ECOLOGICAL IMPACTS OF *PROSOPIS* INVASION IN RIVERINE FORESTS OF KENYA

Gabriel Mukuria Muturi

Thesis committee
Thesis supervisor
Prof. dr. ir. G.M.J. Mohren
Professor of Forest Ecology and Forest Management,
Wageningen University

Thesis co-supervisors
Dr.ir. L. Poorter
Associate professor, Forest Ecology and Forest Management Group
Wageningen University

Dr. B.N. Kigomo
Deputy Director, Research and Development
Kenya forestry Research Institute

Other members
Prof.dr. M. Herold, Wageningen University
Prof.dr. M. van Kleunen, University of Konstanz
Prof.dr. T.M. Kuyper, Wageningen University
Dr. W.F. de Boer, Wageningen University

This research was conducted under the auspices of the C.T. de Wit Graduate School of Production Ecology and Resource Conservation (PE&RC)

ECOLOGICAL IMPACTS OF *PROSOPIS* INVASION IN RIVERINE FORESTS OF KENYA

Gabriel Mukuria Muturi

Thesis
submitted in fulfillment of the requirements for degree of doctor
at Wageningen University
by the authority of Rector Magnificus
Prof.dr. M.J. Kropff
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Wednesday 5 September 2012
at 1.30 p.m. in the Aula.

Gabriel Mukuria Muturi
Ecological impacts of *Prosopis* invasion in Riverine forests of Kenya

Thesis, Wageningen University, Wageningen, NL (2012)
With references, with summaries in English and Dutch

ISBN: **978-94-6173-402-0**

To my parents: Mr. John Muturi Njehu & Mrs Anastacia Wanja Muturi for taking me to school and encouragements in the academic life.

To my wife Beatrice, and Children Winnie, Yvonne, John, Leah and Abigail for your understanding during my absence while pursuing this study.

To all those who be inspired by this Thesis to advance academically.

Abstract

Prosopis chilensis, Prosopis juliflora and *Prosopis pallida* were widely introduced in tropical drylands, where they have become naturalized and invasive. Invasion management is partially hampered by species misidentification because of morphological similarities between species and between species and their hybrids. In Kenya, species identification is even more challenging as several species were introduced within sites. Since biological invasions are invoked by either the susceptibility of a habitat to invasion (invasibility) or the invasive traits of a species (invasiveness), proper knowledge of these two factors is required for proper invasion management. In this dissertation, we used field, greenhouse and laboratory studies to: 1) evaluate invasibility of Turkwel riverine forest, and 2) invasiveness of *Prosopis* species by determining: 2) ecological impacts of *Prosopis* invasion, 3) underlying mechanisms for observed ecological impacts and 4) species composition and genetic diversity of *Prosopis* populations in Kenya.

Invasibility was evaluated by comparing *Prosopis* occurrence between undisturbed invasion resistant forests with invasion susceptible forest gaps; ecological impacts of *Prosopis* invasion determined by comparing herbaceous species and tree regeneration among *Acacia tortilis*, *Prosopis* and a mixture of *A. tortilis* and *Prosopis* species canopies; underlying mechanisms of observed ecological impacts determined by assessing the impact of *A. tortilis* and *Prosopis* litter on *A. tortilis* and *Prosopis* species seed germination and seedling growth; and species composition and genetic diversity of Kenyan *Prosopis* populations determined by comparing Kenyan populations at Bamburi, Bura, Isiolo, Marigat, Taveta and Turkwel with *P. chilensis, P. juliflora* and *P. pallida* references for relatedness and genetic diversity.

