldenladia corymbosa* (14.17%), *Ageratum conyzoides* (7.62%), *Ludwigia abyssinica* (7.38%), *Alternathera sessilis* (6.37%), *Cynodon dactylon* (5.52%) and *Galinsoga parviflora* (5.40%), *Spilanthes costata* (4.68%), *Digitaria nuda* (4.08%), *Bacopa decumbens* (3.48%) and *Fleurya aestuans* (3.42%). Only 27 seedlings of *T. diversifolia* emerged from all samples with 14 of them recorded from the invaded plot at Ibadan. Species richness and diversity were significantly reduced across sites in invaded plots with about 10 speciesless in invaded plots (Table 4.6).

The PERMDISP test did not detect significant differences in the dispersion at each site (F= 2.36, P = 0.07). Site distances to the centroid were 0.53, 0.50, 0.40 0.46 and 0.45 for Abuja, Asaba, Ibadan, Ilorin and Jos respectively. PERMANOVA indicated that species composition was statistically different between site and invasion status (Table 4.7). Non-metric multidimensional scaling illustrating differences in seed bank community structure between invaded and non invaded plots across study sites (Figure 4.12) showed a clear separation in species composition between invaded and non invaded plots only at Jos, Abuja and Asaba. In contrast, seed banks of the remaining two study sites was almost similar in structure between invaded and non-invaded plots.

Table 4.5. Similarity percentage of soil seed banks invaded by *Tithonia diversifolia*

S/N	Species	Invaded?		Average abundance	Dissimilarity SD	Relative contribution	Cumulative contribution
		Yes	No				
1	*Oldenladia corymbosa* Linn.	6.00	5.80	0.09	0.11	0.86	0.10
2	*Cynodon dactylon* (Linn.) Pers.	0.05	4.55	0.09	0.18	0.47	0.19
3	*Ageratum conyzoides* Linn.	3.60	2.75	0.06	0.09	0.66	0.26
4	*Ludwigia abyssinica* A. Rich	4.25	1.90	0.06	0.10	0.59	0.32
5	*Galinsoga parviflora* Cav	2.35	2.15	0.06	0.11	0.52	0.38
6	*Alternathera sessilis* (Linn.) DC.	2.40	2.90	0.04	0.06	0.66	0.43
7	*Spilanthes costata* Benth.	0.10	3.80	0.04	0.07	0.57	0.47
8	*Digitaria nuda* Schumach.	0.55	2.85	0.04	0.07	0.58	0.52
9	*Bacopa decumbens* (Fernald) F.N. Williams	0.15	2.75	0.03	0.08	0.39	0.55
10	*Euphorbia hyssopifolia* Linn.	0.90	1.50	0.02	0.04	0.60	0.58
11	*Fleurya aestuans* [Linn.] ex Miq.	2.55	0.30	0.02	0.04	0.49	0.60
12	*Eleusine indica* L. Gaertn.	0.70	0.75	0.02	0.03	0.59	0.63

Contributions of the twenty most influential species (based on average abundance) that explained the dissimilarity between the seed bank of sites invaded by *T. diversifolia* and those lacking this plant.

Table 4.5. Similarity percentage of soil seed banks invaded by *Tithonia diversifolia*(Continued)

S/N	Species	Invaded?		Average abundance	Dissimilarity SD	Relative contribution	Cumulative contribution
		Yes	No				
13	*Cyperus rotundus* Linn.	0.60	0.60	0.02	0.04	0.44	0.65
14	*Spermacoce ocymoides* Burm. f.	0.20	0.75	0.02	0.04	0.4	0.66
15	*Panicum maximum* Jacq.	0.75	0.25	0.02	0.04	0.48	0.68
16	*Portulaca oleracea* Linn.	0.50	1.55	0.02	0.03	0.58	0.70
17	*Amaranthus spinosus* Linn.	0.40	1.00	0.02	0.03	0.59	0.72
18	*Mollugo nudicaulis* Lam.	0.95	0.25	0.02	0.03	0.47	0.74
19	*Phylanthus amarus* Schum. & Thonn.	0.65	0.80	0.02	0.04	0.41	0.75
20	*Cyperus amabilis* Vahl.	0.00	0.45	0.02	0.05	0.33	0.77
21	*Brachiara lata* (Schumach.) C.E. Hubbard	0.40	0.35	0.01	0.03	0.48	0.79
22	*Tithonia diversifolia* (Hemsl) A. Gray	1.25	0.10	0.01	0.03	0.49	0.80
23	*Cyperus tuberosus* Linn.	0.35	0.75	0.01	0.02	0.58	0.82
24	*Celosia leptostachya* Benth.	0.05	0.35	0.01	0.05	0.26	0.83

Contributions of the twenty most influential species (based on average abundance) that explained the dissimilarity between the seed bank of sites invaded by *T. diversifolia* and those lacking this plant.

Table 4.5. Similarity percentage of soil seed banks invaded by *Tithonia diversifolia*(Continued)

S/N	Species	Invaded?		Average abundance	Dissimilarity SD	Relative contribution	Cumulative contribution
		Yes	No				
25	*Spigelia anthelmia* Linn.	1.10	0.25	0.01	0.02	0.51	0.84
26	*Pepperomia pellucida* (L.) H.B. & K.	0.00	1.35	0.01	0.03	0.33	0.85
27	*Acalypha fimbriata* Schum. & Thonn.	0.75	0.30	0.01	0.03	0.39	0.86
28	*Gomphrena celosiodes* Mart.	0.00	1.05	0.01	0.03	0.35	0.87
29	*Digitaria horizontalis* Willd.	1.00	0.05	0.01	0.02	0.42	0.88
30	*Cyperus iria* Linn	0.05	0.75	0.01	0.02	0.45	0.89
31	*Digitaria ciliaris* (Retz.) Koel.	0.30	0.50	0.01	0.02	0.38	0.90
32	*Chromolaena odorata* (L.) R.M. King & Robinson	0.10	0.60	0.01	0.02	0.39	0.91
33	*Setaria pumila* (Poir) Roem & Schult.	0.40	0.20	0.01	0.01	0.41	0.92
34	*Pycreus lanceolatus* (Poir.) C.B. Clarke	0.05	0.15	0.01	0.02	0.29	0.92
35	*Hyptis suaveolens* Poit	0.10	0.15	0.01	0.02	0.27	0.93
36	*Cyperus longibracteatus* Cherm.	0.35	0.25	0.01	0.01	0.47	0.94

Contributions of the twenty most influential species (based on average abundance) that explained the dissimilarity between the seed bank of sites invaded by *T. diversifolia* and those lacking this plant.

Table 4.5. Similarity percentage of soil seed banks invaded by *Tithonia diversifolia*(Continued)

S/N	Species	Invaded?		Average abundance	Dissimilarity SD	Relative contribution	Cumulative contribution
		Yes	No				
37	*Croton lobatus* Linn	0.20	0.15	0.00	0.01	0.39	0.94
38	*Eragrostis tremula* Hochst. ex Steud.	0.00	0.10	0.00	0.02	0.26	0.95
39	*Panicum repens* Linn	0.20	0.05	0.00	0.01	0.33	0.95
40	*Sida acuta* Burn. f.	0.00	0.55	0.00	0.02	0.22	0.95
41	*Lindernia crustacea* (L.) F. Muell.	0.00	0.40	0.00	0.01	0.38	0.96
42	*Setaria longiseta* P. Beauv.	0.30	0.00	0.00	0.01	0.22	0.96
43	*Sida garckeana* Polak.	0.10	0.05	0.00	0.01	0.27	0.96
44	*Vernonia ambigua* Kotschy & Peyr	0.00	0.20	0.00	0.01	0.39	0.97
45	*Kyllinga erecta*Schumach	0.25	0.10	0.00	0.01	0.30	0.97
46	*Physalis angulata* Linn	0.25	0.00	0.00	0.01	0.39	0.97
47	*Setaria barbata* (Lam.) Kunth.	0.10	0.15	0.00	0.00	0.45	0.97
48	*Talinum triangulare* (Jacq.) Willd.	0.00	0.20	0.00	0.01	0.32	0.98

Contributions of the twenty most influential species (based on average abundance) that explained the dissimilarity between the seed bank of sites invaded by *T. diversifolia* and those lacking this plant.

Table 4.5. Similarity percentage of soil seed banks invaded by *Tithonia diversifolia*(Continued)

S/N	Species	Invaded?		Average abundance	Dissimilarity SD	Relative contribution	Cumulative contribution
		Yes	No				
49	*Boerhavia erecta* Linn.	0.05	0.05	0.00	0.01	0.24	0.98
50	*Sida rhombifolia* Linn.	0.00	0.15	0.00	0.01	0.31	0.98
51	*Solanum erianthum* D. Don	0.10	0.05	0.00	0.00	0.37	0.98
52	*Dactyloctnium aegyptum* (Linn.) P. Beauv.	0.00	0.20	0.00	0.01	0.29	0.98
53	*Andropogon gayanus* Kunth.	0.00	0.10	0.00	0.01	0.21	0.99
54	*Pouzolzia guineensis* Benth.	0.10	0.00	0.00	0.01	0.28	0.99
55	*Synedrella nodiflora* Gaertn.	0.10	0.00	0.00	0.01	0.22	0.99
56	*Brachiara deflexa* (Schumach.) C.E. Hubbard ex Robyns	0.05	0.00	0.00	0.01	0.20	0.99
57	*Heliotropium ovalifolium* Forssk.	0.05	0.00	0.00	0.01	0.20	0.99
58	*Bidens pilosa* Linn.	0.05	0.05	0.00	0.00	0.31	0.99
59	*Oldenladia lancifolia* (Schumach.) D.C.	0.00	0.05	0.00	0.00	0.21	0.99
60	*Tridax procumbens* Linn.	0.05	0.05	0.00	0.00	0.31	0.99

Contributions of the twenty most influential species (based on average abundance) that explained the dissimilarity between the seed bank of sites invaded by *T. diversifolia* and those lacking this plant.

Table 4.5. Similarity percentage of soil seed banks invaded by *Tithonia diversifolia*(Continued)

S/N	Species	Invaded?		Average abundance	Dissimilarity SD	Relative contribution	Cumulative contribution
		Yes	No				
61	*Paspalum scrobiculatum* Linn.	0.00	0.05	0.00	0.00	0.21	1.00
62	*Passiflora foetida* Linn.	0.05	0.05	0.00	0.00	0.31	1.00
63	*Ludwigia decurrens* Walt.	0.05	0.00	0.00	0.00	0.22	1.00
64	*Ludwigia hyssopifolia* (G. Don) Exell	0.00	0.05	0.00	0.00	0.22	1.00
65	*Asystasia gangetica* (Linn.) T. Anders	0.00	0.05	0.00	0.00	0.22	1.00
66	*Centrosema molle* Mart. ex Benth	0.00	0.05	0.00	0.00	0.22	1.00
67	*Mimosa invisa* Mart.	0.00	0.05	0.00	0.00	0.22	1.00
68	*Chamaecrista mimosoides* (L.) Greene	0.00	0.05	0.00	0.00	0.22	1.00
69	*Cenhrus biflorus* Roxb.	0.00	0.05	0.00	0.00	0.22	1.00

Contributions of the twenty most influential species (based on average abundance) that explained the dissimilarity between the seed bank of sites invaded by *T. diversifolia* and those lacking this plant.

Table 4.6. ANOVA results testing invasion effect on species richness and diversity

	Significance (summary ANOVA)			Group mean ± SE (n=5)	
	Site (S)	Invasion (I)	S × I	Invaded	Non-invaded
Richness	**	***	n.s	36 ± 8	48 ± 7
Diversity	***	*	***	1.45 ± 0.15	1.74 ± 0.11

Results of species richness and diversity in plots invaded by *T. diversifolia* across five sites in Nigeria. ***P*<0.01; ****P*<0.001; n.s., non-significant

Table 4.7. Effect of *Tithonia diversifolia* on seed bank composition

Source of variation	*df*	SS	MS	F	R^2	*P*
Status	1	0.6584	0.6584	3.4708	0.0412	0.0001
Site	4	6.6134	1.6534	8.7152	0.4140	0.0001
Status × Site	4	3.0116	0.7529	3.9687	0.1886	0.0001
Residuals	30	5.6912	0.1897		0.3562	
Total	39	15.9747			1.0000	

Invasion effects based on Permutational Analysis of Variance **(**PERMANOVA) for thecomposition of soil seed banks collected at five sites in areas invaded by *Tithonia diversifolia*

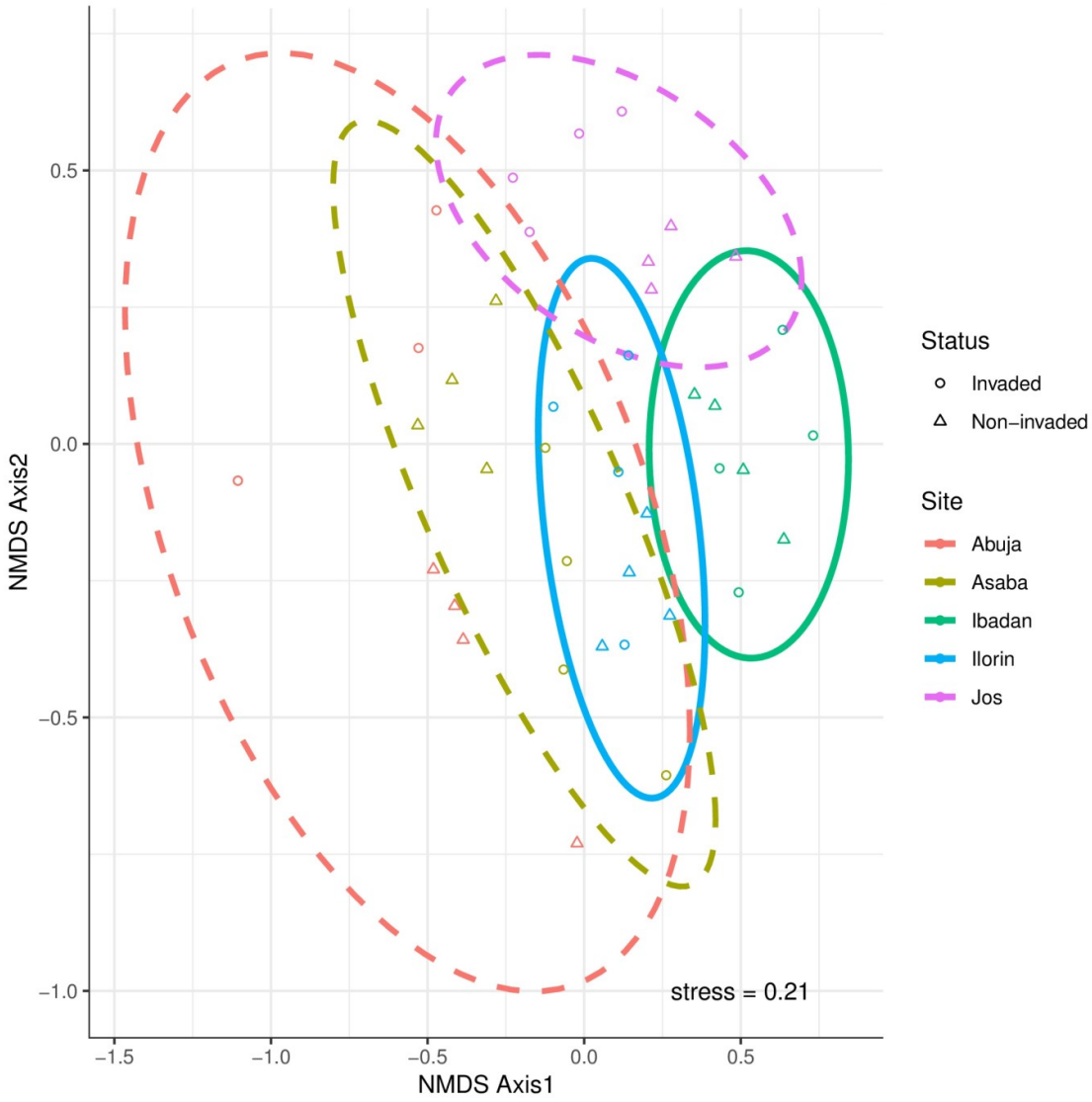

Figure 4.12. Non-metric Dimensional Scaling of seed banks of *Tithonia diversifolia*

Each ellipse represents a site. Circles and triangles within each ellipse represent invaded and non-invaded quadrats respectively. Points close together in the ordination space indicate similarity in terms of community composition. The solid lines show sites where the seed bank structure between invaded and non-invaded quadrats is not significantly different.

4. 2. 2Soil physico-chemical properties of sites invaded by *T. diversifolia*

Soils from study sites were classified as sandy (>78% sand content). All soil physical properties showed no differences between invaded and non-invaded plotsacross all study sites (Table 4.8). Among the chemical properties investigated, Electrical conductivity, Nitrate nitrogen and Manganese were not significantly different between invaded and non-invaded plots at all sites. Other chemical properties that were statistically different across sites and between invasion status were pH, Total Nitrogen, effective CEC, organic carbon, available phosphorus, phosphate, Iron, Copper and Zinc. All invaded plots showed elevated levels of chemical properties except for Iron, Copper and Zinc (Table 4.8). There was non-significant effect of invasion status on Ammonium and Nitrite nitrogen. However, different site effects caused a significantly different interaction between site and invasion for these two properties.

4. 3 Variation of N, P,K and reproductive Allocation in *T.diversifolia*

4. 3. 1 Nitrogen levels in soils and tissues of *T.diversifolia*

Percentage Nitrogen in soils at the study sites and organs of *T. diversifolia* harvested from these locations is shown in Table 4.9. Percentage Nitrogen in the studied soils ranged from 1.54 ± 0.01in Ikere to 3.20 ± 0.03in Shagamu. Nitrogen levels were significantly different across most study sites ($p< 0.05$) except between Odeda and Ekanmeje; Okoafon and Fiditi as well as between Ifo and Ikere. Nitrogen levels in roots, stems, leaves and flowers of *T. diversifolia* differed significant regardless of the site with the highest percentage found in leaves (1.31 ± 0.14) and the lowest in flowers (0.33 ± 0.04). Linear regression analysis revealed that the soil Nitrogen was related to Nitrogen in roots and leaves of the plant with a coefficient of determination of 65% and 50% respectively (Figure 4.13 a). The association between soil Nitrogen and these two variables was significant and could be described by the equations:$N_r = 0.78N_s - 0.60$ and$N_l = 0.84N_s - 0.66$

Where N_r, N_l and N_s are root, leaf and soil Nitrogen (in percentage), respectively.

Table 4.8. ANOVA summary of soil physico-chemical properties

	Significance (summary ANOVA)			Group mean ± SE (n=5)	
	Site (S)	Invasion (I)	S × I	Invaded	Non-invaded
pH	***	***	***	7.76 ± 0.15	6.8 ± 0.12
EC (µS/cm)	***	n.s	n.s	116.08 ± 6.69	113.67 ± 8.81
Total N (%)	***	***	***	3.25 ± 0.19	2.57 ± 0.20
NO_3-N (ppm)	***	n.s.	n.s.	1.11 ± 0.04	1.11 ± 0.06
NO_2-N (ppm)	***	n.s.	***	0.22 ± 0.01	0.22 ± 0.02
NH_4-N (ppm)	***	n.s.	***	0.16 ± 0.01	0.16 ± 0.01
PO_4 (ppm)	***	*	***	0.32 ± 0.01	0.32 ± 0.01
CEC (Cmol/kg)	***	***	***	6.43 ± 0.23	3.48 ± 0.11
Org C (%)	***	***	***	30.77 ± 1.88	25.66 ± 1.98
P (ppm)	***	***	n.s.	283.09 ± 15.65	262.69 ± 14.22
Mn (ppm)	***	n.s.	n.s	120.52 ± 6.24	119.65 ± 6.17
Fe (ppm)	***	***	***	102.77 ± 3.36	123.53 ± 5.36
Zn (ppm)	***	***	***	62.44 ± 2.18	102.78 ± 4.06
Cu (ppm)	***	***	***	26.56 ± 0.53	33.66 ± 0.66
Sand (%)	***	n.s	n.s	78.93 ± 0.42	79.27 ± 0.38
Silt (%)	***	n.s	n.s	10.27 ± 0.33	9.87 ± 0.34
Clay (%)	***	n.s	n.s	12.00 ± 0.73	11.67 ± 0.81

Results of soil physico-chemical properties between plots invaded and non-invaded by *Tithonia diversifolia* at across five sites in Nigeria.

*P<0.05; **P<0.01; ***P<0.001; n.s., not significant

Table 4.9. Nitrogen in soil and tissues of *Tithonia diversifolia* in Southwest Nigeria

	Nitrogen (%)				
	Soil	Root	Stem	Leaf	Flower
Badore	2.88 ± 0.00^{b}	1.60 ± 0.00^{a}	0.74 ± 0.00^{c}	2.32 ± 0.0^{a}	0.39 ± 0.02^{d}
Shagamu	3.20 ± 0.00^{a}	1.57 ± 0.00^{bc}	0.64 ± 0.00^{d}	2.15 ± 0.00^{ab}	0.37 ± 0.00^{de}
Epe	2.55 ± 0.01^{e}	1.58 ± 0.01^{b}	0.54 ± 0.00^{f}	1.97 ± 0.07^{abc}	0.37 ± 0.00^{de}
Okoafon	1.97 ± 0.00^{h}	1.47 ± 0.00^{e}	0.53 ± 0.00^{fg}	1.32 ± 0.00^{cd}	0.22 ± 0.00^{g}
Ekanmeje	2.45 ± 0.00^{f}	1.43 ± 0.00^{f}	0.56 ± 0.00^{e}	1.36 ± 0.00^{cd}	0.31 ± 0.00^{f}
Ifo	1.75 ± 0.00^{i}	0.39 ± 0.00^{j}	0.79 ± 0.00^{j}	0.94 ± 0.01^{d}	0.21 ± 0.00^{g}
Odeda	2.46 ± 0.00^{f}	1.48 ± 0.00^{e}	0.21 ± 0.00^{m}	1.46 ± 0.00^{bcd}	0.66 ± 0.00^{a}
Gbogan	2.15 ± 0.01^{g}	1.22 ± 0.01^{g}	0.53 ± 0.00^{g}	1.24 ± 0.00^{d}	0.33 ± 0.00^{ef}
Ofosi	2.15 ± 0.01^{g}	1.21 ± 0.01^{h}	0.43 ± 0.00^{i}	0.97 ± 0.00^{d}	0.22 ± 0.00^{g}
Omotosho	1.96 ± 0.01^{h}	0.69 ± 0.01^{i}	0.32 ± 0.00^{k}	0.08 ± 0.00^{e}	0.14 ± 0.00^{h}
Ikere	1.54 ± 0.01^{j}	0.21 ± 0.01^{k}	0.27 ± 0.00^{l}	0.83 ± 0.00^{d}	0.14 ± 0.00^{h}
Ajibode	2.74 ± 0.00^{d}	1.53 ± 0.01^{d}	0.99 ± 0.00^{a}	1.45 ± 0.01^{bcd}	0.61 ± 0.00^{b}
Fiditi	1.96 ± 0.00^{h}	1.22 ± 0.00^{gh}	0.78 ± 0.01^{b}	1.12 ± 0.00^{d}	0.48 ± 0.01^{c}

Values are mean percentage ± standard error. Means followed by the same superscript within a column are not significantly different ($p > 0.05$).

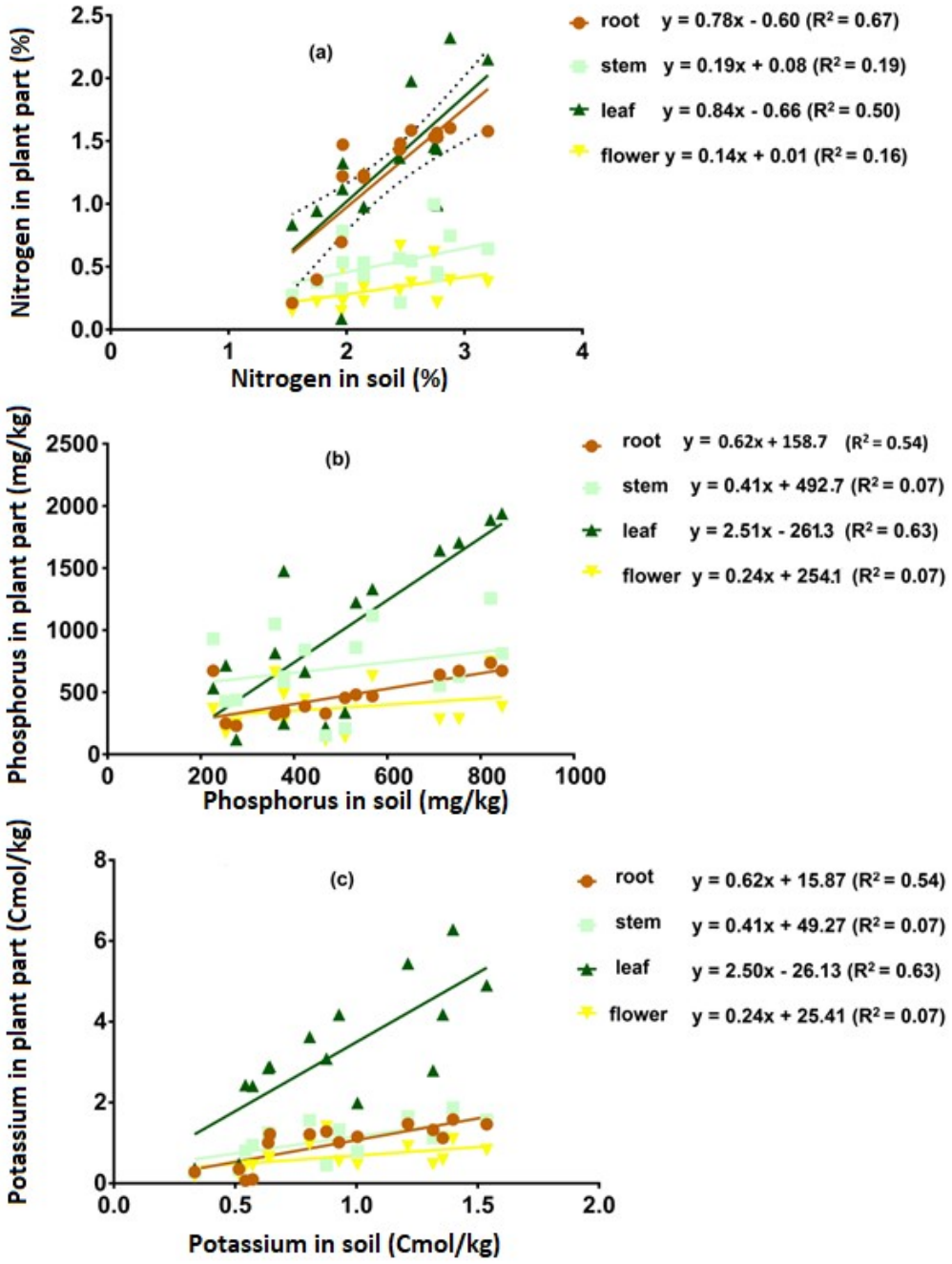

Figure 4.13. Relationships between nutrients in soils and tissues of *T. diversifolia*

4. 3. 2 Phosphorus levels in soils and tissues of *T.diversifolia*

Soil Phosphorus levels ranged from 226.58 ± 18.83 ppm to 845.72 ± 9.16ppm and differed significantly at nine out of the thirteen sites (Table 4.10). The lowest values were recorded at Ifo and Odeda (< 300 pmm). This plant accumulated the highest amounts of Phosphorus in its leaves. Changes in Phosphorus levels followed the same pattern in both soil and leaves, almost twice that found in soils (Table 4.10). For example, plants growing on sites with the highest soil Phosphorus (Shagamu and Omotosho) had the highest leaf Phosphorus while those on Phosphorus-poor soil presented the lowest leaf Phosphorus levels. At all sites, Phosphorus level in flowers of the study species was significantly lower than that of stems. As shown in Figure 4.13 b, the relationship between soil, leaf and root Phosphorus were significant (R = 63% and 54% respectively) and were defined by the following equations:

$$P_l = 2.51P_s - 261.3$$

$$P_r = 0.61P_s + 158.7$$

Where P_l , P_r and P_s are leaf, root and soil Phosphorus respectively.

4. 3. 3 Potassium levels in soils and tissues of *T.diversifolia*

Soil Potassium levels differed across sites and ranged from 0.33 ± 0.01 Cmol/kg to 1.54 ± 0.01Cmol/kg (Table 4.11). As with Nitrogen and Phosphorus significantly higher Potassium levels were detected in the leaves of this plant across all sites. Root and leaf Potassium were related to soil Potassium levels (Figure 4.13 c). The relationships could be described by the following equations:

$$K_r = 0.62K_s + 15.87$$

$$K_l = 2.50K_s - 26.13$$

Where K_r and K_l and K_s are root, soil and leaf Potassium respectively.

Across all sites, *T. diversifolia* showed significantly higher leaf Nitrogen, Potassium and Phosphorus concentrations. Nutrient levels in other parts of this plant were not significantly different (Table 4.12).

Table 4.10. Phosphorus in soil and tissues of *Tithonia diversifolia* in Southwest Nigeria

	Phosphorus (mg/kg)				
Location	Soil	Root	Stem	Leaf	Flower
Badore	423.13 ± 6.91 ^{fg}	387.30 ± 5.10 ^{d}	841.47 ± 11.94 ^{cd}	666.73 ± 8.65 ^{f}	438.69 ± 7.94 ^{cd}
Shagamu	821.35 ± 5.13 ^{ab}	736.16 ± 2.83 ^{a}	1256.85 ± 2.05 ^{a}	1888.73 ± 0.19 ^{a}	746.62 ± 17.22 ^{a}
Epe	377.8 ± 10.66 ^{g}	354.34 ± 16.61 ^{de}	626.32 ± 22.63 ^{e}	249.39 ± 29.54 ^{h}	484.00 ± 13.42 ^{bc}
Okoafon	377.77 ± 21.64 ^{g}	337.78 ± 16.81 ^{e}	588.50 ± 3.05 ^{e}	1477.51 ± 7.08 ^{c}	255.73 ± 10.98 ^{efg}
Ekanmeje	567.79± 6.56 ^{d}	469.40 ± 9.38 ^{c}	1117.55 ± 10.35 ^{b}	1331.86 ± 2.97 ^{d}	627.75 ± 25.66 ^{ab}
Ifo	275.92 ± 3.98 ^{h}	230.87 ± 3.01 ^{f}	438.67 ± 20.26 ^{f}	121.47 ± 16.43 ^{i}	250.38 ± 11.76 ^{efg}
Odeda	253.39 ± 15.50^{h}	249.45 ± 9.46 ^{f}	426.30 ± 2.49 ^{f}	717.67 ± 1.04 ^{ef}	171.85 ± 2.81 ^{fg}
Gbogan	359.08 ± 11.01 ^{g}	322.57 ± 5.23 ^{e}	1050.67 ± 8.23 ^{b}	817.0 ± 11.72 ^{e}	657.99 ± 13.85 ^{a}
Ofosi	532.69 ± 7.40 ^{de}	480.82 ± 6.31 ^{c}	861.01 ± 17.90 ^{cd}	1224.98 ± 29.54 ^{d}	452.00 ± 23.75 ^{c}
Omotosho	753.64 ± 12.00 ^{bc}	672.63 ± 9.76 ^{b}	628.26 ± 4.77 ^{e}	1705.85 ± 10.11 ^{def}	282.91 ± 4.46 ^{def}
Ikere	712.21 ± 8.68 ^{c}	641.43 ± 1.57 ^{b}	553.30 ± 15.66 ^{e}	1643.25 ± 15.46 ^{b}	280.02 ± 1.84 ^{def}
Ajibode	509.27 ± 6.93 ^{de}	455.80 ± 2.04 ^{c}	208.34 ± 10.70 ^{g}	339.54 ± 50.06 ^{h}	136.13 ± 19.39 ^{fg}
Fiditi	467.48 ± 21.24 ^{ef}	329.08 ± 1.84 ^{e}	152.11 ± 4.26 ^{g}	220.5 ± 1.80 ^{hi}	110.86 ± 17.72 ^{g}

Values are mean percentage ± standard error. Meanswith the same superscript within a column are not significantly different ($p< 0.05$).

Table 4.11. Potassium in soil and tissues of *Tithonia diversifolia* in Southwest Nigeria

	Potassium (Cmol/kg)				
Location	Soil	Root	Stem	Leaf	Flower
Badore	1.54 ± 0.01^{a}	1.46 ± 0.04^{b}	1.57 ± 0.00^{c}	4.90 ± 0.00^{c}	0.82 ± 0.00^{d}
Shagamu	1.4 ± 0.00^{b}	1.58 ± 0.00^{a}	1.87 ± 0.00^{a}	6.28 ± 0.00^{a}	1.09 ± 0.00^{b}
Epe	1.36 ± 0.00^{c}	1.12 ± 0.00^{e}	1.14 ± 0.00^{g}	4.18 ± 0.00^{d}	0.58 ± 0.00^{ef}
Okoafon	1.32 ± 0.01^{d}	1.32 ± 0.00^{c}	1.12 ± 0.00^{h}	2.79 ± 0.00^{g}	0.47 ± 0.00^{fg}
Ekanmeje	1.21 ± 0.01^{e}	1.47 ± 0.01^{b}	1.43 ± 0.00^{f}	5.44 ± 0.13^{b}	0.91 ± 0.13^{cd}
Ifo	1.00 ± 0.00^{f}	1.15 ± 0.00^{e}	0.79 ± 0.00^{j}	2.00 ± 0.00^{i}	0.46 ± 0.00^{fg}
Odeda	0.88 ± 0.00^{h}	1.28 ± 0.00^{c}	0.45 ± 0.00^{k}	3.09 ± 0.00^{f}	1.40 ± 0.00^{a}
Gbogan	0.81 ± 0.00^{i}	1.21 ± 0.00^{d}	1.55 ± 0.0^{c}	3.62 ± 0.00^{e}	0.98 ± 0.00^{bc}
Ofosi	0.64 ± 0.01^{kj}	1.00 ± 0.01^{f}	1.26 ± 0.00^{e}	2.85 ± 0.00^{g}	0.65 ± 0.00^{e}
Omotosho	0.57 ± 0.00^{k}	0.09 ± 0.00^{i}	0.94 ± 0.0^{i}	2.41 ± 0.21^{h}	0.43 ± 0.02^{g}
Ikere	0.54 ± 0.00^{l}	0.06 ± 0.02^{i}	0.80 ± 0.00^{j}	2.43 ± 0.00^{h}	0.42 ± 0.00^{g}
Ajibode	0.52 ± 0.00^{m}	0.35 ± 0.00^{g}	0.33 ± 0.00^{l}	0.48 ± 0.00^{j}	0.20 ± 0.00^{h}
Fiditi	0.33 ± 0.01^{n}	0.28 ± 0.01^{h}	0.27 ± 0.01^{m}	0.37 ± 0.00^{j}	0.16 ± 0.01^{h}

Values are mean percentage ± standard error. Means with the same superscript within a column are not significantly different ($p< 0.05$).

Table 4.12. Allocation of N, P and K in *Tithonia diversifolia*

	Nitrogen (%)	Phosphorus (mg/kg)	Potassium (Cmol/kg)
Root	1.25 ± 0.12 [a]	467.7 0 ± 44.17 [b]	0.98 ± 0.12 [b]
Stem	0.52 ± 0.05 [b]	699.50 ± 83.08 [b]	1.09 ± 0.12 [b]
Leaf	1.314 ± 0.14 [a]	991.90 ± 161.10 [a]	3.20 ± 0.40 [a]
Flower	0.33 ± 0.04 [b]	375.90 ± 49.73 [b]	0.65 ± 0.08 [b]

Means with the same superscript within columns are not significantly different ($p<$ 0.05)

4. 3. 4 Reproductive allocation of N, P and K in *T.diversifolia*

T. diversifolia was found to allocate Nitrogen, Phosphorus and Potassium in varying percentages depending on the concentrations of these nutrients in soil. Reproductive allocation varied significantly depending on the element with phosphorus being the most allocated element to reproduction parts with the highest percentage (15.64%) while Nitrogen was lowest (9.76%) (Table 4.13). This plant allocated between 5.8 % and 17.4 % of Nitrogen to reproductive structures. Reproductive allocation for Phosphorus ranged between 8.6 % to 31.6 % while that of and Potassium ranged between 7.7 % to 22.5. Linear regression analysis showed that there was no significant relationships between soil nutrient and reproductive allocation of respective nutrients ($R^2 < 0.21$).

4. 4 Some aspects of the reproductive biology and ecology of *T. diversifolia*

4. 4. 1 Pollen to ovule ratio and pollination mode in *T. diversifolia*

The number of pollen grains recorded in florets of *T. diversifolia* ranged between 3,000 and 4,000 (4,167 ± 76, mean ± SD, n = 30 florets). Table 4.14 shows the number of viable and non-viable achenes in bagged and control capitula of *T. diversifolia.* The Chi-square test provided strong evidence to suggest that achene viability in *T. diversifolia* differed between bagged and open pollinated capitula, χ^2 (1, N = 5180) = 4518 , $p < 0.01$. In bagged capitula, viability was very low (0.17%) whereas the percentage of non-viable achenes was high (58.78%). On the other hand, 37.97% of the 5180 capitula were viable for control plants while only 3.07 % were non-viable.

Table 4.13. Reproductive allocation of N, P and K in *Tithonia diversifolia*

	RA_N (%)	RA_P (%)	RA_K (%)
Mean ± SEM	9.76 ± 0.82 [a]	15.64 ± 1.69 [b]	11.61 ± 0.97 [c]
Minimum	5.88	8.60	7.73
Maximum	17.40	31.65	22.53

Meanswithin rows with similar superscript are not statistically different (p = 0.05).

Table 4.14. Seed setand viability of *Tithonia.diversifolia*

Treatment	Bagged	Control	Total	χ^2 test
Non-viable	3045 (58.78 %)	159 (3.07 %)	3204	0.000**
Viable	9 (0.17 %)	1967 (37.97 %)	1976	
Total	3054	2126	5180	

Number and percentage (in brackets) of viable and non-viable achenes in bagged and open-pollinated capitula of *Tithonia diversifolia* (**$p < 0.01$).

4. 4. 2 Floral phenology and reproductive output of *T. diversifolia*

In the population studied, *T. diversifolia* bloomed from the end of August through December. Dispersal was from October to January. Mature capitula of this plant measure between 10 and 22 mm (Table 4.15). Capitula development was basipetal, on the branch of an individual plant. They are heterogamous with marginal sterile ray florets and bisexual disk florets which are protogynous. A capitulum contains on the average 8 and 75 ray and disk florets respectively (Table 4.15). Floral development within capitulastarted with the opening of the marginal ray florets before that of the central disk florets. The total number of achenes produced by an individual plant was estimated between 488 and 8,736 that is, 3675 achenes on the average. With 93% of achenes of *T. diversifolia* viable at maturity (Table 4.14), the total number of viable achenes per plant would range between 454 and 8,124 (3,418 on the average). This would amount to between 7,320 and 131,040 achenes/m^2 (51,270 achenes/m^2 on the average), considering the average observed density of 15 plants m^2.

Within a capitulum, disk florets open from the periphery to the centre row after row. The average lifespan of capitula (from visible bud appearance to withering) was 38 days. It took 2 to 6 days for a bud to appear on the branch apex (Plate 4.1 A) and 10-20 days for buds to mature and reach preanthesis (Plate 4.1 B), which lasted for 1 to 4 days (Plate4.1 C). Anthesis lasted for 2 to 5 days during which pollen is shed (Plate 4.1 D-E). Achene filling took 12 to 17 days before dispersal (Plate4.1 F). The floral phenology of a capitulum of *T. diversifolia* could be divided into the following stages:1) capitulum with closed involucral (Plate 4.1 A - B), 2) involucral bracts and ray florets gradually opening to expose disk florets just before pollen shedding (Plate 4.1 C-D) and 3) Anthesis during which ray florets wither, disk florets shed pollen and achene filling starts (Plate 4.1E).

Table 4.15. Basic floral metrics of *Tithonia diversifolia*

Metric	Minimum	Maximum	Mean ± SE (cm)	Sample size
Capitulum diameter (mm)	10.12	22.03	18.81 ± 0.22	100
Number of capitula/plant	8	104	49 ± 3	60
Number of ray florets	6	12	8 ± 0.00	50
Number of disk florets	61	84	75 ± 1.00	50

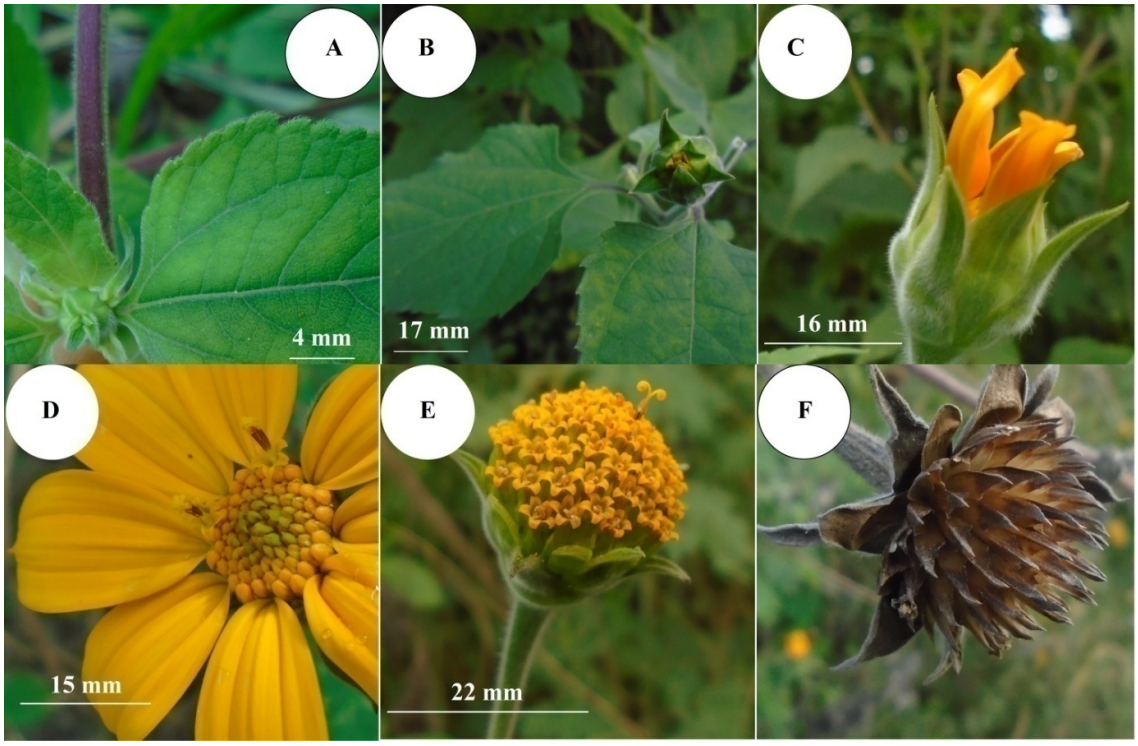

Plate 4.1. Flowering phenophases of *Tithonia diversifolia*

Floral bud with capitulum enclosed in involucral bracts (A - B); In B, involucral bracts gradually open revealing newly formed ray florets. Preanthesis (C - D); capitulum showing two newly opened disk (C) and ray (D) florets. Anthesis (E); capitulum after ray florets have senesced and disk florets have shed pollen. Dispersal (F) dry and empty capitulum after achene dispersal.

4. 4. 3 Germination ecology of *T. diversifolia*

4. 4. 3. 1. Seed type of *T. diversifolia*

Achenes of *T. diversifolia* is fully developed with a radicle two thick cotyledons.The embryo is erect does not grow in the achene prior to germination; it is spoon-shaped with its stalk slightly invested/enveloped by cotyledons (Plate 4.2). Achenes of *T. diversifolia* can thus be classified based on embryo morphology following the Martin (1946) key for seed type modified by Baskin and Baskin (2014) as spatulate fully developed.

4. 4. 3. 2 Effect of scarification on imbibition of achenes of *T. diversifolia*

Figure 4.14 shows the time course of imbibition in mechanically scarified and non-scarified achenes of achenes of *T. diversifolia.* After 6 hours of imbibition, the batch of 20 scarified achenes absorbed 62.5 ± 4.79mg of water. This was significantly different from the control batch, which absorbed 45 ± 5.00g of water. However, at 12, 24 and 48 hours, water imbibition was higher in scarified achenes but not significantly different from intact achenes. Water uptake was equal (97.50 ± 4.79) in both groups from 72 hours after imbibition.