We found that both the forest and the forest gaps were equally susceptible to *Prosopis* invasion, suggesting that invasion was spontaneous and independent of the assumed habitat invasibility variation. The ecological impact study revealed reduction of ground vegetation cover, herbaceous species diversity and termination of *A. tortilis* regeneration by *Prosopis*. Termination of *A. tortilis* regeneration may be attributed to strong reduction of *A. tortilis* and *Prosopis* species seed germination by increasing *Prosopis* litter concentration in the

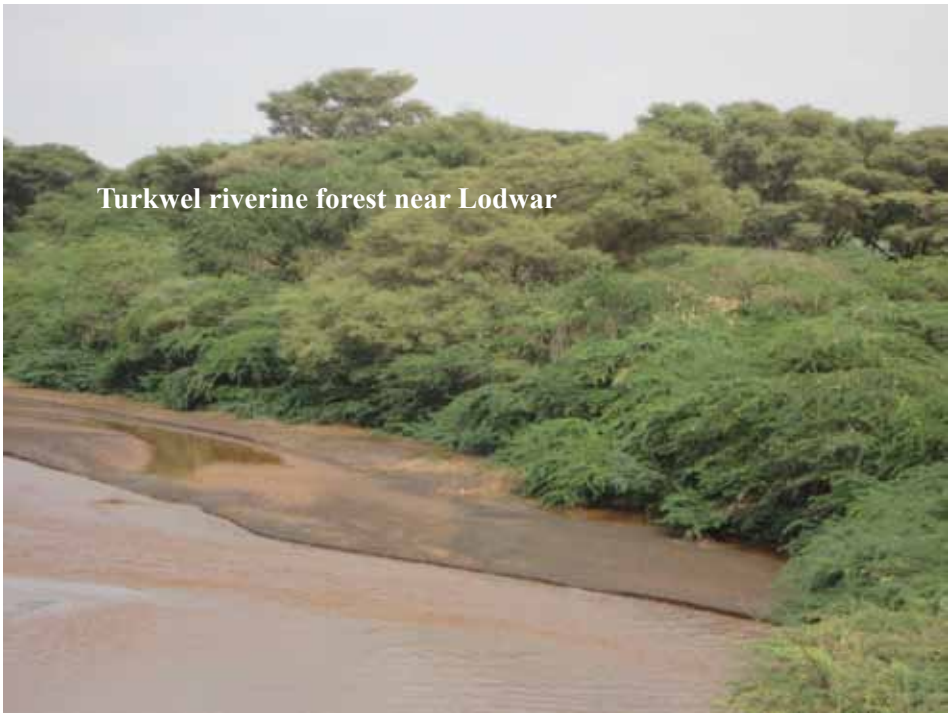
soil in greenhouse studies. Relatedness studies between the Kenya *Prosopis* populations and the reference species revealed the clustering of *P. chilensis* with Taveta population, *P. juliflora* with Bura, Marigat and Isiolo and *P. pallida* with Bamburi. Results suggested that Turkwel population was a likely hybrid between *P. chilensis* and *P. juliflora.* Genetic diversity of populations at Bamburi, Isiolo and Marigat was higher than that of the reference species that they clustered with. Bamburi, Isiolo, Taveta and Turkwel populations revealed genetic uniqueness, as demonstrated by generation of private markers by a specific primer in each of the population. *Prosopis juliflora* and its hybrid occurred in areas currently classified as most invaded.

Based on the results, we concluded that *P. juliflora* and its hybrid are the most aggressive invaders and that riverine forest invasion was invoked more by species invasiveness and not habitat invasibility. The invasiveness traits found in our study were: 1) Allelopathy of *Prosopis* litter which reduces herbaceous species ground vegetation cover and herbaceous species diversity; and inhibited regeneration of *A. tortilis*. 2) Unique site adaptations of introduced germplasm evident from the genetic differentiation of introduced germplasm depending on site, and 3) hybridization that was evident from a *P. chilensis –P. juliflora* hybrid in Turkwel.