4. 4. 3. 3 Effect of osmotic stress and GA_3 on germination of *T. diversifolia*

Germinability of GA_3-treated achenes of *T. diversifolia* over the course of four weeks was significantly higher compared to mechanically scarified and control achenes (Table 4.16) The differences between these two treatments was statistically significant. On the average it took 9 days for freshly collected achenes to germinate. This time was significantly reduced when achenes were treated with GA_3 or scarified, that is, 6.08 ± 0.05 and7.09 ± 0.36days respectively.Germination index of achenes of *T. diversifolia* was significantly enhanced after treatment with GA_3 as 6 achenes germinated per day as opposed to 4 and 1 in mechanically scarified and control achenes respectively. No germination was noted under osmotic stress (-0.5 Mpa and -1.0 MPa).Because, achenes of *T. diversifolia* imbibe water, do no germinate considerably in the course of the recommended four-week period and embryo does no grow prior to radicle emergence, the dormancy type identified following the hierarchical classification system of classification of seed dormancy (Baskin and Baskin 2014) is physiological (PD) and more precisely Physiological Regular Dormancy.

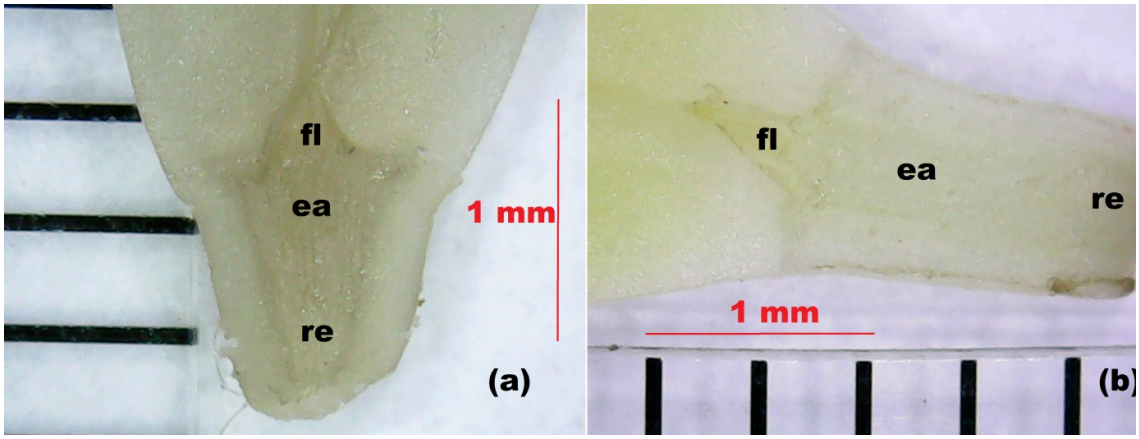

Plate 4.2. Embryo of *Tithonia diversifolia*

Longitudinal section through an ungerminated (a) and newly germinated achene (b).

Key: e = embryonic axis, fl= first leaves, r = radicular end.

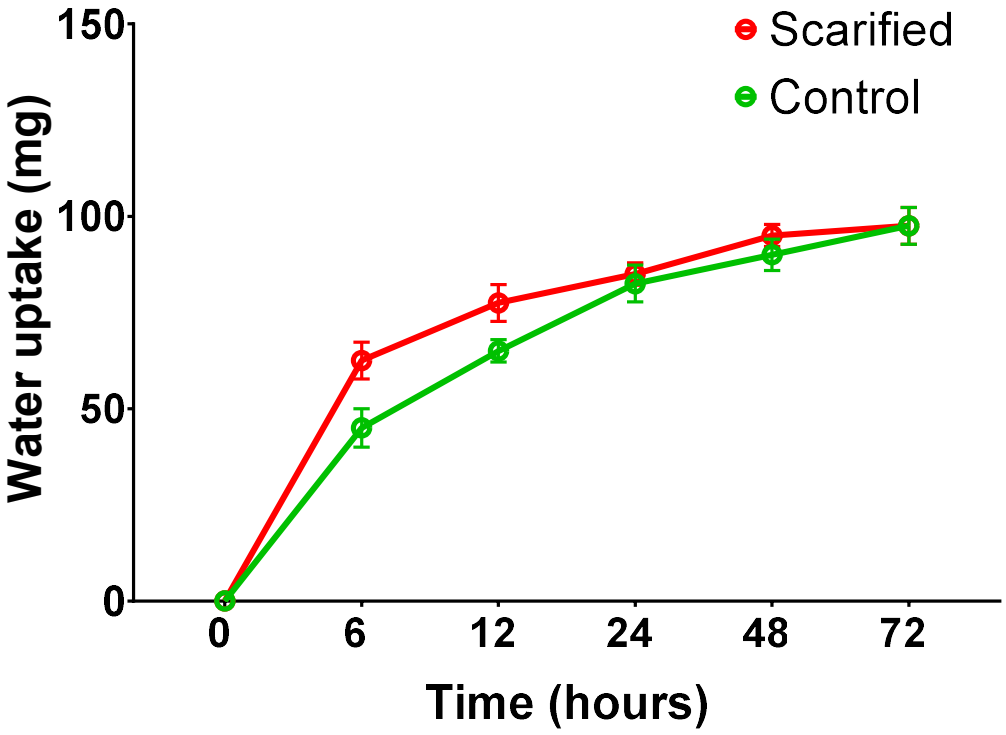

Figure 4.14: Imbibition pattern in achenes of *Tithonia diversifolia*

The red and green curves depict mechanically scarified and intactachenes of *Tithonia diversifolia.*Bars indicate standard error of the mean.

Table 4.16. Germination indices of *Tithonia diversifolia*

	Control	Mechanical Scarification	GA_3
Germinability(%)	8.67 ± 2.91^{a}	48.67 ± 4.37^{b}	65.33 ± 1.76^{c}
Germination Time(Days)	8.93 ± 0.54^{a}	7.09 ± 0.36^{b}	6.08 ± 0.05^{b}
Germination index(Achene/day^{-1})	1 ± 0.00^{a}	4 ± 0.00^{b}	6 ± 0.00^{c}

Effect of mechanical scarification and GA_3 on the germination of *T. diversifolia*. Statistically different means are denoted by different superscript across each row. Values were obtained from three replicates each of 50 achenes. No germination occurred in solutions of osmotic -0.5, and -1.0 MPa and as such results are not shown.

4. 4. 3. 4 Temporal patterns in germinability of achenes of *T. diversifolia*

A gradual increase was noted in the germinability of achenes of *T. diversifolia* in the study (Figure 4.15). The mean germination percentage (± SE) tested in December 2017, one month after exposure to field and room conditions ranged between 4.00 ± 0.40 and 8.00 ± 2.30 for all groups and did not differ statistically. Germinability increased almost uniformly across all groups with no significant differences in January and February 2018. However, statistically significant differences in germination percentages were noted in March and April 2018.

In March, the highest difference in germinability was observed in achenes at the Ajibode site (over 50%) as opposed to those at the Research Farm and the control (less than 30%). A similar pattern was noted in April with germination percentage at Ajibode above 60% whereas that of the Research farm averaged 42% (Figure 4.15). Achenes stored at room temperature for five months had lower germination percentage (36%) compared to those exposed to field conditions. In May, six months after the beginning of the study, achenes subjected to the test conditions showed no statistical difference in germinability.

4. 4. 3. 5Temporal pattern in seed bank of *T. diversifolia*

Figure 4.16 shows the temporal variation in the number of achenes in the seed bank of *T. diversifolia* per square metre at a depth of 5 cm. For the total sampled area, that is 12 m^2, 1059 achenes were recovered from the seed bank during the study period (1 March - 1 May). Mean seed bank density (mean number of achene/m^3) at each sampling date is represented in Figure 4.16. At each sampling date, there was a rapid decreased in seed bank density. For example, on 1 March, density was 54 ± 3 achenes/m^3. This decreased to 23 ± 3 (about 57%) two weeks later. On May 1, 8, weeks after the beginning of the experiment, the seed bank was depleted with an average seed density of 1 m^2 (Appendix 6) The temporal pattern in seed bank density of *T. diversifolia* was best fit (R^2 = 0.95) by an exponential decay model:

$$s = e^{3.9(\pm 0.28) - 0.89(\pm 0.12)t}$$

Where *s*: mean seed bank density (achenes/m^2) and

t : time in weeks after field emergence.

Without the uncertainty estimates, this equation can also be written as:

$$s = 49.4e^{-0.89t}$$

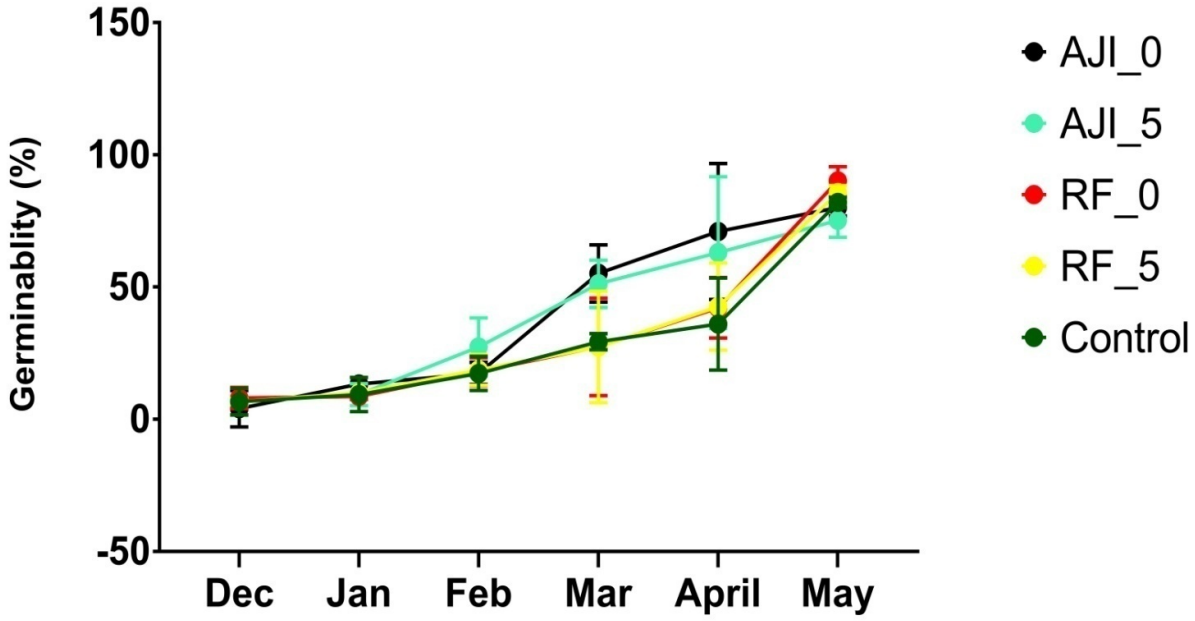

Figure 4.15. Germination of bagged achenes of *Tithonia diversifolia*

AJI_5 and RF_5 denote bags buried 5 cm deep while AJI_0 and RF_0 are bags left on the soil surface at the Ajibode and the Botany Research Farm respectively.

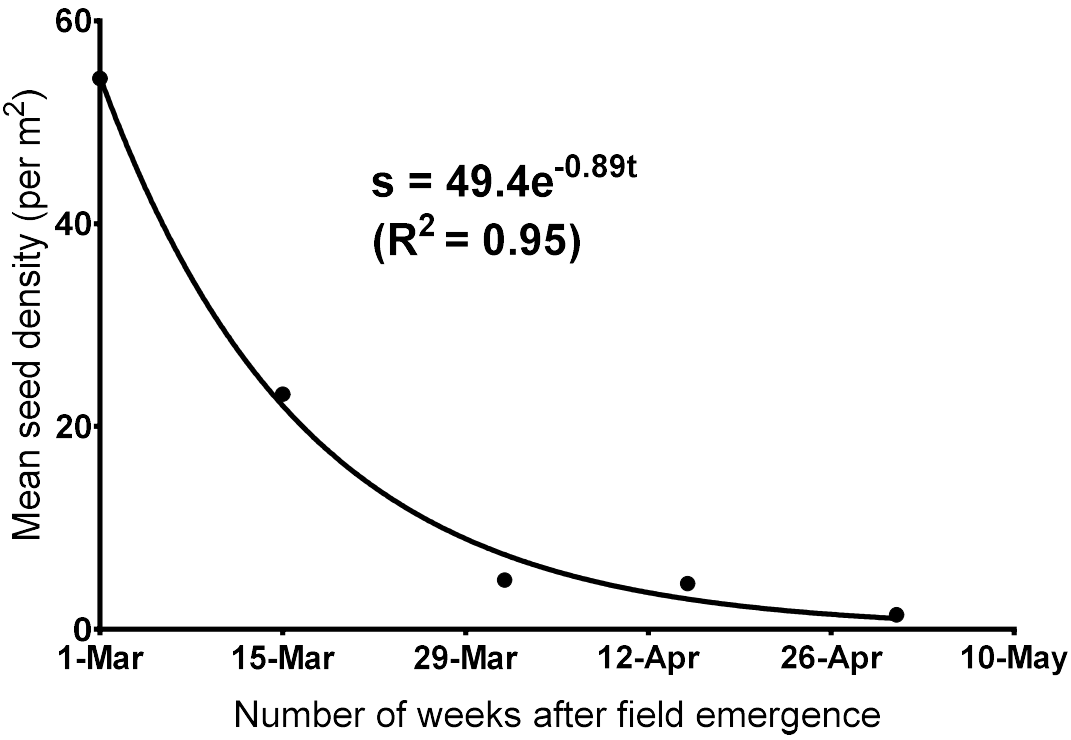

Figure 4.16. Seed bank depletion model of *Tithonia diversifolia*

The seed bank was sampled at two weeks intervals prior to field emergence through when no further emergence was noted in the experiment plot. The depletion followed an exponential decay model, $\boldsymbol{s = 49.4e^{-0.89t}}$ ($R^2 = 0.95$).

4. 5 Biomass structure and response of *T. diversifolia* to management

4. 5. 1 Effects of control measures on growth of *T. diversifolia*

The effect of paraquat dichloride, fire and manual weeding compared to untreated plants on the density of *T. diversifolia* are shown in Table 4.17. In March, before treatment application, the number of seedlings recorded across all quadrats was not significantly different and ranged between 119 and 178. Subsequently, statistically significant differences were observed in the density of *T. diversifolia* across treatments. For example, one month after the plants were subjected to the different treatments, the lowest density was obtained from quadrats in which herbicide and fire were used (10 ± 4 and 22 ± 5 plants respectively). This translated to mortality rates over 80% compared to 4% in control plants.

Mortality followed the same trend throughout the duration of the study, with no further mortality and emergence in quadrats treated with fire and herbicide. Little variations in density were observed in control quadrats.Significant differences were observed in the height of *T. diversifolia* after treatment with fire, manual weeding and paraquat dichloride (Table 4.16).After one month, that is in April, the least height of plants was recorded in quadrats treated with herbicide (12.67 ± 0.75 cm) while the highest plant height was recorded in control plants (47.15 ± 1.81 cm). Plants in manual weeding and fire treatments did not differ in their height (Table 4.18).

Two months after treatment application, that is, in May, the same effect (47.15 ± 1.81 cm). Plants in manual weeding and fire treatments did not differ in their height (Table 4.17). Two months after treatment application, that is in May, the same effect was observed with 50% reduction in the height of herbicide-treated plant compared to control. In June, the growth-retarding effect ofparaquat dichloride persisted, as plants in this group were significantly shorter than those in the three other groups.

Unlike density and height, the inhibitory effects of paraquat dichloride application and fire were pronounced only at one month after treatment application (Table 4.19). From May to August, stem girth of plants treated with this herbicide were comparable to those in two groups (control and manual weeding). The girth of plants in these three groups statistically differed from that of plants treated with fire.

Table 4.17. Effect of control measures on density of *Tithonia diversifolia*

	Manual weeding	Fire	Control	Herbicide
March	137 ± 18 [a]	160 ± 7 [a]	163 ± 15 [a]	168 ± 6 [a]
April	69 ± 10 [a]	22 ± 5 [b]	156 ± 13 [c]	10 ± 4 [b]
May	68 ± 11 [a]	21 ± 4 [b]	182 ± 13 [c]	8 ± 3 [b]
June	58 ± 6 [a]	20 ± 5 [b]	186 ± 16 [c]	8 ± 3 [b]
July	63 ± 9 [a]	20 ± 5 [b]	153 ± 5 [c]	8 ± 4 [b]
August	60 ± 12 [a]	20 ± 5 [b]	162 ± 15 [c]	8 ± 3 [b]

Effect of manual weeding, fire and herbicide (Paraquat dichloride) on density (number of individuals/m^2) of *T. diversifolia.* Means and SE were computed for 3 to 10 plants per quadrats in each of the sixteen quadrats. Values followed by the same superscript in each row are not significantly different.

Table 4.18. Effect of control measures on height of *Tithonia diversifolia*

	April	May	June
Manual weeding	21.68 ± 1.05 [b]	87.83 ± 2.48 [b]	159.60 ± 3.90 [b]
Fire	20.49 ± 0.91 [b]	95.24 ± 3.36 [bc]	170.40 ± 5.49 [b]
Control	47.15 ± 1.81 [c]	105.3 ± 3.80 [c]	154.00 ± 4.68 [b]
Herbicide	12.67 ± 0.75 [a]	47.1 ± 2.47 [a]	109.50 ± 3.46 [a]

Effect of manual weeding, fire and herbicide (Paraquat dichloride) on height (cm) of *T. diversifolia.* Means ± SE with different superscript within a column are statistically different ($p < 0.05$) Values were averaged across each of the four 1m × 1 m quadrats per treatment, equivalent to a total of 21 to 40 plants per treatment.

Table 4.19. Effect of control measures on the stem girth of *Tithonia diversifolia*

	April	May	June	July	August
Manual weeding	3.63 ± 0.17^{ab}	9.31 ± 0.47^{a}	12.81 ± 0.69^{a}	15.9 ± 1.10^{ab}	16.67 ± 1.05^{ab}
Fire	4.11 ± 0.23^{b}	11.38 ± 0.54^{b}	15.81 ± 0.95^{b}	20.15 ± 1.31^{c}	20.59 ± 1.34^{b}
Control	5.749 ± 0.24^{c}	9.00 ± 0.39^{a}	11.26 ± 0.53^{a}	13.13 ± 0.69^{a}	13.79 ± 0.80^{a}
Herbicide	2.90 ± 0.24^{a}	8.29 ± 0.56^{a}	13.15 ± 0.69^{ab}	18.20 ± 1.04^{bc}	19.64 ± 1.39^{b}

Effect of manual weeding, fire and herbicide (Paraquat dichloride) on the stem girth (mm) of *T. diversifolia.* Means ± SE with different superscript within a column are statistically different ($p < 0.056$) Values were averaged across each of the four 1 m × 1 m quadrats per treatment, equivalent to a total of 21 to 40 plants per treatment.

4. 5. 2 Growth and biomass allocation of *T. diversifolia*

4. 5. 2. 1 Growth parameters of *T. diversifolia*

The temporal patterns in the height, stem girth, leaf area and biomass of *T. diversifolia* are shown in Table 4.20. The plant grew significantly taller at each sampling date. For example in May, a rapid growth, from 30.7 ± 2.63 cm to 105.1 ± 5.26 cm, that is about 70 % increase in one month was obtained. Lower but significantly different increases in height (< 40 %) were recorded in subsequent months. At the end of September only 7% increase in height was obtained. As with height, stem girth abruptly increased during the first month by about 68 %.

At the end June, July and August, stem girth significantly increased to 13 %, 12 % and 17 % respectively. However, a decrease was noted at the end of September by about 17%. Leaf area of the test species significantly increased by 79 % (from 33.53 ± 3.67cm^2 to 163 ± 15.08 cm^2) between April 30th and May 30th 2018. Mean leaf area in May, June and September were significant lower than mean leaf area in July and August 2018. The relationship between leaf central lobe length and leaf area was impressive (Figure 4.17). The prediction equations was:

$$\log(\text{leaf area}) = 2.09\log(\text{central lobe length}) - 0.49.$$

Table 4.20. Time course of growth parameters of *Tithonia diversifolia*

	Plant height (cm)	Stem girth (mm)	Leaf Area (cm^2)
April	30.7 ± 2.63^{a}	3.57 ± 0.31^{a}	33.53 ± 3.67^{a}
May	105.1 ± 5.26^{b}	11.41 ± 0.518^{b}	163 ± 15.08^{bc}
June	167.5 ± 5.93^{c}	13.24 ± 0.759^{bc}	197.2 ± 17.30^{b}
July	273.2 ± 6.08^{d}	15.17 ± 0.91^{cd}	307.9 ± 30.45^{d}
August	315.1 ± 9.52^{e}	18.29 ± 0.951^{e}	336.5 ± 24.25^{d}
September	341.2 ± 6.86^{f}	17.17 ± 0.79^{de}	248.48 ± 15.99^{b}

Time course of height, stem girth and leaf area of *T. diversifolia.*Means ± SE with different superscript within a column are statistically different ($p < 0.05$) Values were averaged for 30 individual plants, harvested on a monthly interval.

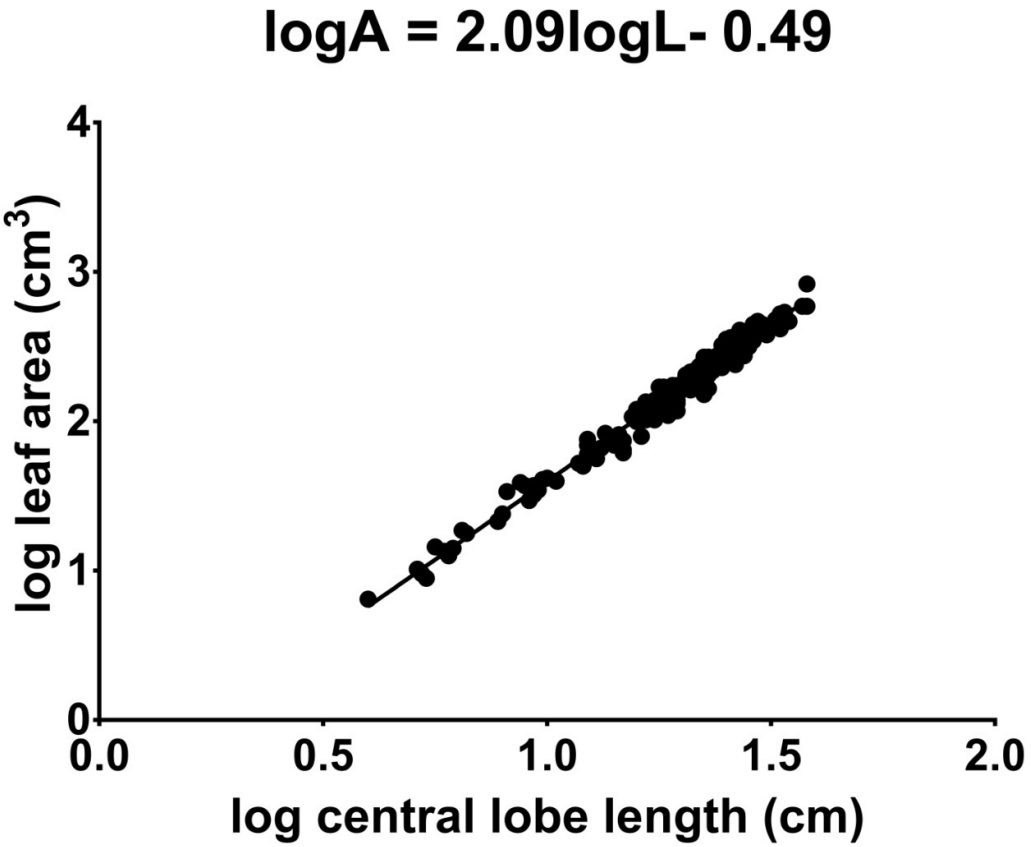

Figure 4.17. Relationship between leaf lobe length and area of *Tithonia diversifolia*

Leaf measurements were taken from three fully expanded leaves harvested from 30 individual on a monthly basis from April to September.

4. 5. 2. 2 Biomass of *T. diversifolia*

Biomass allocation to vegetative structures of *T. diversifolia* is shown in Table 4.21 and Figure 4.18. The mean biomass of one month-old *T. diversifolia* seedlings was 2.36 ± 0.38. At this stage, the study species had the highest amount of biomass in its leaves(53.78%) compared to 33.4% and 12.78% recorded in shoots and roots respectively (Figure 4.18).These values were not did not significantly differ from each other. For the rest of the study, shoot biomass was significantly higher than that of root and leaf. For example, two months after emergence in May 2018, total biomass increased by more than 10 folds (28.33 ± 4.38). At this stage, biomass allocation to roots, shoots and leaves was 13.92 ± 0.09, 51.22 ± 0.12 and 34.85 ± 0.08% respectively.

Between July and August 2018, there an increase in total biomass from 134.23 ± 17.91 to 179.56 ± 22.54 g. This corresponded to root, shoot and leaf allocations of about 14, 67 and 18% respectively. For the last sampling date, six months after the emergence of *T. diversifolia,* no further increase in total biomass was recorded. At this stage, the study species had allocated the highest amount of biomass to its shoot system (72.91 ± 0.08%). Non-linear regression showed that biomass data was best fit by a logistic model:

$$biomass = 179.7/(1 + 855.4e^{-2.25t})$$ (Figure 4.19).

The Allometric equations developed at each sampling date to predict total biomass using either stem girth or plant height are shown in Table 4.22. Most of these were second order polynomials that were linearized using a logarithmic transformation. At each measurements date, stem girth was a better predictor of biomass compared to plant height with R^2 values ranging from 0.84 to 0.92. As shown in Figure 4.20 and Table 4.21, the biomass of *T. diversifolia* at any time could be predicted from its stem girth more accurately than plant height. The prediction equations are as follows:

$$\log(biomass) = 2.5logd - 1.09$$

$$\log(biomass) = 1.8logh - 2.39$$

Where *d*: stem girth (mm) and *h*: plant height (cm).

Table 4.21. Time course of biomass allocation in *Tithonia diversifolia*

	Leaf biomass	Shoot biomass	Root biomass	Total biomass
April	1.27 ± 0.199^{a}	0.79 ± 0.13^{a}	0.30 ± 0.06^{a}	2.36 ± 0.38
May	9.877 ± 1.23^{ab}	14.52 ± 2.77^{b}	3.95 ± 0.56^{a}	28.33 ± 4.38
June	14.15 ± 2.25^{ab}	24.25 ± 3.91^{b}	6.81 ± 1.42^{a}	45.21 ± 7.40
July	24.69 ± 3.71^{cd}	90.74 ± 11.74^{b}	18.80 ± 2.90^{b}	134.23 ± 17.91
August	33.54 ± 4.40^{d}	121.30 ± 14.97^{b}	24.73 ± 3.80^{b}	179.56 ± 22.54
September	25.44 ± 2.99^{cd}	130.70 ± 13.29^{b}	23.11 ± 2.57^{b}	179.20 ± 18.37

Total biomass (in mg) and biomass allocation to organs (in mg)of *T. diversifolia.* Means ± SE with different superscript within a row are statistically different ($p < 0.05$). Values were averaged for 30 individual plants, harvested on a monthly interval.

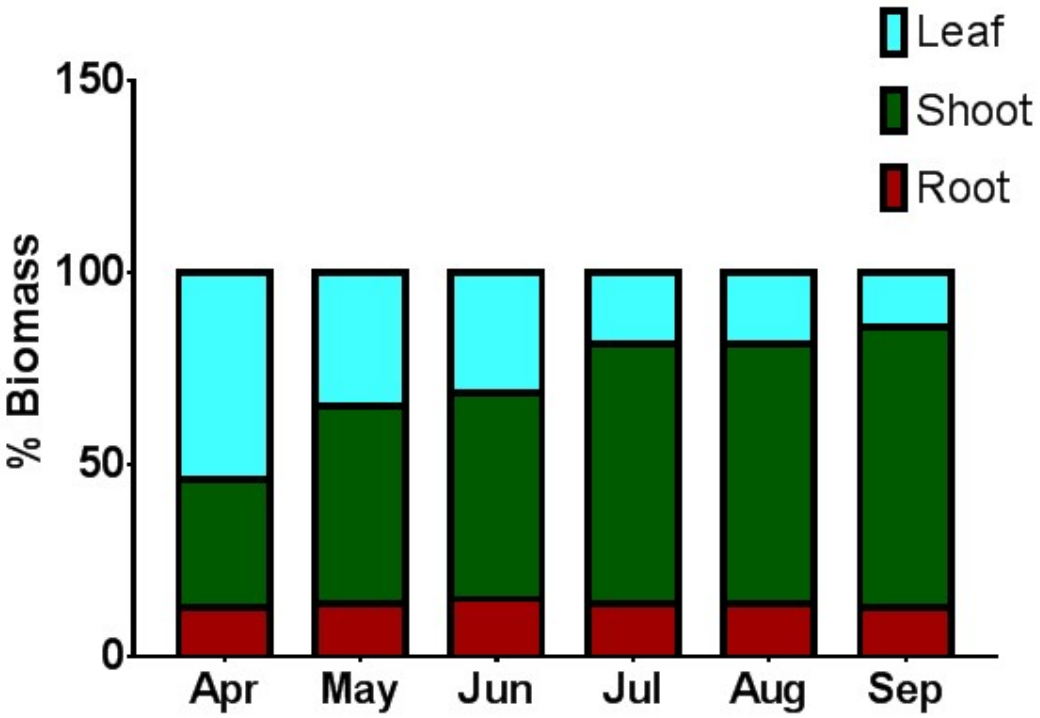

Figure 4.18. Relative biomass allocation in parts of *Tithonia diversifolia* with time

Data were collected destructively on a monthly basis using 30 individual from emergence to maturity.

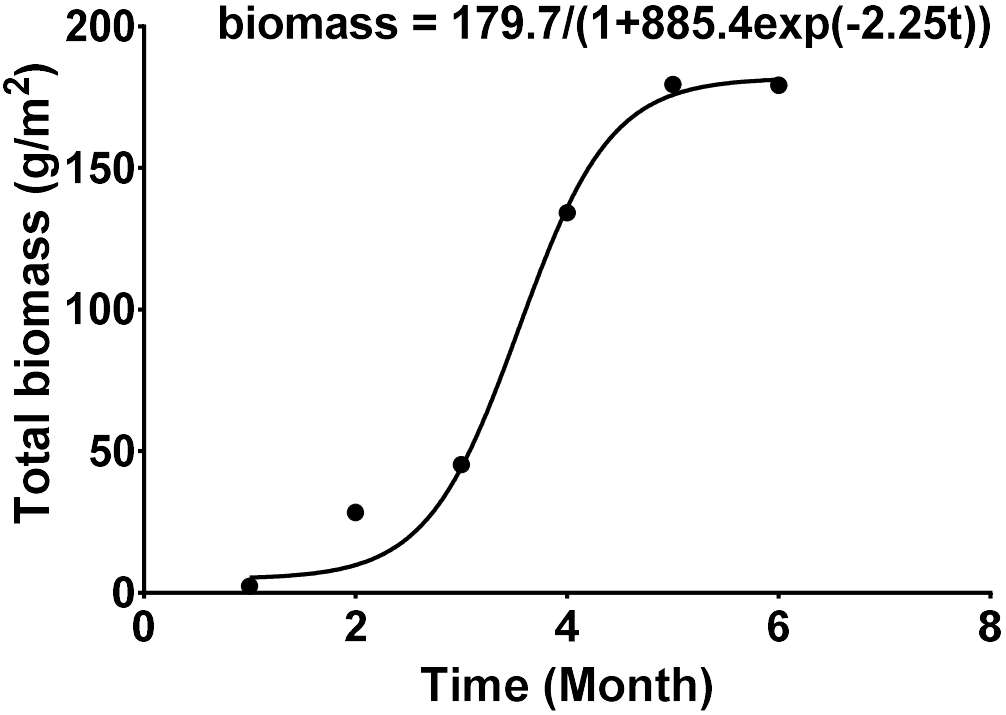

Figure 4.19. Total biomass model of *Tithonia diversifolia*

Monthly biomass followed a logistic model: $\frac{179.7}{1+855.4e^{-2.25t}}$ Data were collecteddestructively on a monthly basis using 30 individual from emergence to maturity.

Table 4.22. Allometric equations for biomass of *Tithonia diversifolia*

Month	predictor	R^2	F	y-intercept	slope	equation
April	*d*	0.92	333	-0.79 ± 0.06	1.90 ± 0.11	$logm = 1.9logd - 0.79$
	h	0.72	72	-2.20 ± 0.28	1.60 ± 0.19	$logm = 1.6logh - 2.2$
May	*d*	0.84	143	-3.50 ± 0.55	2.70 ± 0.23	$lnm = 2.7lnd - 3.5$
	h	0.19	6.4	-0.82 ± 0.85	1.10 ± 0.42	$logm = 1.1logh - 0.82$
June	*d*	0.89	220	-1.40 ± 0.19	2.60 ± 0.17	$logm = 2.6logd - 1.4$
	h	0.36	16	-4.60 ± 1.5	2.80 ± 0.69	$logm = 2.8logh - 4.6$
July	*d*	0.95	560	-0.65 ± 0.11	2.30 ± 0.10	$logm = 2.3logd - 0.65$
	h	0.38	17	-7.70 ± 2.40	4.00 ± 0.97	$logm = 4logh - 7.7$
August	*d*	0.92	326	-0.81 ± 0.16	2.40 ± 0.13	$logm = 2.4logd - 0.81$
	h	0.53	31	-6.10 ± 1.50	-3.30 ± 0.59	$logm = -3.3logh - 6.1$

Model summary and parameter estimates using stem girth, d (mm) and shoot height, h (cm) of *T. diversifolia* as predictors for total biomass m in grams. N = 30 individual were used at each sampling date , DFn = 1, DFd = 28, $p < 0.01$.

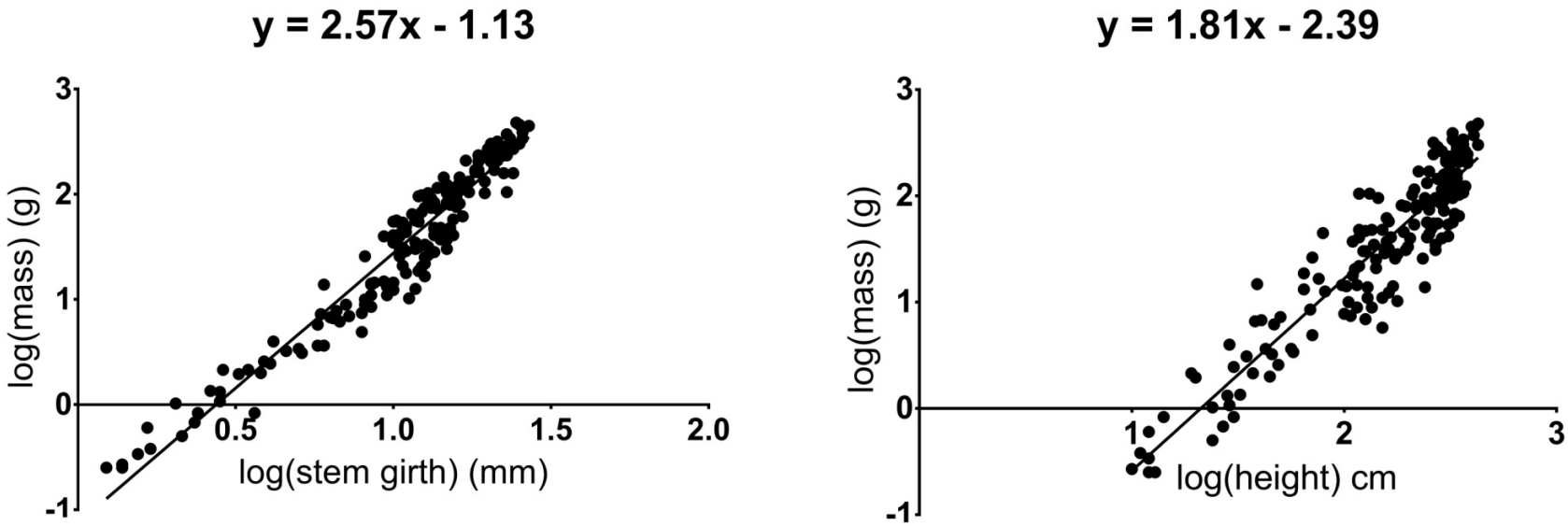

Figure 4.20. Relationship between stem girth, height and biomass of *Tithonia diversifolia*

Data were collected destructively on a monthly basis using 30 individual from emergence to maturity.

4. 6 Leaf area model of *T. diversifolia*

Figure 4.21 shows the variation of leaf length and breadth of *T. diversifolia* from the four selected populations across the University of Ibadan Campus. Manually measured leaf lengths ranged from 31.40 cm − 53.30 cm, 29.00 cm − 51.80 cm, 38.3 cm − 71.00 cm and 32.7 cm − 64.50 cm at AJ1, AJ2, UI1 and UI2 respectively. Leaf breadth showed the same pattern as follows: 18.5 cm − 38.4 cm, 16.0 cm − 34.9 cm, 20.0 cm − 35.60 cm and 16.3 cm − 41.20 cm (Figure 4.21).

Site-specific differences in manual leaf metrics estimates were evident as both length and breadth were significantly different and increased in magnitude from AJ2 to AJ1 to UI1 and to UI2 (Table 4.23). Photographically measured leaf length of *T. diversifolia* (45.82 ± 0.66 cm) was significantly higher than manually measured leaf length (45.62 ± 0.66 cm). However, there were no significant differences between manually and image-derived leaf breadth (26.90 ± 0.49 cm and 26.95± 0.47 cm respectively).The relative mean absolute error between both measurement methods washigher (-0.44) for the leaf length compared to the breadth (-0.18).

The five selected leaf area models of *T. diversifolia* and theirparameter estimates using leaf length and breadth as independent variables are presented in Table 4.24 whereas their fitting results are shown in Table 4.25. At calibration, all models showed a good fit to the data and explained at least 80 % of the observed variability (R^2_{adj}), with considerably low RMA values (below 12 %), RMSE values below 58 cm^2 and AIC values ranging from 1127.41 to 1303.17 (Table 4.25). Based on the aforementioned criteria, the power model (Model 6) and the linear model with the product of the length and the breadth (Model 3) gave the most satisfactory leaf area predictions thereby performed best with calibration ranks of 4 and 7 respectively. The two least-performing leaf area models of the study species were the simple linear models based on leaf breadth with calibration ranks of 15 and 18 respectively. The multiple linear models based on both metric showed an intermediary performance.

Model performance criteria based on a validation dataset of 80 measurements are also shown in Table 4.25. Generally, there wasa decrease in model predictive power. At this stage, Model 6 and Model 3 had the highest ranks (5 and 8 respectively). The other models had a similar performance to that of calibration. The overall ranking of models is also shown in Table 4.25, with model 6 and 3 being the top two least performing

models at calibration except forModel 1 whose rank increased from (performed poorly at calibration)which was ranked second. Similar to the calibration stage, Model 3 provided the best performance at the validation stage. Globally, Model 3 followed by model 5 were the most robust for describing leaf area of *T. diversifolia.*

Leaf area predictions from the best first model was significantly different from observed area (316.2 ± 4.96 and 413.8±6.14 cm^2 respectively). On the contrary, predictions from the second best model were not significantly different from observed values (415±6.316 and 413.8±6.14 cm^2 respectively) as shown in Figures4.22, 4.23 and 4.24.

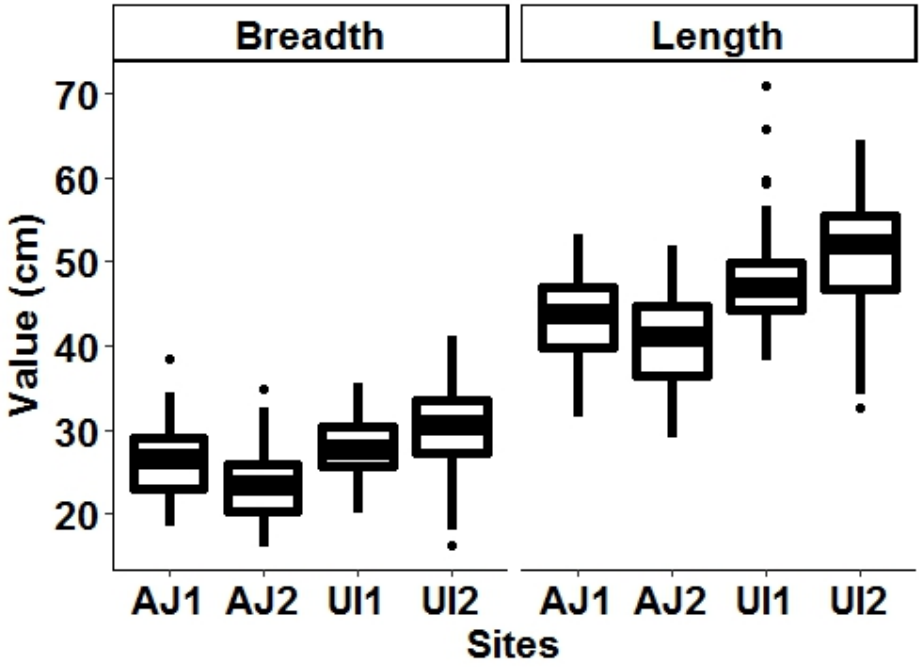

Figure 4.21. Variation in leaf length and breadth of *Tithonia diversifolia*

Key: UI1 = Department of Botany;
UI2 = Nnamdi Azikiwe Hall
AJ1 = UI Research Farm;
UI2 = Runsewe Olatunde Hall

Table 4.23. Comparison of leaf metrics of *Tithonia diversifolia*

Population	Length (cm)	Breadth (cm)
AJ1	43.69 ± 0.50 [a]	26.09 ± 0.40 [a]
AJ2	40.54 ± 0.53 [b]	23.47 ± 0.40 [b]
UI1	47.39 ± 0.52 [c]	27.62 ± 0.35 [c]
UI2	50.86 ± 0.60 [d]	30.41 ± 0.50 [d]

Comparison based on four populations randomly selected across the University of Ibadan Campus. Metrics across columns with the same letter are not significantly different.