Contents

Chapter 1

Introduction



Turkwel riverine forest near Lodwar

Drylands degradation, desertification and mitigation

Drylands are globally important, as they occupy 41% of the world land surface. The majority of the drylands are found in Africa and Asia (each accounting for 32% of the global total), whereas the remainder is distributed over, Australia, Europe, North America and South America (Table 1.1). According to Sombroek et al., (1982), drylands occupy 87% of the total land in Kenya (Table 1.1). Of the Kenyan drylands, 46% are classified as very arid, 22% as arid, 15% as semi-arid and 5% as semi humid to semi-arid (Sombroek et al., 1982). In both Africa and Asia, over 40% of the population lives in drylands, compared to 25 – 30% in other continents (White and Nackoney 2003). In Kenya, drylands support 30% of human population and 70% of livestock and the bulk of wildlife that supports the tourism sector (GoK 2007).

Pastoralism is the main economic activity in drylands, whereas agropastoralism is also practiced but has high incidents of crop failures (Darkoh 1998, Speranza et al., 2008 Eriksen and Lind 2009). As livestock depends on the natural range resource and crop failure is frequent, then local communities rely more on natural resources for livelihoods than on crop production (Eriksen and Lind 2009, Sietz et al., 2011). Because of overstocking, the range resource is often degraded. Resource degradation is further exacerbated by cyclic droughts (Darkoh 1998, UNEP 2000, Dregne 2002). Land degradation in drylands, also called desertification, leads to loss of biological productivity (Dregne 2002). Land degradation includes vegetation deterioration, soil erosion by wind and water, and salinization of water and soil. Because these environmental challenges are widespread (Darkoh 1998, Dregne 2002), the United Nations Convention to combat desertification was specifically dedicated to mitigate desertification.

The introduction of drought tolerant multipurpose trees and shrubs has been an important tool to mitigate large-scale loss of ground vegetation cover in drylands. Trees from the genus *Prosopis* were extensively introduced in many tropical drylands (Pasiecznik et al., 2001), because they met the criteria of environmental stresses tolerance, fast growth, soil amelioration, fodder provision and fuelwood supply (Rosenschein et al., 1999, Pasiecznik et al., 2001, Gallaher and Merlin 2010). *Prosopis* species are now naturalized in many introduced regions where they have become invasive (Zimmerman 1991, Pasiecznik et al., 2001, Shiferaw et al., 2004, van Klinken et al, 2006, Mwangi and Swallow 2008).

Biological invasions

Biological invasion is defined as the movement of a species beyond its natural range as result of anthropogenic factors or a natural process (Lockwood et al., 2007). However, most biological invasions are anthropogenic, either through intentional or accidental introductions. Patterns of plant invasions are conceptualized around invasiveness and invasibility (Erfmeier and Bruelheide 2010, Warren et al., 2011). Invasiveness deals with attributes such as fast growth rates, prolific seeding, allelopathy and hybridization that make a species invasive (Shiferaw et al., 2004, Callaway and Ridenour 2004, Schierenbeck and Ellstrand 2009, Dawson et al., 2011). On the other hand, invasibility deals with characteristics such as absence of natural enemies, resource availability and the conditions of physical environment that makes a habitat/ community susceptible to invasion (Lockwood et al, 2007, van Kleunen et al., 2010). Although conceptually differentiated, invasiveness and invasibility are not mutually exclusive as there are many overlaps among invasion mechanisms (van Kleunen et al., 2010). Species that out-compete other species through any or combination of invasiveness attributes are more invasive than those that co-exist with other species. Regions that have more non-native species are more invasible than areas with fewer invasive alien species (Lockwood et al., 2007).

Propagule pressure, colonization pressure and genetic diversity

Invasion is initiated by the arrival of a propagule to a site. A propagule is any material by which plants regenerate and includes seeds, cuttings and rhizomes. In invasion ecology, the definition of a propagule is expanded to include individual organisms (Lockwood et al., 2007). Also, propagule pressure is a commonly used inclusive term for frequency, size, spatial and temporal patterns of propagules arrival when dealing with a single species (Lockwood et al. 2009, Simberloff 2009). On the other hand, colonization pressure is commonly used in reference to the frequency, size, spatial and temporal patterns of propagules arrival when dealing with several species (Lockwood et al 2009). Propagule pressures increases the probability of invasive species establishment as some propagules within the pool may adapt to the prevailing environmental conditions even if others fail to adapt (Lockwood et al., 2009, Pairon et al., 2010. In addition, repeated spatial and temporal arrival of propagules to a site increases the establishment probability through mitigation of spatial and temporal establishment barriers (Blackburn et