Key: UI1 = Department of Botany;
UI2 = Nnamdi Azikiwe Hall
AJ1 = UI Research Farm;
UI2 = Runsewe Olatunde Hall

Table 4.24. Parameter estimates of leaf area model parameters of *Tithonia diversifolia*

Model	Equation	Model parameters		
		a	b	c
1	$A = aL + b$	17.16 ± 0.49	− 370.37 ± 22.63	-
2	$A = aB + b$	25.52 ± 0.55	− 273.48 ± 15.15	-
3	$A = aLB + b$	0.33 ± 0.01	4.28 ± 6.55	-
4	$A = aL + bB + c$	7.77 ± 0.48	16.68 ± 0.68	−391.01 ± 13.33
5	$A = aB^2 + bL + c$	0.30 ± 0.01	8.00 ± 0.46	−175.34 ± 15.31
6	$A = a(LB)^b$	0.37± 0.04	0.98± 0.02	-

Key: A = leaf area (cm^2); L = leaf length (cm); B = leaf breadth (cm)

Table 4.25. Comparison of leaf area models for*Tithonia diversifolia*

	Calibration percentage = 80%					Validationpercentage = 20 %					
Model	R^2_{Adj}	RMA (%)	RMSE	AIC	Rank	R^2_{Adj}	RMA (%)	RMSE	AIC	Rank	Total Rank
1	0.80(2)	11.37 (5)	57.97 (6)	1303.17 (6)	19	0.87 (2)	11.01 (5)	398.85 (3)	483.09 (2)	12	15
2	0.87 (3)	8.76 (4)	46.1 (5)	1229.84 (3)	15	0.84 (3)	14.80 (6)	456.64 (6)	495.91 (6)	21	18
3	0.93 (1)	6.27 (1)	33.5 (2)	1127.72 (2)	6	0.87 (2)	6.15 (1)	397.65 (2)	484.84 (3)	8	7
4	0.93 (1)	6.85 (3)	34.08 (4)	1135.22 (5)	11	0.87 (2)	7.12 (4)	401.10 (4)	485.53 (4)	14	13
5	0.93 (1)	6.36 (2)	33.73 (3)	1131.88 (4)	10	0.87 (2)	6.46 (3)	402.66 (5)	485.85 (5)	15	12
6	0.93 (1)	6.27 (1)	33.47 (1)	1127.41 (1)	4	0.93 (1)	6.24 (2)	394.06 (1)	482.12 (1)	5	4

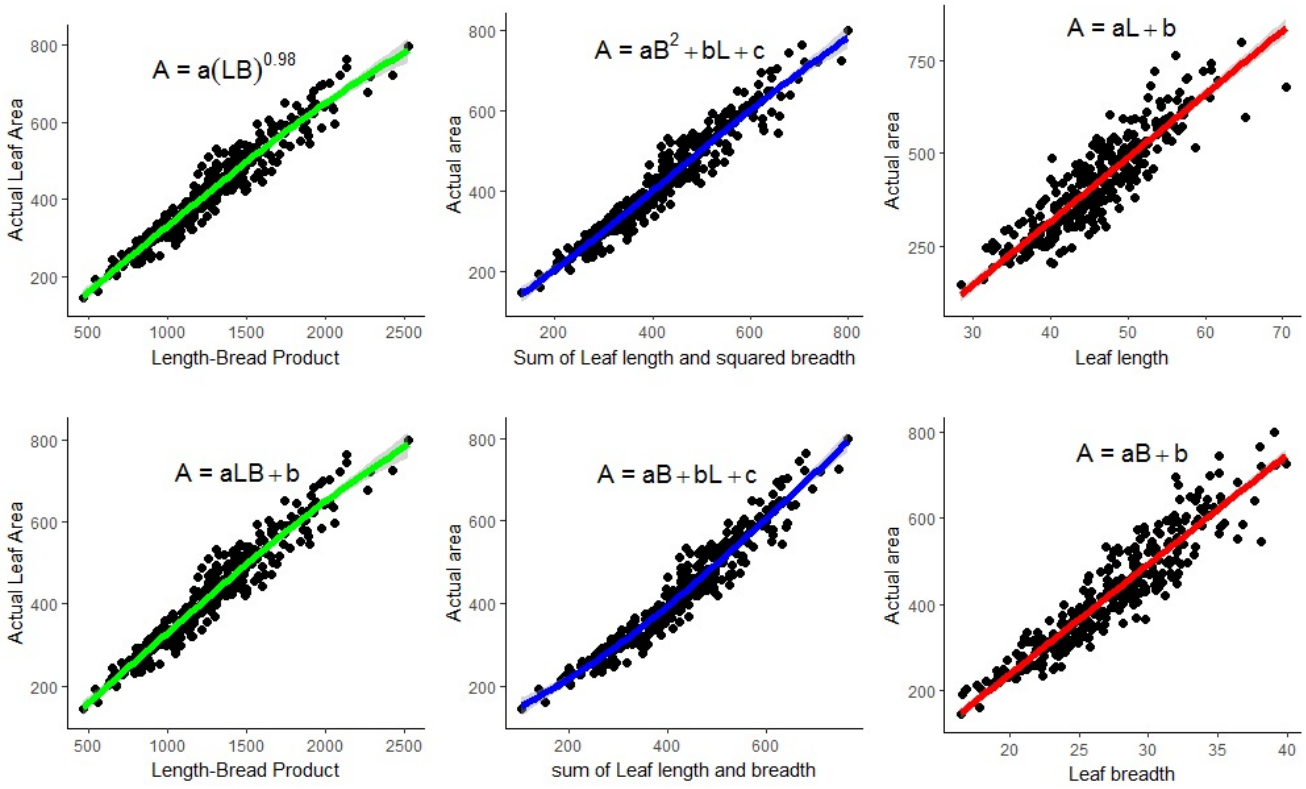

Figure 4.22. Leaf models of *T. diversifolia*

Models were developed from 400 leaf samples collected within the University of Ibadan Campus. Models were ranked based on their predictive performance from the left to right in the first to the third columns**.**

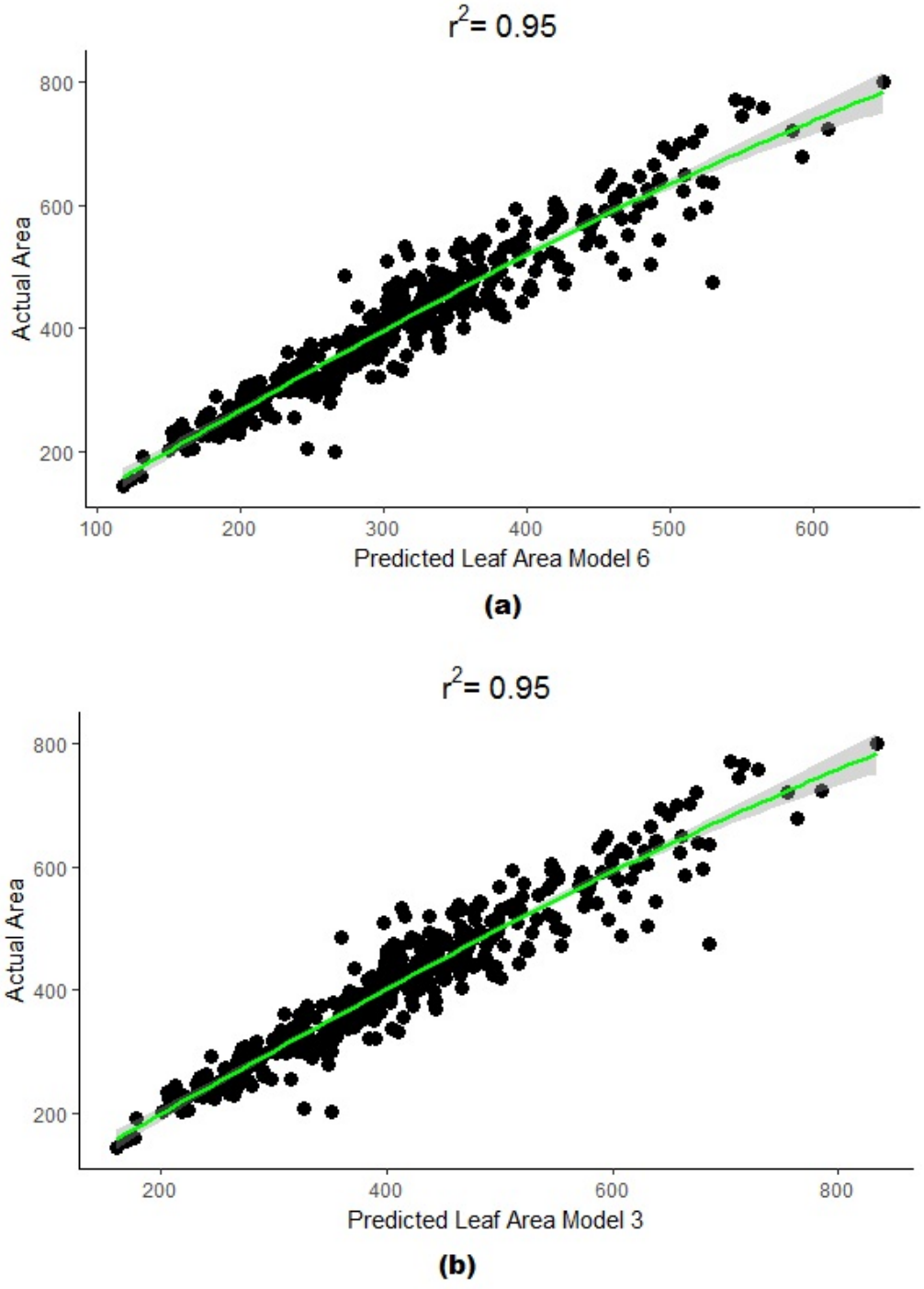

Figure 4.23. Correlation between predicted and actual leaf area of *T. diversifolia* Leaf areas predicted by the power model (a) and the length-breadth product model (b)

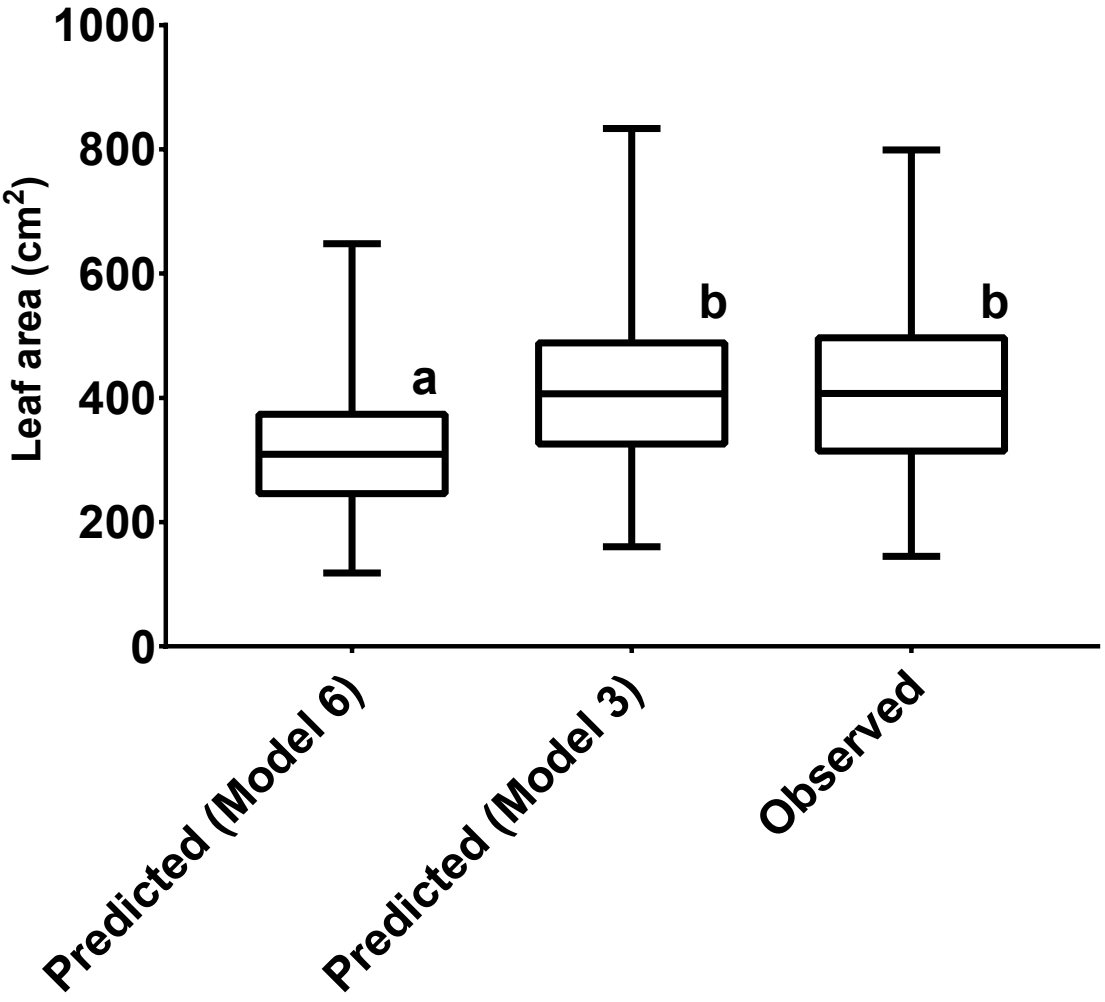

Figure 4.24. Variation in predicted and observed lead area of *T. diversifolia*

CHAPTER 5
DISCUSSION

5. 1 Niche and potential ecological distribution of *T. diversifolia* in Nigeria

This study showed that the ecological niche that *T. diversifolia* currently occupies in Nigeria is different from its native niche in Mexico. This suggests that this species was able to expand its niche upon introduction into Nigeria. This is in consonance with previous studies, for example, Early and Sax (2014) andAtwater *et al*. (2018) who reported that niche shifts are frequent in invasive plants. The time span since the first known introduction of *T. diversifolia* below 50 years in Nigeria (Akobundu *et al*., 2016). Although niche conservatism was expected because this observation is typical over short period of timeafter the introduction of a species into novel habitats (Peterson, 2011). Therefore, over the study area,*T. diversifolia* presenteda new case of niche shift in invasive plants.

As pointed out by Goncalves *et al.*(2014), further analyses outside Nigeria may yield different results. Although *T. diversifolia* is widespread in Mexico, these resultsshow that it has yettofill all native habitats withsuitable abiotic conditions thereby signifying an important geographic range unfilling, which can hamper spatial predictions into new areas (Guisan *et al.,* 2014). The invasive potential of*T. diversifolia* can be further inferredfrom its capacity to form hybrids with related species such as*T. tubaeformis* and *T. rotundifolia* (Tovar-Sánchez *et al.,* 2012; López-Caamal *et al*., 2013). However, climatic projections between 2014 and 2060 showed that this plant is not likely to expand its range further since its future potential distribution does not considerably exceed the current potential distribution under most severe climate change scenario.

Although the native climatic niche model of *T. diversifolia* had a good predictive performance upon projection to Nigeria, a better predictive performance was attained by merging both reciprocal climatic niche models by their maximum predicted values. This is in line with the findings of Broennimann and Guisan (2008) who advocated that data from both introduced andnative ranges should be taken into account in predicting biological invasions.It is noteworthy that this study provided evidence contrary to this recommendationas a lower predictive performance as given by the Boyce index was obtained when merging both reciprocal edaphic Nigerian models. Therefore, the widespread approach of using models trained with native range data for prediction into new ranges holds true in this case for soil physico-chemical properties. Finally, a mergerof the best climatic and edaphic models produced a robust prediction of suitable habitats for the study species in Nigeria. This is in line with the results ofVelazco *et al*. (2017) who highlighted the importance of incorporating soil data alongside climatic variables in species distribution models. In the present study, we opted to merge separate models based on their maximum predicted value.

Climatic models of *T. diversifolia* in Nigeria revealed that the derived savannah zone and the northern limits of the forest zone of this country are the mostsuitable ecological zones for this species. These zones correspond to southwestern Nigerian region where this plant was first introduced. Here, *T. diversifolia*grows luxuriantly during the rainy season and completes its growth cycle at the onset of the dry season, spanning from December to early March. This periodcoincides with the driest quarter of the year. Multi-colinearity was detected in the dataset of 19 climatic layers. This dataset wasdiminished to seven uncorrelated variables as in many other studies where at least four bioclimatic variables were considered uncorrelated (Suárez-Mota *et al*., 2016; Hernández-Lambraño*et al*., 2017). Climate-only distribution models showed that in Nigeria, *T. diversifolia* was constrained by three hydricvariables (Bio 14, Bio 19, and Bio 18) and only one thermal variable (Bio 11). Strikingly, the hydrothermal variables identified as the most important for the survival of *T. diversifolia* in Nigeria, namelyBio 14 (precipitation of the driest month), Bio 19 (precipitation of coldest quarter) and Bio 11 (mean temperature of coldest quarter) all correspond to the dry season in the derived savanna zone. These findingsare in line with those of Suárez-Mota *et al*. (2016) who reported that three hydrothermal variables (Bio 11, Bio 6 and

Bio 18) constrain the distribution of the invasive *Chromolaena odorata* in South Africa.

Contrary to the climatic models built in this study, using soil physico-chemical properties to model the geographic distribution of *T. diversifolia* showed a different result. In effect, based on edaphic variables at 15 cm depth, a much greater extent of the Nigerian environmental space, distributed throughout the southern region of the country were found highly suitable for the development of this species.It was therefore necessary to combine prediction from both edaphic and climatic models in order to have an all inclusive representation of the geographical distribution of this species in Nigeria. The prediction obtained from this merger was also found reliable given its very high Boyce index. Recently, Velazco *et al*. (2017) showed that combining edaphic and climatic variables to generateecological niche models produced a increased accuracy compared to when only climate variables are used. The present study therefore highlighted the importance of using non-climate data in modelling the ecological niche of invasive species.

5. 2 Seed bank and Soil properties of sites infested by *T. diversifolia*

5. 2. 1 Seed bank diversity of sites infested by *T. diversifolia*

The results of this study indicated that *T. diversifolia* exerts no reductive effect on the seed bank structure of invaded sites as opposed to many other invasive species such as *Lantana camara* (Ruwanza 2016), *Gunneratinctoria,Fallopiajaponica* and *Heracleummantegazzianum* (Gioria and Osborne 2009, 2010). Though rare, the absence of structural changes in seed bank community due to invasive species has also been reported with *Solidago canadensis* and *Solidago gigantea*(Kundel *et al.,* 2014). Although the species richness and diversity of seed banks decreased across all *T. diversifolia* dominated plots in relation to non-invaded plots, these changes were clearly not due to the presence of its propagules in the soil.

In contrast, Oke *et al.*(2009) in a similar study carried out in Ile-Ife, obtained a relatively higher seedling density of *T. diversifolia* in invaded plots. This discrepancy may be attributed to differences in timing of sample collection in relation to seasons. In the study species, seed dispersal starts from early December and lasts until late January while field emergence takes place at the onset of the rainy season from April. Oke and colleaguescollected soil samples in July, understandably, in line with their objective

which was to compare belowground and aboveground vegetation diversity. An important seed bank depletion could have occurred in during the 2 month difference between both our studies, thereby supporting the discrepancy between above ground and belowground species diversity obtained here. The seed bank of *T. diversifolia* is atypical of many invasive species as it comprises seeds (achenes in this case) that quickly lose dormancy after dispersal. Therefore, *T. diversifolia* forms a transient seed bank (Thompson *et al*., 1997) given the very low number of emergents reported here about six month from the beginning of field emergence.

5. 2. 2 Physico-chemical properties of soils infested by *T. diversifolia*

Overall, *T. diversifolia* showed a considerable impact on soil physico-chemical properties as nine out of the fourteen soil chemical properties measured were found to be different across sites and between invasion status. The levels of pH, total nitrogen, organic carbon and phosphorus obtained across the invaded and non-invaded sites in this study compare well with those reported by Oludare and Muoghalu (2014), in a more localized assessment of the impacts of this species, in Ile-Ife (south-western Nigeria).

Previous studies report similar findings whereby plant invasions were associated with shifts in soil physico-chemical properties. For example, Perrett *et al.* (2012) showed that about ten of the twenty four soil properties they investigated showed significant differences between plots invaded by *Macfadyena unguis-cati* and non-invaded areas. The variation in some soil traits in the presence of *M. unguis-cati* (Perrett *et al.* 2012) and *Chromolaena odorata* (Mandal and Joshi 2014, Wei *et al.,* 2017) is in agreement with the results of our study, namely higher organic carbon, Nitrogen, pH and electrical conductivity and lower levels of iron in invaded plots. Similarly, soil texture was also found unaltered by the presence of *T. diversifolia.* In the same vein, prior studies (Ruwanza and Shackleton 2016; Muvengwi and Ndagurwa 2015) assessing the effects of the invasive *Lantana camara* in South Africa and Zimbabwe respectively showed that this plant is capable to significantly alter soil chemistry by increasing the levels of several properties including total carbon, total phosphorus, Calcium, Magnesium, sodium and ammonium. Although, invasive species could readily alter soil chemistry, with some cases of drastic changes, ranging from two to eightfold higher in invaded areas, there is evidence that this is not always the case even for the same species in different habitats (Muvengwi & Ndagurwa 2015; Abella *et al.,* 2012).

Therefore, it is worthy to note that such changes depend on several factors including host community biotic and abiotic characteristic as well as invader traits. In effect, a global evaluation of the impacts of 167 invasive plant species on native communities showed that short-statured plants and annual plants are least likely to significantly affect soil physico-chemical properties in invaded habitats (Pyšek *et al.,* 2012). This study suggests that the persistence of *Tithonia diversifolia,* whichis a shrub-like annual plant with a tremendous growth and spread potential comparable to the world's worst invasive species (*C. odorata* and *L. camara*) may have profound effects on soil chemistry. It appears that invasive species may transform soil properties of their host communities in order to favour their establishment and further spread to the detriment of native species. The higher soil Nitrogen and phosphorus levels in tandem with reduced metals concentrations observed in sites invaded by *T. diversifolia* explain the widespread usage of this plant as a source of green manure (Jama *et al.,* 2000; Partey *et al.,* 2011) and heavy metal remediation (Ayesa *et al.,* 2018). Improved soil fertility has been also reported in areas invaded by *L. camara* (Fan *et al.,* 2010).

Among the changes in soil chemistry with regards to plant invasions, we noted a pattern in the variation of pH between invaded and non-invaded areas. For *T. diversifolia,* the higher pH values found across all sites in this study concur with the findings of Cong and Merckx (2005) who showed that incorporation of leaves of this plant into soil caused an immediate increase in pH in Vietnam. Similarly, in studies involving *L camara,* Osunkoya *et al.* (2012) reported an increase in the pH of invaded soil in Australia. Soil pH stood out as the trait with most discriminating power between invaded and non-invaded patches for *Lantana camara* (Osunkoya and Perrett, 2011). Similarly, higher soil pH values were recorded in areas invaded by *Centaurea stoebe* and *Euphorbia esula* (Gibbons *et al.* 2017).

In our case, the observed changes in pH and other chemical properties are directly linked to the presence of *T. diversifolia* given the similarity in soil type and texture between invaded and non-invaded areas. Therefore, the pathway by which this species increases soil pH requires further investigation. Because soil pH influences litter decomposition and subsequent nutrient availability, the higher pH in invaded plots could have positively affected soil electrical conductivity and total Nitrogen. This is in agreement with the results of Osunkoya and Perrett (2011) who reported a positive correlation between electrical conductivity and pH in Lantana-invaded soils. Given

that leaves of *T. diversifolia* are a major source of nutrients especially Phosphorus, it was expected that this major nutrient would be higher in plots invaded by this plant. This finding support the hypothesis that high litter accumulation by plant invaders results in increased soil nutrients (Ehrenfeld, 2010). As pointed out above, the impacts of invasive plants on soil physico-chemical properties depend more on the context in which the study is conducted and several other factors such as the species traits and life form (Osunkoya *et al.,* 2012; Pyšek *et al.,* 2012). The absence of changes in some soil physico-chemical properties reported in our study buttresses the idiosyncratic nature of this the effects of plant invaders on soil traits.

5. 3. Variation of N, P and K and reproductive Allocation in *T.diversifolia*

5. 3. 1 Variation of N, P and K in *T. diversifolia*

Total soil N within the study area varied between 1.54 to 3.20% while P and K ranged from 207.74 to 835.56 ppm and 0.33 to 1.53 Cmol/kg respectively. This concurs with the results of Salami and Sangoyomi (2013) who analyzed the properties of soils from two major ecological zones in the study area and reported closely related mean values for total soil nitrogen (1.5%), potassium (0.4 Cmol/kg) and available phosphorus (600 ppm). Similarly, Watanabe *et al*., (2015) showed that nitrogen, phosphorus and potassium levels in subsoil (50 cm depth) in this region fall within similar ranges. Soils samples analysed in the present study were found to be relatively rich in nitrogen, phosphorus and potassium as these macronutrients are well above the critical levels for Nigerian soils (Adepetu, 1996).

T. diversifolia had the highest levels of Nitrogen, Phosphorus and Potassium in its leaves. This is in consonance with the reports of Jama *et al.,* (2000) and Partey *et al.,* (2011) who demonstrated the use of this plant in soil fertility improvement in Africa.The range of leaf Nitrogen was wider (0.08 to 2.32%) but far below 2.56 to 4.38% and 3.1 to 4.0% reported by George *et al*.(2001) and Jama *et al*.(2000) respectively. The same trend was observed in mean leaf Nitrogen, which was lower compared to the values reported by these authors.

In the same vein, the values of leaf Phosphorus (range 226 to 847 ppm) and Potassium levels (range 0.33 to 1.54 Cmol/kg) in this study tend to be lower than those (2000 to 5000 ppm and 6.92 to 12.30 Cmol/Kg) reportedby Jama *et al*. (2000). Similarly, the mean leaf Phosphorus and Potassium concentrations in this study (991.90 ± 161.10

and 3.20 ± 0.40 Cmol/kg) were also lower than the means reported by George *et al* (2001). The differences in concentrations of nutrients in tissues of *T. diversifolia*obtained in this study is obviously due to differences in soil fertility levels. In effect, the data of Jama *et al.*(2000) and George *et al.*(2001) show that nutrient concentrations were higher in theirstudy soils.

The discrepancy between our results and those reported by George*et al*. (2001) and Jama *et al*. (2000) may be due to differences in soil Nitrogen level. Indeed, changes in leaf Nitrogen of *T. diversifolia* in relation to soil Nitrogen as reported in thesestudies also appear here as leaf Nitrogen was found to be significantly correlated with soil Nitrogen. In other words, we found that higher soil Nitrogen levels led to higher leaf Nitrogen in *T. diversifolia*. This reflects the ability of this plant to occupy a wide array of soil conditions and evidence of plasticity, which is known as an important trait in other invasive species (Claridge and Franklin, 2002).In the same way, Nutrients in other parts of this plants were found to be lower.

5. 3. 2Reproductive allocation of N, P and K in *T.diversifolia*

The results demonstrate that RA_N RA_P and RA_K in *T. diversifolia* do not vary with soil N, P and R levels respectively and that Nitrogen, Phosphorus and Potassium are not equivalent currencies for measuring RA in this species. This suggests that these elements are suitable currencies for estimating Reproductive allocation mainly because they strongly control the growth and development of this species (Chukwuka *etal*., 2007b). Méndez and Karlsson (2007) showed that reproductive allocation of nitrogen in *Pinguicula vulgaris* is equivalent to either allocation to biomass or phosphorus. The lack of association between RA_N and $RA_P$and RA_Kfound in the present study does not agree with the existence of redundant RA currencies as suggested by these authors. Also, this does not reflect the well-known interaction between N and K in crops (Milford and Johnston 2007).

A limited number of studies have explored resource allocation patterns in invasive species using nutrients as currencies. However, many studies in this context focus on biomass solely (Claridge and Franklin 2002, Qi *etal*., 2008; Gupta and Narayan 2012). It is therefore hard to directly compare our results with previous studies. Using the more accurate ‘‘dynamic’’ approach to biomass allocation as recommended by Ashman (1994a), Muoghalu (2008) showed that *T. diversifolia* allocates 5-7.6% of its

biomass to reproduction. This range and the ones obtained here for nitrogen (5.88 - 17.40%), phosphorus (8.60 - 31.65%) and potassium (7.73 - 22.53%) indicate that this species invests more nutrients in its reproductive structure compared to biomass. This trend is in agreement with the findings of Abrahamson and Caswell (1982) who, in a comparative study on biomass and nutrient allocation to reproduction in the semelparous *Verbascum thapsus* and five iteroparous Solidago species showed that mineral elements are allocated differently than biomass.

Our results also concur with those of Ashman (1994b) who showed that the quantity of N, P and K allotted to reproduction in *Sidalcea oregana spp.Spicata* do not significantly differ. Using an approach similar to ours, Méndez and Karlsson (2007) reported significantly different and relatively higher RA_N (21.0 –34.6%) and RA_P (27.6 – 40.6%) in relation to biomass (21.1–26.5%) across 11 population of *Pinguicula vulgaris* in northern Scandinavia. Such relatively high and wide-ranging RA values are species-specific and as such cannot be compared with the ones recorded in our study. In cases whereby such comparisons are inevitable, soil nutrients status will be valuable.

The unaltered Reproductive Allocation of important nutrients across various soil conditions indicates that *T. diversifolia* does not rely on this trait to expand its range. This is in contrast with the widely held view that plasticity in resource allocation to reproduction is selected during the invasion process (Gupta and Narayan 2012; Medeiros *et al.,* 2016). Investigations aimed at estimating inter-individual or inter-population patterns of resource allocation would be more robust if allocation in several currencies, particularly limiting nutrients is considered. Further research on the "currency issue" is greatly needed especially with advances in plant nutrient analysis techniques.

5. 4. Reproductive biology and ecology of *T. diversifolia*

5. 4. 1 Pollen to ovule ratio and pollination mode in *T. diversifolia*

The inability of *T. diversifolia* to produce viable achenes in bagged capitula intimates that this plant isincapable of autonomous seed production and therefore depends on external agencies for pollination. The near absence of viable achenes in bagged capitula of *T. diversifolia* was also in observed in bagged capitula of the invasive *Bidens pilosa* (Huang and Kao 2014).These finding do not agree with Baker's (1955)

predictions about the characteristics of the breeding system of invasive species.Our results also disagree with the findings of Rambuda and Johnson (2004) who have shown that that many plant species invading south African landscape including *C.odorata* and *A. adenophora* are capable of autonomous seed production. Although pollinator diversity was not assessed, insects mainly bees, butterflies and flies were encountered in the course of the study. These groups of insects have been reported to visit many Asteraceae (Yan *et al*., 2016).

The high P/O of *T. diversifolia* suggests that this plant is a facultativelyxenogamous species (Cruden, 1977; Dafni, 1992).A similar P/O ratio was reported by Hong *et al.* (2007) for the invasive *Mikania micrantha*in China.The findings of Hao *et al.* (2011) suggest that Asteraceae appear to have a wide range of breeding systems. These authors reported autogamy as the major breeding system in twelve invasive species in China including the annuals *Ageratum conyzoides* and *Bidens pilosa.*However, in a recent study involving the genus Bidens, Yan *et al*. (2016) reported that the invasive *B. frondasa* is facultative xenogamous whereas three Chinese varieties of *B. pilosa* exhibited autogamy (*B. pilosa var pilosa*) and xenogamy (*B. pilosa var radiata*) according to Huang and Kao (2013). Although, pollinator diversity was not investigated in thepresent study, it appears that, contrary to Baker's law, *T. diversifolia* seems to depend on pollinators during its invasion. A possible explanation is that this plant may havebeen pre-adapted to a wide range of pollinators given its inherently high levels of genetic diversity (Yang *et al*., 2012) and its ability to hybridize with related taxa (Tovar-Sánchez *et al.,* 2012; López-Caamal *et al*., 2013).

In their comparison of the breeding systems between the native and exotic rangesof some important invasive species such as *Echiumplantagineum*, *Solanumelaeagnifolium*, and *Centaureasolstitialis*), Petanidou*et al.* (2012) showed that *E. plantagineum* and *C. solstitialis* were self incompatible in the native range but self compatible in novel habitats whereas the reverse was true for *S. elaeagnifolium.* This implies that breeding systems may not be the only factor contributing to plant invasiness. Although our P/O ratio and pollinator exclusion experiments are effective methods of inferring xenogamous reproduction in *T. diversifolia,* they do not tell the real breeding system of this plant as emphasized by Baker (1955). This author pointed out that the actual breeding system of a plant *in situ* is as a result of both the ability of a plant to cross/self pollinate and the behaviour of pollinators. One of the weaknesses

of this study lies in our inability to investigate pollinators that facilitate xenogamy in the study species.

5. 4. 2 Floral phenology and reproductive output of *T. diversifolia*

In the studied population, seed set of open-pollinated capitula of *T. diversifolia*was 93%. A similar value (92.5%) was reported by Tiebre *et al.*(2012) in Côte d'Ivoire. Similarly, Wang*et al.*(2004) showed that seed set in this species varied according to site characteristics in China and could reach 82%. The high reproductive potential, through the production of large amounts of viable achenes may be the major reason for the spread and persistence of *T. diversifolia* in Nigeria. Seed production is a characteristics of invasive speciesmechanisms for plant invasions.Mean capitulum diameter in five Chinese populations of *T. diversifolia* ranged between 26.22 ± 0.36 and 32.32 ± 0.36 mm (Wang *et al.,* 2008). This value is higher than the one reported in the present study 18.81 ± 0.22 mm. Capitulum number per plant found in this study (49 ± 3) was comparable to that reported by Muoghalu (2008) in Zambia (52 ± 14). Wang *et al.* (2008) found a notably highernumber of achenes per capitula (between 164 ± 6 and 231 ± 9) compared to 75 ± 1 found here. In the same vein, Tiebre *et al.*(2012) found that this species produced 146 ± 28 achenes per capitulum. Although this metric was lower here, personal observations, madeon solitary individualsof *T. diversifolia* provided enough evidence to support disproportionate seed production in this plant. Solitary individuals of *T.diversifolia* are very rarely encountered; only three of such were found after surveying the University of Ibadan Campus and environs and above 800 capitulumwere recorded from each of them (Obiakara personal observation).The trend in achene number per square metres is as follows: 7,320 - 131,040in this study, 10,296 - 58,520 (Tiebre *et al.,*2012) and 80,000 - 160,000 (Wang *et al.,* 2004).Differences in reproductive metrics of the study plant among studies are not surprising and can be mainly attributed to site differences. This is in consonance with the results reported in section 4.3 of this thesis and illustrated in Figure 4.13depicting the correlation between soil and tissue nutrient.*Tithonia diversifolia* is therefore a highly plastic plant in terms of reproductive output.

5. 4. 3 Germination ecology of *T. diversifolia*

5. 4. 3. 1 Effect of scarification on imbibition of achenes of *T. diversifolia*

Our results suggest that water imbibition byintact, freshly harvested achenes of *T. diversifolia* is similar to mechanically scarified.This is in line with the findings of

Upfold and van Staden (1990) who reported that freshly harvested intact and mechanically scarified achenes of *T. rotundifolia* imbibed water rapidly and reached full imbibition after 48 hours. In contrast, Presotto *et al.* (2014) showed that water imbibition was increased by 19% after pericarp scarification in the invasive *Helianthus annuus*.Upfoldand van Staden (1990) investigated the microscopic structure of the pericarp of achenes of *T.* diversifolia usingscanning electron microscopy. This revealed an outer layer of porous tissues and a macrosclerid bundles packed in an inner, thicker layer. The macrosclerid layer may serve as a mechanical protection for the delicate embryo of this species and not as an impermeable barrier.

5.4. 3. 2 Seed type and dormancy of *T. diversifolia*

Unlike many other studies where germination is assessed using germinability (germination percentage) only, we used in addition, mean germination time and germination index as recommended by Ranal and Santana (2006) in order to fullycharacterize germination in the study species. Mean germinability of freshly harvested achenes of *T. diversifolia* was very low (8.67 ± 2.91 %) as reported in previous studies: 16.3% after 30 days (Muoghalu and Chuba, 2005), 21.20 % after 30 days (Tiebre *et al.,* 2012). It can be concluded that achenes of this plant are dormant (Baskin and Baskin 2014). It was observed that mechanical scarification significantly increased all germination indices of achenes of the study species. Since fresh intact achenes of the study species fail to germinate even upon imbibition, Physical Dormancy, PYD (i.e. failure to take up water) is not the cause of dormancy in this plant (Baskin and Baskin 2014).

We observed a 40% difference between mean germination percentage of scarified and intact achenes. A comparable outcome was reported by Muoghalu and Chuba (2005) with 40 and 62% of achenes germinating after chemical scarification with sulphuric acid for 6 and 10 minutes respectively. This could be explained by the inability of the embryo to rupture the thick macrosclerid bundle layers of the achenes of the congener of *T. diversifolia* (Upfold and van Staden 1990). Therefore, mechanical/chemical scarificationmay enhance germinability of *T. diversifolia* mainly by weakening the thick layer of macrosclerids. Indeed, physiologically dormant seed take more than four weeks to germinate largely (at least 50 % germinability); in such seeds, the embryo does not have enough growth potential. This is what Baskin and Baskin (2014) referred to as "embryo push power". In other words, after receiving appropriate testa-

weakening mechanical and chemical treatments, the embryo is abe to emerge through this barrier.

The significant increase of germination percentage (from 8 to 65%) of GA_3-treated achenes of *T. diversifolia* has been reported in *T. rotundifolia* (Upfold and van Staden, 1990). This indicates that the type of dormancy in this plant is physiological (PD) according to the classification scheme of Baskin and Baskin (2014). Physiological dormancy is characterised by 1) water imbibition, 2) a relatively low embryo length/seed length ratio, and 3) no embryo growth preceding radicle emergence (Baskin and Baskin, 2014).In conclusion, *T. diversifolia* exhibit PD. This result is in line with those reported in studies. For example, Muoghalu and Chuba (2005) concluded that achenes of *T. diversifolia* "displayed a kind of dormancy" after low germination (16.3 %) of fresh achenes.

It was shown that osmotically stressed achenes of *T. diversifolia* were not able to germinate. A similar result was reported by Javaid and Tanveer (2014) who showed that germination of the two invasive *Emex spinosa* and *E. australis* was completely inhibited at -1 Mpa. In the same vein, Chahan (2013) showed that germination percentage of *Eragrostis tenella* could be fit by a linear model y= 98 + 69x where x and y are osmotic potential in (MPa) and germination percentage. This equation shows that germination percentage is 98 % at 0 MPa and can decrease to 1.4% at -1 MPa. Our results thus suggest that water stress is an important limiting factor in the germination of the study species. This may explain the relationship between the time of highest emergence of *T. diversifolia* in the field, which is between the end of March and April when rain start to abound and the dry spell that precedes this period (from November).The spread of *T. diversifolia* may be limited to rainfall given its inabiity to germinate at low water potentials.

For the first time, this study characterized the type of seed of *T. diversifolia* and its dormancy as opposed to previous works. Based on embryo morphology, the type of seed determined here was Spatulate Fully Developed. This is in line with the review of Finch-Savageand Leubner-Metzger (2006) who established the phylogeny of angiosperm seeds based on on the internal morphology of the embryo and endosperm. In their work, these authors classified the Asteraceae family in the FA-1 group. All

seeds in this category store their nutrient in cotyledons and these were observed in Plate 4.2.

Dormancy type identified in this species has been known as one of the most prevalent in angiosperms (Finch-Savage and Leubner-Metzger2006). The results of this present study are in line with the phylogenetic tree of angiosperm seed evolution constructed by the Angiosperm Phylogeny Group II (2003) according to which PD is widespread in the Asteraceae. Although most studies (e. g. ,Muoghalu and Chuba, 2005; Tiebre *et al.,* 2012) have only reported the presence of dormancy in *T. diversifolia,* this work has gone a step further to pinpoint the actual type of dormancy as Physiological dormancy. Physiological dormancy has been divided into three levels namely, deep, non-deep and intermediate physiological dormancy based on embryo behaviour with respect to some dormancy-breaking treatments (Baskin and Baskin, 2014). This suggests an opportunity for further research on this subject.

5. 4. 3. 3 Temporal patterns in germinability of achenes of *T. diversifolia*

The gradual increase in germinability of achenes of *T. diversifolia* with time also confirms the presence of dormancy. A similar pattern of germination was reported by Tamado *et al.*(2002) for *Parthenium hysterophorus* in Ethiopia. The high germination percentage obtained six months after the onset of the rainy season suggests that *T. diversifolia* forms a transient seedbank and as unlike many other invasive species. For instance, Tamado *et al.,* (2002) reported that after 26 months of burial only 50 % of seeds of *P. hysterophorus*could still germinate. This implies that a strategy aimed a depleting the seed bank of this species would be an effective control measure against this plant.

Germinability of dry-stored achenes was generally similar to those exposed to field conditions both on the soil surface and at 5 cm depth. This is in consonance with the results of Mendes-Rodrigues *et al.* (2008) who found that the viability of *Clidemia hirta* was similar ina seed samples kept at ambient conditionin the laboratory for two years and those buried inbags for the same duration. Achenes of *T. diversifolia* gradually break dormancy with age, a phenomenon known as after ripening. Our findings are in line with the few works of weedy and invasive Asteraceae from tropical and subtropical regions demonstrating that most of these species with dormant achenes

need an after-ripening period to overcome dormancy(Schütz *et al.,* 2002; Presotto *et al.,* 2014)

5. 4. 3. 4 Seed bank depletion

Seed bank decreased drastically with more rains from March when rainfall was highest. This implies that achenes of this species require under field conditions 3 to 4 months of after-ripening after which they need relatively low moisture to start germination. A comparable pattern was reported by Tamado *et al.* (2002) where *P. hysterophorus* required about 2 months from dispersal date to start emergence in the field. From dispersal to emergence, aftersufficient amounts of moisture and after-ripening is necessary to initiate mass germination of on the field. The predicted "half-life" of the seed bank of *T. diversifolia* (20.6 days.) suggests that eradication of this plant can be easily achieved because of its short-lived or transient seed bank (Thompson *et al.,* 1997). A similar result was obtained with seeds of *Heracleum. mantegazzianum* (Moravcová*et al.,* 2006).

5. 5 Effect of control measure on the growth of *T. diversifolia*

5. 5. 1 Effects of control measures on growth parameters of *T. diversifolia*

Results suggest that the use of paraquat dichloride and fireinduced high mortality in seedlings of *T. diversifolia*and reduced the height of this plant. However, the stem girth was not affected by these two treatments. Some of these results agree with the findings of Ayeni *et al.* (1997b) who reported an inhibitory effect of herbicide (a mixture of imazethapyr and pendimethalin)on the height of *T. diversifolia*4 weeks after application. In the present study, *T. diversifolia* took advantage of the reduced competition induced by the treatments to increase its stem girth. This was evidenced by the fast increase in stem girth in treated plants (paraquat dichloride, fire and manual weeding) as opposed to control plants,a process referred to as density-dependent growth. This finding is in line with the report of Spitters (1989). This author showed that density was inversely proportional to plant size and fecundity. A similar finding was reported in the meta-analysis of Poorter *et al.* (2012) who quantified the pattern of biomass allocation to stems, leaves and roots and found that plants grown at higher densities have a marked increase in the stem biomass.

5. 5. 2 Biomass of *T. diversifolia*

Biomass allocation pattern is an important trait associated with invasiveness (Van Kleunen *et al.,* 2010). In this study, the invasive *T. diversifolia* allocated the largest portion of biomass to its shoot. This is in line with the report of Muoghalu (2008) who found similar biomass (66%) allocation to shoots of this species in Zambia. These results also agree with the findings of van Kleunen*et al.* (2010) who reported that increased plant size and biomass allocation to shoot were fitness traits inherent to many invasive species. In contrast, Wilsey and Polley (2006) found that a greater amount of biomass is allocated to leaves in manysuccessful invasive species.Although leaf biomass allocation reduced with time in the study species, the pattern of allocation observed here may be a strategy forbetter sunlight capture. The high growth rate and leaf expansion of *T. diversifolia* observed here are in line with the report of Zheng *et al.* (2009) who reported that*Chromolaena odorata* presents a strong competitive advantage and the ability to form dense monospecific stands thereby, out-shading native plants.The logistic growth of *T. diversifolia* is in line with the findings of Spitters (1989)who reported that, as a result of intraspecific competition, plant growth increases following an S-shaped rather than exponential model.

5. 6. Leaf area model of *T. diversifolia*

Linear leaf metrics of *T. diversifolia* varied with respect to location within the University of Ibadan Campus. The observed difference in leaf metrics across the four studied population is probably due to different land use types. The UI1 and UI2 populations were established on recently cultivated or abandoned arable lands as opposed to AJ1 and AJ2, which were roadside populations. It noteworthy that the UI1 population, which has the highest leaf metrics was an arable land highly coveted by local farmers due to the high yields commonly recorded there. The soil on this land may be nutrient-rich and liable to support a luxuriant growth of *T. diversifolia.*

The variation leaf length and breadth recorded in this study is an evidence of plasticity in *T. diversifolia*. Plasticity is an important attribute of invasive plants (Claridge and Franklin, 2002). We recall that plasticity was also recorded in the nutrient pattern acquisition and storage with respect to different organs of this species (section 4.3). Therefore, plasticity may play a vital role in the invasiveness of *T. diversifolia.*

The difference between the photographic and manual methods of leaf metrics estimation in the case of leaf length was more likely as a result deviations in manual estimates. Although precaution was taken to ensure that the rule was positioned along the midrib, from the end of the petiole to the leaf apex, it was often difficult to obtain consistent values as the caudate leaf apex of *T. diversifolia* readily bends thereby making it hard to measure accurately. Such difficulty was not encountered when measuring leaf breadth and this is reflected in the lower bias obtained for this metric.

This study tested a series of linear and non-linear models for the prediction of leaf area of *T. diversifolia* using leaf length and breadth as independent variables. It was observed that a power model based on the product of the length and breadth gave the best prediction of leaf area as:

$$Leaf\ area = 0.37 \times (lenght \times breadth)^{0.98}$$

(R_{Adj}^2= 0.93, RMA = 6.27, RMSE = 33.47 and AIC = 1127.41)

This was closely followed by a simple linear model also based on the length and breadth product as:

$$Leaf\ area = 0.33 \times length \times breadth + 4.28$$

(AdjR^2 = 0.87, RMA = 6.27, RMSE = 33.5 and AIC = 1127.72).

These results are in line with those of Holguín *et al.,* (2019) whose predictive model for the same species in Columbia was:

$$Leaf\ area = 0.44 \times length \times breadth + 0.76.$$

Although the power model (model 6) outranked thesimple linear model using the product of leaf length and breadth, the former may not be biologically meaningful given the statistically significant differences found predicted and observed means as shown in Table 4.24and Figure 4.22.

The basic formula for leaf area calculation was proposed by Montgomery (1911). This formula is based on the product of its length and breadth and a leaf shape coefficient. This leaf shape coefficient varies according to species. The difference (though not considerable) reported by Holguín *et al.,* (2019) in their linear model may be accounted for by environmental factors. This is supported by our results that showed

that even within an area as restively small as the University of Ibadan Campus and environs; we found significant differences in the leaf area of this species. This would then be expected since these authors carried their study with Colombian populations of *T. diversifolia.* Thus it may be concluded that leaf shape coefficient of a species varies according to its environment. This variation may tend to be wide given that the study species is morphologically plastic.

In a related study using sunflower, (*Helianthus annuus* L.), Rouphael *et al.*(2007) showed that a linear model with the squared leaf breadth as independent variable produced the most accurate values of leaf area of this plant (R^2= 0.98). In the present study, we found that all models based on leaf breadth had a better overall performance than those based on length. In effect, the simple linear model having breadth (model 2) in this study outperformed the one having length (mode 1) at validation with R^2_{Adj} = 0.87 and 0.84 respectively. This was also evident with the multiple linear models. Thus, the use of the square of the leaf breadth in combination with leaf length is an informative leaf area model in line with Rouphael *et al.* (2007).

The very high predictive performance of the leaf area model based on thepower product of the leaf length and bread obtained here has been reported in previous studies (Cornet*et al.,* 2015; Oliveira*et al.,* 2019). In their assessment of allometric models for the leaf area determination of yam species (*Dioscorea alata* L. and *D. rotundata* Poir.), Cornet *et al.* (2015) found that leaf area of these species was best predicted by a powerfunction of the square of the product of the leaf width and leaf length (bias of 5.4% R^2 = 0.987). The robustness of power-based models for leaf area estimations was also demonstrated by Oliveira *et al.*(2019). These authors reported that the best equation for predicting the leaf area of *Garcinia brasiliensis* Mart. is a power model in the form $0.7470\times(\text{lenght}\times\text{breadth})^{0.9842}$($R^2$= 0.995). For our study, the multiple linear would be the most preferred model because of its simplicity. This choice is based on the principle of Parsimony (also known as Occam's Razor). This principle advocates for the use of simpler, linear models rather than non-linear models in statistics (Crawley, 2007).

This study has shown the use of a simple photographic method for estimating the leaf area of *T. diversifolia.* It was shown that the photogrammetric method was invaluable to model the leaf area of this species, which is why many previous studies rely on it.

For example, in a comparative analysis of the accuracy of several leaf area determination methods, Easlon and Bloom (2014) showed that this method can produce overestimations of leaf area due to lens distortions. They reported a difference of -4.89 % between their reference values and those derived from images taken with a digital camera with a 25-mm focal length. They also attributed this bias to shadows round leaf margins. In our study, care was taken to use a lens with a focal distance known to generate less distortion (50 mm). Additionally, the built-in flash of the camera was set to automatically work in less illuminated conditions. Several other studies have shown the robustness of photogrammetrically-derived leaf area (Cornet *et al.,* 2015; Oliveira *et al.,* 2019).

CHAPTER 6
SUMMARY AND CONCLUSIONS

6. 1. Summary

*Tithonia diversifolia*is an invasive plant species originating from Mexico. Since its introduction in Nigeria in the 1970s, this planthas posed an increasing threat to crop production and native species diversity. This study investigated some autecological and reproductive traits of *T. diversifolia*with a view to controlling itsspread in Nigeria's major ecological zones.

In this study, the ecological niche of *T. diversifolia* was assessed in Nigeria, in relation to that of its native range in Mexico, and the current and future potential geographic distributions of this species were modelled using MaxEnt. The ecological impacts of *T. diversifolia*on seed bank species diversity and soil physico-chemical properties were investigated in the Nigeria Lowland Forest, Derived Savanna and Jos Plateau Forest-grassland Mosaic ecological zones.Autecological traits such as reproductive allocation of primary nutrients (Nitrogen, Phosphorus and Potassium), pollination Mode of pollination, fecundity, germination, dormancy, seed bank behaviour and biomass accumulationof the study species were investigated. Finally, control of *T. diversifolia* using chemical and mechanical methods were assessed.

The niche of *Tithonia diversifolia*in Nigeria was different from that of its native range. Ecological conditions in the Derived Savanna zone of Nigeria were ideal for the spread of this species.Surprisingly, the presence of *T. diversifolia* did not affect the diversity and composition ofnative seed banks.However, this species had the tendency to alternumerous soil physico-chemical properties including pH, cation exchange capacity total N, PO_4, organic C, available P, Fe, Zn and Cu. The leaves of *T. diversifolia* had significantly high levels of N, P and K compared to other plant parts. Reproductive allocation of nutrients varied widely thereby suggesting plasticity, a traits that reflect the ability of this species to grow in soils with a wide range nutrient concentrations.

Tithonia diversifolia is a facultatively xenogamous species with very high fruit set (93%) in open-pollinated capitula and a high pollen-ovule ratio (4,167±76). The average number of capitula produced per plant ranged between 46 and 52, which translated to 454-8,124 achenes/plant. Achenes of *T. diversifolia* were permeable but showed morphological dormancy with low germinability (8.67%). Mechanical scarification and Gibberellic acid increased the germination percentage by 40 and 65%, respectively. The seed bank of *Tithonia diversifolia*was classified as a transient seed bank, with a longevity of less than 6 months and 2,811±201 achenes/m^2. Seed bank density was best fit with exponential decay model.

The study species had a fast vegetative growth with biomass increasing from 2.36±0.38 g/m^2,one month after seedling emergence to 179.56±22.54 g/m^2 two months thereafter. The largest proportion of this biomass (67%) was found in the shoot of *T. diversifolia.* Paraquat dichloride application was most efficient in controlling this species on-farm, with over 80% seedling mortality and 50% reduction in plant height.

6. 2. Conclusions

The invasiveness of *Tithonia diversifolia*is a result of its ability to shift its ancestral niche and invade new habitats in Nigeria. Although this plant species has been recorded in other ecological zones such as the Jos Plateau Forest-grassland mosaic and the Lowland forest zone, in the eastern part of Nigeria,the climate of the derived savanna provides ideal conditions for its establishment. This study failed to link seed bank diversity and structural changes to the presence of *T. diversifolia* in the studied ecozones. This can be attributed to the transient nature of the seed bank of this species, which cannot exceed 6 months.

Unlike many other invader that rely on a seed bank to sustain infestations, *T. diversifolia* may adversely affect species diversity through changes in the aboveground vegetation usually mediated by the formation of large, monospecific stands and the production of important standing biomass. This specieson the other hand appears to alter soil chemistry via increases in pH, CEC, Total nitrogen, organic carbon and available phosphorus thereby showing a biofertilizer potential.

Like many invasive species, the vegetative and reproductive traits of *T. diversifolia*greatly contribute to its invasiveness.These may promote future range expansions of this species in Nigeria if adequate measures are implemented. In contrast

to many invasive plants, this species does not possess the ability to cause long-term changes in native species richness due to its short-lived seed bank. The high amounts of nutrients, especially phosphorus found in the leaves of this *T. diversifolia* confirms its suitability as green manure.

6. 3. Recommendations

Further use of *T. diversifolia*as a source ofgreen manure, as observed in other countries such as Kenya should be discouraged given its effects on soil.However, this practice could serve as a control measure, especially in areas encompassing the south-western region of Nigeria where the species has already naturalized. Owing to the transient nature of the seed bank of *T. diversifolia,* any management strategies that are focused at depleting this element might not produce desirable results.Thus, control of this species should instead be primarily focused on stopping its luxuriant vegetative growth, especially at the seedling and juvenile stages.In cases where herbicide application is impossiblein the control of *T. diversifolia,* alternative means aimed at preventing seed production and reducing seed bank densities are recommended.

6. 4. Contributions to knowledge

1. This study revealed that there is a shift in the ecological niche of *Tithonia diversifolia*Nigeria.

2. *Tithonia diversifolia* has no ability to alter the diversity and composition of invaded seed bank communities in Nigeria.

3. The study established that *T. diversifolia* can modify soil pH, CEC, Total nitrogen, organic carbon and available phosphorus in invaded areas.

4. This study showed *T. diversifolia* can adapt to various soil nutrient concentration by modifying its reproductive allocation of soil macronutrients.

4. The major traits that contribute to invasiveness in *T. diversifolia* are a rapid vegetative growth and prolific seed production.

5. Chemical control is the most effective form of management of *T. diversifolia* infestations.

6. 5. Suggestions for further studies

Further studies are needed to understand the traits that make *T. diversifolia* invasive in Nigeria. For example, research on the reproductive biology of *T. diversifolia*, especiallythe role of pollinators in its seed production is yet to be fully understood, owing to its reliance on a prolific reproduction to colonise new habitats, Studies that investigate the spatial variation of reproductive traits of *T. diversifolia* across a wide range of population, including achene morphology, fruiting and seeing characteristicswould shed more insight into the invasiveness of this species. So far, no comprehensive study on thekaryomorphology of this species has been done in Nigeria. In addition, this aspect, alongside the genetic diversity assessment of *T. diversifolia* would provide more information for the management of this species. Control measures other that chemical, that is, integratedbiological control, which hasproduced desirableresults in other African countries also needs to explored in Nigeria.

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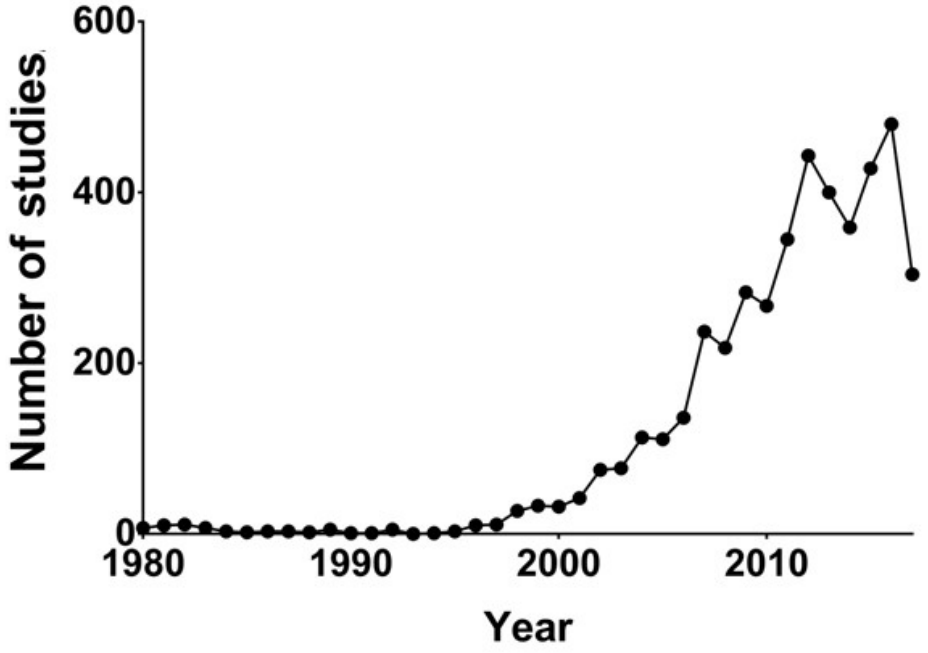
APPENDICES

Appendix 1: A typical stand of *T. diversifolia*

This species typically forms dense monospecific stands in open and sunlit area. Photo taken at the University of Ibadan Campus in October 2017.

Appendix 2:Number of published studies on *T. diversifolia* between 1980 and 2017



Data source: https://www.webofknowledge.com. Figure done using GraphPad Prism 7.

Appendix 3: Occurrences of *T. diversifolia* in Nigeria along major highways

S/N	Longitude	Latitude	S/N	Longitude	Latitude	S/N	Longitude	Latitude
1	7.35204	10.25506	19	4.77810	8.41345	37	6.78245	7.40151
2	3.89882	7.46182	20	6.64883	6.21767	38	6.88130	7.41504
3	5.37131	7.25856	21	8.86441	9.80899	39	7.03781	7.40174
4	6.32143	7.48097	22	6.92325	8.66043	40	7.05042	7.39380
5	6.10125	7.44790	23	3.91342	7.49035	41	7.87010	7.36807
6	5.36425	7.26089	24	7.35204	10.25506	42	7.11601	7.35656
7	6.10127	7.44790	25	3.89882	7.46182	43	7.28719	7.30826
8	6.75831	7.95693	26	5.37131	7.25856	44	7.43968	7.24621
9	6.65875	7.43735	27	6.32143	7.48097	45	4.04204	7.94700
10	6.69389	7.43326	28	6.10125	7.44790	46	4.04655	7.94963
11	6.78245	7.40151	29	5.36425	7.26089	47	4.09558	7.99454
12	6.88130	7.41504	30	6.10127	7.44790	48	4.13776	8.04545
13	7.03781	7.40174	31	6.75831	7.95693	49	4.13776	8.04545
14	7.05042	7.39380	32	6.65875	7.43735	50	4.21814	8.11344
15	7.87010	7.36807	33	6.69389	7.43326	51	4.22858	8.15736
16	7.11601	7.35656	34	4.04655	7.94963	52	4.21814	8.11344
17	7.28719	7.30826	35	4.09558	7.99454	53	4.22858	8.15736
18	7.43968	7.24621	36	4.04204	7.94700			

These geo-referenced populations of *T. diversifolia* were obtained during field surveys

Appendix 4: Various computational R scripts used in analyses

1. Bioclimatic variable processing (Subsection 3. 1. 2)

```
## Bioclimatic variable processing, 23 May 2018

# to ensure hicth-free running, increase memory allocation
to R and Jave and clear global environment.

memory.limit(size=100000)

rm(list = ls())

options(java.parameters = "-Xmx8000m")

# load package "raster"

library(raster)

# set the working directory to the path that contains all
.tif files

setwd("C:/Users/Maxwell
Obiakara/Desktop/SDM/current_climate")

# create a list of all .tif files that exist in the wd

files <- list.files(pattern='\\.tif$', full.names=TRUE)

# combine all list elements into a raster stack

bioclim_stack <- stack(files)

# check plot

plot(bioclim_stack)

# assess multicolinearity using 10,000 random samples
drawn over the world

set.seed(0)

random.points <- sampleRandom(bioclim_stack, size = 10000)

correlation.test <- cor(random.points, method = "pearson")

write.csv(correlation.test, "corr.mat.bioclim.stack.csv")
```

2. Acquiring occurrence records from GBIF (subsection 3. 1. 1)

```
## 2. Download occurrence records from GBIF (internet
connection required) (subsection 3.1.1)

# load package "rgbif"

library(rgbif)

# records from Nigeria

Ng <- occ_search(scientificName = 'Tithonia diversifolia',

                 country = "NG", hasCoordinate = TRUE,

                 hasGeospatialIssue = FALSE,

                 eventDate = "1970,2013")

# save a copy

Ng.gbif.occ <- write.csv(Ng$data, "Ng.gbif.occ.csv")

# records from Mexico

Mx <- occ_search(scientificName = 'Tithonia diversifolia',

                 country = "MX", hasCoordinate = TRUE,

                 hasGeospatialIssue = FALSE,

                 eventDate = "1970,2013")

# save a copy

Mx.gbif.occ <- write.csv(Mx$data, "Mx.gbif.occ.csv")

# occurrence records from MEX

Mex.occ <- data.frame(Sp= rep("Tithonia_diversifolia",
nrow(Mx$data)), LON=Mx$data$decimalLongitude,
LAT=Mx$data$decimalLatitude, row.names = NULL)

# load occurence records from NGN, with literature and
herbarium records
```

```
Ng.gbif.occ <- data.frame(Sp= rep("Tithonia_diversifolia",
nrow(Ng$data)), LON= Ng$data$decimalLongitude,
LAT=Ng$data$decimalLatitude, row.names = NULL)

Ng.lit.herb <- read.csv("C:/Users/Maxwell
Obiakara/Desktop/SDM/Occu/Ng_unthinned.csv")

Ng.occ <- rbind(Ng.lit.herb, Ng.gbif.occ)

# check plot

plot(wrld_simpl, xlim=c(-118,15), ylim=c(4,33), axes=TRUE,
col="white")

points(Ng.occ$LON, Ng.occ$LAT, col='red', pch=20,
cex=0.75)

points(Mex.occ$LON, Mex.occ$LAT, col="green", pch=20,
cex=0.75)
```

3. Thinning occurrence records using a distance of 1 Km (subsection 3.1.1)

```
# load package "spThin"

library(spThin)

# thin occurrence records from Nigeria

thinned_occ_Ng <-

  thin( loc.data= Ng.occ, lat.col = "x", long.col = "y",

        spec.col = "Sp",

        thin.par = 1, reps = 100,

        locs.thinned.list.return = TRUE,

        write.files = TRUE,

        max.files = 1, verbose = TRUE,

        out.dir = "Tithonia_thinned_Ng/",

        write.log.file = FALSE,

    log.file = "Tithonia_thin_log_file_Ng.txt")
```

```
# thin occurence records from Mexico using the same
process as above
```

4. MaxEnt Modelling with current and future bioclimatic variables (subsection 3.1.5)

```
#load required packages

library(dismo)

library(ENMeval)

# import thinned presence records

Ng.pres <- read.csv("C:/Users/Maxwell
Obiakara/Desktop/SDM/current_climate/Tithonia_thinned_Ng/t
hinned_data_thin1.csv")

Mx.pres <- read.csv("C:/Users/Maxwell
Obiakara/Desktop/SDM/current_climate/Tithonia_thinned_Mx/t
hinned_data_thin1.csv")

# arrange dataset according to ENMeval specifications

Ng.pres <- Ng.pres[,-1]

names(Ng.pres) <- c("x", "y")

Mx.pres <- Mx.pres[,-1]

names(Mx.pres) <- c("x", "y")

# keep uncorrelated bioclimatic variables and raster
stacks

bioclim_stack <- bioclim_stack[[c(2,7,11,14,15,18,19)]]

# crop to study areas and split Nigeria from Mexico

extent_NGN <- c(2, 15, 4, 14)

extent_MEX <- c(-119, -85, 14, 33)

NGN_range <- crop(bioclim_stack, extent_NGN)

MEX_range <- crop(bioclim_stack, extent_MEX)
```

```
# check plot

plot(NGN_range)

plot(MEX_range)

# Build Mexicanclimatic candidate models

mod.mx.test<- ENMevaluate(occ = Mx.pres, env = MEX_range,
method = "block", rasterPreds = TRUE,parallel = T,
numCores = 3)

# extract results

results_mx <- mod.mx.test@results

head(results_mx[order(results_mx$delta.AICc),])

# Keep a copy

write.csv(results_mx, "mx_eval.csv", row.names = F)

# select the best performing Mexican climatic model based
on AICc and LQHPT feature class combination (the simpler
the better!)

mod_mx <- mod.mx.test@models[[which(results_mx$delta.AICc
== 0 and results_mx$features == "LQH")]]

# project MCM to Mexico and Nigeria (using the recommended
cloglog transformation)

MxToMx <- predict(mod_mx, MEX_range,
args=c("outputformat=cloglog"))

# check plot

plot(MxToMx)

MxToNg <- predict(mod_mx, NGN_range,
args=c("outputformat=cloglog"))

plot(MxToNg)

# export both models

writeRaster(MxToMx, "./MxToMx.asc")
```

```
writeRaster(MxToNg, "./MxToNg.asc")

# Build Nigerian candidate climatic models

mod.ng.test<- ENMevaluate(occ = Ng.pres, env = NGN_range,
method = "block", rasterPreds = TRUE, parallel = T,
numCores = 3)

# extract results

results_ng <- mod.ng.test@results

head(results_ng[order(results_ng$delta.AICc),])

# Keep a copy

write.csv(results_ng, "ng_eval.csv", row.names = F)

# select the best performing NCM model based on AICc and
LQHPT feature class combination

mod_ng <- mod.ng.test@models[[which(results_ng$delta.AICc
== 0 and results_ng$features == "LQHP")]]

# project NCM model to Nigeria and Mexico (using the
recommended cloglog transformation)

NgToNg <- predict(mod_ng, NGN_range,
args=c("outputformat=cloglog"))

# check plot

plot(NgToNg)

NgToMx <- predict(mod_ng, MEX_range,
args=c("outputformat=cloglog"))

plot(NgToMx)

# merge both NCM and rNCM models and plot

merged.ng <- mosaic(NgToNg, MxToNg, fun=max)

plot(merged.ng)

# export all models

writeRaster(NgToNg, "./NgToNg.asc")
```

```
writeRaster(NgToMx, "./NgToMx.asc")

writeRaster(merged.ng, "./merged.ng.asc")

#boyce index using

# load package "ecospat"

library(ecospat)

boyce.index.NgToNg <- ecospat.boyce(NgToNg, Ng.pres,
nclass=0, window.w="default", res=100, PEplot=FALSE)

#Keep a copy

write.csv(boyce.index.NgToNg, "boyce.index.NgToNg.csv")

write.csv(boyce.index.MxToMx, "boyce.index.MxToMx.csv")

#boyce index using model projected models

#boyce index for merged reciprocal models in Nigeria

write.csv(boyce.index.merged.ng,
"boyce.index.merged.ng.csv")

# variable contribution and response curves for both
models

# the following piece of code was written by Dr. Yoan
Fourcade It serves to combine the response curves from
both Ng and Mx models

# set variable names

names.var <- c(

  "Bio 2: Mean Diurnal Range",

  "Bio 7: Temperature Annual Range",

  "Bio 11 : Mean Temperature of Coldest Quarter",

  "Bio 14 : Precipitation of Driest Month",

  "Bio 15 : Precipitation Seasonality",

  "Bio 18 : Precipitation of Warmest Quarter",
```

```
  "Bio 19 : Precipitation of Coldest Quarter")

# find the minimal and maximal values of each variable in
presence and background points of both models, this will
be used to define the range of x values

minVal <-
apply(rbind(apply(rbind(mod_mx@presence,mod_mx@absence),
2, function(x){min(x, na.rm
=T)}),apply(rbind(mod_ng@presence,mod_ng@absence), 2,
function(x){min(x, na.rm =T)})), 2, function(x){min(x,
na.rm =T)})
maxVal <-
apply(rbind(apply(rbind(mod_mx@presence,mod_mx@absence),
2, function(x){max(x, na.rm
=T)}),apply(rbind(mod_ng@presence,mod_ng@absence), 2,
function(x){max(x, na.rm =T)})), 2, function(x){max(x,
na.rm =T)})

# export as tiff

tiff(filename = "Response_plot.tiff", 7.5, 6.5, units =
"in", res = 300, compression = "lzw")

# recursive plot for each variable

par(mfrow = c(3,3), mar = c(4, 4, 2, 2))

for(i in 1:7){

  # call MEX plot first

response(mod_mx, i, col = "#009ACD", xlim =
c(minVal[i]*.9, maxVal[i]*1.08), ann = F, lty = 1)

title(ylab = "Predicted suitability")

title(xlab = names.var[i])

# overlay Nigerian plot

par(new = TRUE)
```

```
  response(mod_ng, i, col = "#EE2C2C", xlim =
c(minVal[i]*.9, maxVal[i]*1.1), ann = F, axes = F, lty =
2)

  # on the first plot, add a legend

  if( i == 1){legend("topright", legend = c("Native
model", "Invasive model"),lty = c(1,2), col = c("#009ACD",
"#EE2C2C"), bty = "n")}}

# close the plot to write the file on the disk

dev.off()

# future projections: Because the main objective is to
assess whether or not there would be a potential
shift/expansion in the future in Nigeria, I merge the
native and invasive models (by keeping the maximum
predicted value) and project them in the future using the
extreme, RCP8.5 of the HaGEM2-CC and MIROC-ESM-CHEM models

# importing future climate data

hadgem <- stack(list.files("C:/Users/Maxwell
Obiakara/Desktop/SDM/future_climate/HadGem", full.names =
T))

miroc <- stack(list.files("C:/Users/Maxwell
Obiakara/Desktop/SDM/future_climate/MIROC", full.names =
T))

# native and invasive models projected in Nigeria for
2041-2060, according to the HadGEM2-CC circulation model
and for the 8.5 RCP

ng.hadgem <- predict(mod_ng, crop(hadgem, NGN_range),
args=c("outputformat=cloglog"))

mx.hadgem <- predict(mod_mx, crop(hadgem, NGN_range),
args=c("outputformat=cloglog"))

projection_HadGEM2_CC <- mosaic(ng.hadgem, mx.hadgem, fun
= max)

plot(projection_HadGEM2_CC)
```

```
writeRaster(projection_HadGEM2_CC,
"projection_HadGEM2_CC.asc")

# native and invasive models projected in Nigeria for
2041-2060, according to the MIROC-ESM-CHEM model and for
the 8.5 RCP

ng.miroc <- predict(mod_ng, crop(miroc, NGN_range),
args=c("outputformat=cloglog"))

mx.miroc <- predict(mod_mx, crop(miroc, NGN_range),
args=c("outputformat=cloglog"))

projection_MIROC_ESM_CHEM <- mosaic(ng.miroc, mx.miroc,
fun = max)

plot(projection_MIROC_ESM_CHEM)

writeRaster(projection_MIROC_ESM_CHEM,
"projection_MIROC_ESM_CHEM.asc")
```

5. MaxEnt Modelling with edaphic variables (subsection 3.1.5)

```
# import soil data from Mx and Ng

soil.ng <- stack(list.files("C:/Users/Maxwell
Obiakara/Desktop/SDM/soil_data/SOIL NGN", full.names = T))

soil.mx <- stack(list.files("C:/Users/Maxwell
Obiakara/Desktop/SDM/soil_data/SOIL MEX", full.names = T))

# Select only variables at 15 cm depth

soil.mx <- soil.mx[[15:21]]

soil.ng <- soil.ng[[15:21]]

# build candidate Edaphic Native models

mod.ng.test.edaph <- ENMevaluate(occ = Ng.pres, env =
soil.ng, method = "block", rasterPreds = TRUE)

mod.mx.test.edaph <- ENMevaluate(occ = Mx.pres, env =
soil.mx, method = "block", rasterPreds = TRUE)

# view and exporting results
```

```
results.ng.edaph <- mod.ng.test.edaph@results

write.csv(results.ng.edaph, "ng.eval.edaph.csv")

results.mx.edaph <- mod.mx.test.edaph@results

write.csv(results.mx.edaph, "mx.eval.edaph.csv")

# select the best performing Ng model based on AICc and
LQHPT feature class combination

mod_ng.edaph <-
mod.ng.test.edaph@models[[which(results.ng.edaph$delta.AIC
c == 0 and results.ng.edaph$features == "H")]]

# projecting invasive model onto Nigeria and Mexico

edaph.NgToNg <- predict(mod_ng.edaph, soil.ng,
args=c("outputformat=cloglog"))

plot(edaph.NgToNg)

edaph.NgToMx <- predict(mod_ng.edaph, soil.mx,
args=c("outputformat=cloglog"))

plot(edaph.NgToMx)

# export both models

writeRaster(edaph.NgToNg, "./edaph.NgToNg.asc")

writeRaster(edaph.NgToMx, "./edaph.NgToMx.asc")

# select the best performing Mx model based on AICc and
LQHPT feature class combination

mod_mx.edaph <-
mod.mx.test.edaph@models[[which(results.mx.edaph$delta.AIC
c == 0 and results.mx.edaph$features == "LQHP")]]

# project invasive model Nigeria and Mexico

edaph.MxToMx <- predict(mod_mx.edaph, soil.mx,
args=c("outputformat=cloglog"))

plot(edaph.MxToMx)
```

```
edaph.MxToNg <- predict(mod_mx.edaph, soil.ng,
args=c("outputformat=cloglog"))

plot(edaph.MxToNg)

# merge both invasive and projected invasive models

merged.ng.edaph <- mosaic(edaph.NgToNg, edaph.MxToNg,
fun=max)

plot(merged.ng.edaph)

# export both models

writeRaster(edaph.MxToMx, "./edaph.MexToMex.asc")

writeRaster(edaph.MxToNg, "./edaph.MexToNg.asc")

writeRaster(merged.ng.edaph, "./merged.ng.edaph.asc")

# variable contribution and response curves for both
models

#boyce index using occurrences in the same area as model
calibration

#Keep a copy

write.csv(boyce.index.edaph.NgToNg,
"boyce.index.edaph.NgToNg.csv")

write.csv(boyce.index.edaph.MxToMx,
"boyce.index.edaph.MxToMx.csv")

#boyce index using model projected models

write.csv(boyce.index.edaph.NgToMx,
"boyce.index.edaph.NgToMx.csv")

write.csv(boyce.index.edaph.MxToNg,
"boyce.index.edaph.MxToNg.csv")

#boyce index for merged reciprocal models in Nigeria

# variable contributions

# set variable names
```

```
names.var <- c("BLDFIE: Bulk density","SNDPPT: Sand
content",

  "SLTPPT: Silt content","CLYPPT: Clay content","PHIHOX:
pH*10","CECSOL: CEC","ORCDRC: Org Carbon Content")

minVal <-
apply(rbind(apply(rbind(mod_mx.edaph@presence,mod_mx.edaph
@absence), 2, function(x){min(x, na.rm =T)}),
apply(rbind(mod_ng.edaph@presence,mod_ng.edaph@absence),
2, function(x){min(x, na.rm =T)})),
2, function(x){min(x, na.rm =T)})

maxVal <-
apply(rbind(apply(rbind(mod_mx.edaph@presence,mod_mx.edaph
@absence), 2, function(x){max(x, na.rm =T)}),
apply(rbind(mod_ng.edaph@presence,mod_ng.edaph@absence),
2, function(x){max(x, na.rm =T)})),
2, function(x){max(x, na.rm =T)})

# export as pdf or tiff for 0 cm depth

tiff(filename = "Response_plot_edaph.tiff", 7.5, 6.5,
units = "in", res = 400, compression = "lzw")

# recursive plot for each variable

par(mfrow = c(3,3), mar = c(4, 4, 2, 2))

for(j in 1:7){

# call MEX plot first

response(mod_mx.edaph, j, col = "#009ACD", xlim =
c(minVal[j]*.9, maxVal[j]*1.08), ann = F, lty = 1)

title(ylab = "Predicted suitability")

title(xlab = names.var[j])

# overlay MGN plot

par(new = TRUE)
```

```
response(mod_ng.edaph, j, col = "#EE2C2C", xlim =
c(minVal[j]*.9, maxVal[j]*1.1), ann = F, axes = F, lty =
2)

# on the first plot, add a legend

if( j == 1){legend("topright", legend = c("Native model",
"Invasive model"),lty = c(1,2), col = c("#009ACD",
"#EE2C2C"), bty = "n")}}

# close the plot to write the file on the disk

dev.off()

# merging climatic and edaphic models

merged.clim.edaph <- mosaic(merged.ng, edaph.MxToNg,
fun=max)

boyce.index.merged.clim.edaph <-
ecospat.boyce(merged.clim.edaph, Ng.pres, nclass=0,
window.w="default", res=100, PEplot=FALSE)

write.csv(boyce.index.merged.clim.edaph,
"boyce.index.merged.clim.edaph.csv")

plot(merged.clim.edaph)

writeRaster(merged.clim.edaph, "./merged.clim.edaph.asc")
```

6. Climatic niche analysis (Subsection 3. 1. 4)

```
# Loading package ecospat if not already loaded

library(ecospat)

# set same extent for both bioclimatic and edaphic
variables

bioclim.ng <- crop(NGN_range, extent(soil.ng))

bioclim.ng <- mask(bioclim.ng, soil.ng)

bioclim.mx <- crop(MEX_range, extent(soil.mx))

bioclim.mx <- mask(bioclim.mx, soil.mx)
```

```
names(soil.mx) <- names(soil.ng) <- c("BLDFIE", "SNDPPT",
"SLTPPT", "CLYPPT","PHIHOX", "CEC", "ORCDRC")

# stack bioclimatic and edaphic variables

ng.stack <- stack(bioclim.ng, soil.ng)

mx.stack <- stack(bioclim.mx, soil.mx)

# generate 10,000 random background points over each range

set.seed(0)

ng.back <- randomPoints(ng.stack, 10000)

mx.back <- randomPoints(mx.stack, 10000)

# extract background environment from each range.

ng.back.env <- na.omit(extract(ng.stack, ng.back))

mx.back.env <- na.omit(extract(mx.stack, mx.back))

# extract species environment from each range

ng.spec.env <- na.omit(extract(ng.stack, Ng.pres))

mx.spec.env <- na.omit(extract(mx.stack, Mx.pres))

# environmental values all together

ng.data.env <-rbind(ng.spec.env, ng.back.env)

mx.data.env <- rbind(mx.spec.env, mx.back.env)

# weight matrices for both ranges

ng.w <- c(rep(1, nrow(ng.spec.env)), rep(0,
nrow(ng.back.env)))

mx.w <- c(rep(1, nrow(mx.spec.env)), rep(0,
nrow(mx.back.env)))

ng.DATA <- data.frame(cbind(ng.w, ng.data.env))

mx.DATA <- data.frame(cbind(mx.w, mx.data.env))

# run PCA on the entire environment (i.e. the merged
native and invasive ranges)
```

```
pca.env <-dudi.pca(rbind(mx.data.env, ng.data.env), scale
=TRUE,center =TRUE,nf =2, scannf =FALSE)

# extract the scores of the whole area, of the native
area, of the invasive area, of the native

# occurrences and of the invasive occurrences

# PCA scores for study extent

scores.global <- pca.env$li

# PCA scores for the species indigenousrange

scores.sp.mx <-
suprow(pca.env,mx.DATA[which(mx.DATA[,1]==1),-1])$li

# PCA scores for the species invasive distribution

scores.sp.ng <-
suprow(pca.env,ng.DATA[which(ng.DATA[,1]==1),-1])$li

# PCA scores for entire indigenous study extent

scores.mx <- suprow(pca.env,mx.DATA[,-1])$li

# PCA scores for the entireintroduced range

scores.ng <- suprow(pca.env,ng.DATA[,-1])$li

# grid native and invasive environments

grid.mx <- ecospat.grid.clim.dyn(glob=scores.global,
glob1=scores.mx,sp=scores.sp.mx, R=200,th.sp=0)

grid.ng <-
ecospat.grid.clim.dyn(glob=scores.global,glob1=scores.ng,s
p=scores.sp.ng, R=200,th.sp=0)

## Niche dynamics indices

niche.dyn <- ecospat.niche.dyn.index(grid.mx,
grid.ng)$dynamic.index.w

niche.dyn

# Niche overlap
```

```
niche.ov <- ecospat.niche.overlap(grid.mx, grid.ng, cor
=T)

niche.ov

# Niche Equivalency test with recommended minumum of 1000
replications

eq.test <- ecospat.niche.equivalency.test(grid.mx,
grid.ng,

                    rep=100, alternative = "lower")

eq.test

# Niche Similarity Test

sim.test <- ecospat.niche.similarity.test(grid.mx,
grid.ng,

            rep=100, alternative = "lower",rand.type=2)

sim.test

#Plot equivalency and similarity tests

tiff("eq.sim.tests.NG-MEX.tif", 8, 4.5, units = "in", res
= 500, compression = "lzw")

par(mfrow=c(1,2))

ecospat.plot.overlap.test(eq.test, "D", "Equivalency")

ecospat.plot.overlap.test(sim.test, "D", "Similarity")

dev.off()

# export plot showing the niche dynamics between native
and invasive ranges

tiff("niche.tiff", 7, 4.5, units = "in", res = 500,
compression = "lzw")

layout(matrix(c(1,1,1,1,1,1,2,2,2,2), ncol = 5, nrow = 2))

ecospat.plot.niche.dyn (grid.mx, grid.ng, quant = .5,
interest=2,colZ1 = "green", colZ2 = "red",colz1 =
```

```
"orange", colz2 = 'deepskyblue2', colinter = "black",
name.axis1 = "PC 1", name.axis2 = "PC 2")

legend("bottomleft", legend = c("Niche unfilling = 0.99",
"Niche expansion = 0.99", "Overlap = 0.01"), fill =
c("orange", "deepskyblue2", "black"), bty = "n", cex =
1.2, border = "white")

ecospat.shift.centroids(scores.sp.mx, scores.sp.ng,
scores.mx, scores.ng)

s.corcircle(data.frame(pca.env$co, pca.env$eig), grid = F,
clabel = 1.5)

title(xlab = paste("PC 1 = ",
round(pca.env$eig[1]/sum(pca.env$eig) * 100, 2), "% ; ",
"PC 2 = ", round(pca.env$eig[2]/sum(pca.env$eig) * 100,
2), "%"), line = 2)

dev.off()

####### End of sript #######
```

Appendix 5: Species abundance from soil seed banks associated with *T. diversifolia*

S/No.	Species	Invaded					Non-invaded				
		Abuja	Asaba	Ibadan	Ilorin	Jos	Abuja	Asaba	Ibadan	Ilorin	Jos
1	*Acalypha fimbriata* Schum. & Thonn.	0	0	10	5	0	0	0	6	0	0
2	*Ageratum conyzoides* Linn.	0	0	3	31	38	0	0	40	2	13
3	*Alternathera sessilis* (Linn.) DC.	0	0	48	0	0	0	0	53	0	5
4	*Amaranthus spinosus* Linn.	0	3	0	5	0	0	0	1	0	19
5	*Andropogon gayanus* Kunth.	0	0	0	0	0	0	2	0	0	0
6	*Asystasia gangetica* (Linn.) T. Anders	0	0	0	0	0	0	0	1	0	0
7	*Bacopa decumbens* (Fernald) F.N. Williams	0	3	0	0	0	0	3	0	52	0
8	*Bidens pilosa* Linn.	0	0	0	0	1	0	0	0	0	1
9	*Boerhavia erecta* Linn.	0	0	1	0	0	1	0	0	0	0
10	*Brachiara deflexa* (Schumach.) C.E. Hubbard ex Robyns	0	1	0	0	0	0	0	0	0	0
11	*Brachiara lata* (Schumach.) C.E. Hubbard	6	0	0	2	0	4	3	0	0	0
12	*Celosia leptostachya* Benth.	1	0	0	0	0	7	0	0	0	0

Appendix 5: Species abundance from soil seed banks associated with *T. diversifolia*(Continued)

S/No.	Species	Invaded					Non-invaded				
		Abuja	Asaba	Ibadan	Ilorin	Jos	Abuja	Asaba	Ibadan	Ilorin	Jos
13	*Cenhrus biflorus* Roxb.	0	0	0	0	0	0	0	1	0	0
14	*Centrosema molle* Mart. ex Benth	0	0	0	0	0	0	0	1	0	0
15	*Chamaecrista mimosoides* (L.) Greene	0	0	0	0	0	0	0	0	1	0
16	*Chromolaena odorata* (L.) R.M. King & Robinson	0	0	2	0	0	0	0	1	0	11
17	*Croton lobatus* Linn	0	0	0	4	0	2	0	1	0	0
18	*Cynodon dactylon* (Linn.) Pers.	0	0	0	0	1	0	87	0	4	0
19	*Cyperus amabilis* Vahl.	0	0	0	7	0	0	1	0	4	0
20	*Cyperus iria* Linn	0	0	0	0	0	9	0	0	0	0
21	*Cyperus longibracteatus* Cherm.	0	0	1	0	0	0	0	11	0	4
22	*Cyperus rotundus* Linn.	0	3	0	0	9	0	0	0	7	2
23	*Cyperus tuberosus* Linn.	0	0	7	0	0	2	0	5	0	0
24	*Dactyloctnium aegyptum* (Linn.) P. Beauv.	0	0	0	0	0	0	0	0	4	0

Appendix 5: Species abundance from soil seed banks associated with *T. diversifolia*(Continued)

S/No.	Species	Invaded					Non-invaded				
		Abuja	Asaba	Ibadan	Ilorin	Jos	Abuja	Asaba	Ibadan	Ilorin	Jos
25	*Digitaria ciliaris* (Retz.) Koel.	0	0	6	0	0	0	0	0	10	0
26	*Digitaria horizontalis* Willd.	0	0	20	0	0	0	0	1	0	0
27	*Digitaria nuda* Schumach.	0	0	0	10	1	2	1	3	51	0
28	*Eleusine indica* L. Gaertn.	2	3	0	0	9	1	10	1	1	2
29	*Eragrostis tremula* Hochst. ex Steud.	0	0	0	0	0	2	0	0	0	0
30	*Euphorbia hyssopifolia* Linn.	0	0	4	14	0	1	3	0	26	0
31	*Fleurya aestuans* [Linn.] ex Miq.	0	0	49	2	0	0	0	6	0	0
32	*Galinsoga parviflora* Cav	0	0	0	0	47	0	0	0	0	43
33	*Gomphrena celosiodes* Mart.	0	0	0	0	0	0	0	0	21	0
34	*Heliotropium ovalifolium* Forssk.	0	1	0	0	0	0	0	0	0	0
35	*Hyptis suaveolens* Poit	1	0	1	0	0	2	0	1	0	0
36	*Kyllinga erecta* Schumach	0	0	5	0	0	0	0	2	0	0

Appendix 5: Species abundance from soil seed banks associated with *T. diversifolia* (Continued)

S/No.	Species	Invaded					Non-invaded				
		Abuja	Asaba	Ibadan	Ilorin	Jos	Abuja	Asaba	Ibadan	Ilorin	Jos
37	*Lindernia crustacea* (L.) F. Muell.	0	0	0	0	0	0	0	7	1	0
38	*Ludwigia abyssinica* A. Rich	1	0	0	84	0	0	0	0	21	17
39	*Ludwigia decurrens* Walt.	0	0	0	0	1	0	0	0	0	0
40	*Ludwigia hyssopifolia* (G. Don) Exell	0	0	0	0	0	0	0	0	0	1
41	*Mimosa invisa* Mart.	0	0	0	0	0	0	0	1	0	0
42	*Mollugo nudicaulis* Lam.	0	9	0	10	0	1	1	0	3	0
43	*Oldenladia corymbosa* Linn.	0	5	99	16	0	0	1	57	12	46
44	*Oldenladia lancifolia* (Schumach.) D.C.	0	0	0	0	0	0	1	0	0	0
45	*Panicum maximum* Jacq.	0	12	2	1	0	0	1	2	2	0
46	*Panicum repens* Linn	0	0	0	0	4	0	1	0	0	0
47	*Paspalum scrobiculatum* Linn.	0	0	0	0	0	0	1	0	0	0
48	*Passiflora foetida* Linn.	0	0	0	1	0	0	0	0	1	0

Appendix 5: Species abundance from soil seed banks associated with *T. diversifolia*(Continued)

S/No.	Species	Invaded					Non-invaded				
		Abuja	Asaba	Ibadan	Ilorin	Jos	Abuja	Asaba	Ibadan	Ilorin	Jos
49	*Pepperomia pellucida* (L.) H.B. & K.	0	0	0	0	0	0	0	27	0	0
50	*Phylanthus amarus* Schum. & Thonn.	0	0	1	12	0	0	0	2	14	0
51	*Physalis angulata* Linn	0	0	5	0	0	0	0	0	0	0
52	*Portulaca oleracea* Linn.	0	0	6	4	0	0	0	16	11	4
53	*Pouzolzia guineensis* Benth.	0	0	0	1	1	0	0	0	0	0
54	*Pycreus lanceolatus* (Poir.) C.B. Clarke	0	0	0	1	0	3	0	0	0	0
55	*Setaria barbata* (Lam.) Kunth.	0	0	2	0	0	0	0	2	0	1
56	*Setaria longiseta* P. Beauv.	0	0	6	0	0	0	0	0	0	0
57	*Setaria pumila* (Poir) Roem & Schult.	0	0	7	1	0	0	0	0	3	1
58	*Sida acuta* Burn. f.	0	0	0	0	0	0	0	11	0	0
59	*Sida garckeana* Polak.	0	2	0	0	0	0	1	0	0	0
60	*Sida rhombifolia* Linn.	0	0	0	0	0	0	0	0	0	3

Appendix 5: Species abundance from soil seed banks associated with *T. diversifolia* (Continued)

S/No.	Species	Invaded					Non-invaded				
		Abuja	Asaba	Ibadan	Ilorin	Jos	Abuja	Asaba	Ibadan	Ilorin	Jos
60	*Sida rhombifolia* Linn.	0	0	0	0	0	0	0	0	0	3
61	*Solanum erianthum* D. Don	0	0	1	0	1	0	0	0	0	1
62	*Spermacoce ocymoides* Burm. f.	0	2	2	0	0	5	0	8	2	0
63	*Spigelia anthelmia* Linn.	0	0	16	6	0	0	0	0	5	0
64	*Spilanthes costata* Benth.	0	0	1	1	0	0	0	56	5	15
65	*Synedrella nodiflora* Gaertn.	0	0	0	0	2	0	0	0	0	0
66	*Talinum triangulare* (Jacq.) Willd.	0	0	0	0	0	0	0	4	0	0
67	*Tithonia diversifolia* (Hemsl) A. Gray	0	2	14	9	0	0	0	2	0	0
68	*Tridax procumbens* Linn.	0	0	1	0	0	0	0	0	1	0
69	*Vernonia ambigua* Kotschy & Peyr	0	0	0	0	0	0	0	0	0	4

Appendix 6: Seed bank density of model of *T. diversifolia* as a function of time

Coefficients	Estimate¤	Standard error	*P*value	R^2
Intercept (s_0)	49.4	1.32	0.001	0.95
Slope (*b*)	-0.89	0.12	0.004	
Coefficients	Estimate¤	Standard error	*p* value	R^2
Intercept (s_0)	49.4	1.32	0.001	0.95

Exponential regression ($s = s_0 e^{-bt}$) of seed bank density of *T. diversifolia* (s) as a function of time (t). R^2 : Determination coefficient.Estimates are means based on n = 12 quadrats.