al., 2011, Warren et al., 2011). If propagules are sourced from formerly separated geographical regions, hybridization and gene introgression (back-crossing or mating of interspecific hybrids with either parent) increases genetic diversity and invasiveness (Martinez-Ghersa and Ghersa 2006, Lockwood et al., 2009, Pairon et al., 2010). Nevertheless, invasiveness may increase without an increase in genetic diversity if some introduced genotypes are not adapted and are selectively eliminated by prevailing environmental factors (Hunzinker et al., 1986, Besnard et al, 2007).

After establishment, invasive species may sustain propagule pressure by changing their reproductive biology; for example by early reproductive maturity, prolific seeding, seed dispersal efficiency, persistent accumulation of large viable seed banks and coppicing (Shiferaw et al., 2004, Gibson et al., 2011, Mworia et al., 2011). The invaded range is therefore retained through regeneration by coppicing and seed, whereas the invasion range is expanded by long-distance seed dispersal and long -term seed viability. These characteristics have been demonstrated in *Prosopis* species that are invasive in Ethiopia, Kenya and Saudi Arabia (Shiferaw et al., 2004, El-Keblawy Al-Rawai 2005, Mworia et al., 2011).

Enemy release

Population explosions in exotic species can occur due to lack of predation (Blossey and Notzold 1995, Vila et al., 2005). The "evolution of increased competitive ability" hypothesis may explain invasiveness as a result of enemy escape (Blossey and Notzold 1995). This hypothesis postulates that exotic plants allocate resources required for defence to growth, once they are freed from their natural enemies. As the introduction involves genetically diverse germplasm, those varieties that invest more resources to defence against non-existent enemies are classified as less adapted, and are naturally outcompeted by varieties that invest more in growth and reproduction. This hypothesis has been tested in a number of studies with contrasting results (e.g. McKenney et al., 2007, Franks et al., 2008, Zou et al., 2008, MacDonald and Kotanen 2010). However, it is generally found that alien invasive species tend to outperform native species in seed production e.g. in *A. tortilis* and *P. juliflora* (Witkowski and Garner 2000, Shiferaw et al., 2004). This may increase their establishment success, compared to the native species.

In nearly all the introduced landscapes, including Kenya *Prosopis* species are not yet prone to resident pests. Consequently, biological control initiatives are dependent on introduction of bio-control agents from their native range (Zimmerman 1991, Coetzer et al., 1997). Moreover, the species are not yet fully utilized for the purpose they were introduced, either because of lack of knowledge on utilization or due to poor quality of introduced germplasm (Pasiecznik et al., 2001), hence population expands very quickly in introduced environments (van Klinken et al., 2006).

Hybridization and polyploidy

Hybridization may produce more adaptive progenies, eliminate less adaptive genes and increase genetic diversity which contributes to invasiveness (Ellstrand and Schierenbeck 2006, Schierenbeck and Ellstrand 2009). For example, compared to their progenitors, sunflower hybrids have an expanded habitat range (Rieseberg et al., 2007), Mahonia hybrids have higher growth (Ross and Auge 2008), and *Schinus terebinthifolius* Raddi hybrids have both higher germination rates and seedling growth rates in (Geiger et al., 2011). There is a lot of evidence for *Prosopis* species hybridization within the natural range (Vega and Hernandez 2005, Landeras et al., 2006) and invasiveness of *Prosopis* hybrids in introduced environments (Zimmerman 1991, van Klinken et al., 2006). Five of the *Prosopis* species that were introduced to Kenya (*P. alba*, *P. chilensis*, *P. juliflora, P. nigra* and *P. pallida*) hybridize (Hunziker et al. 1986, Vega and Hernandez 2005, Landeras et al., 2006). Therefore, it is plausible that *Prosopis* hybrids exist in Kenya.

Polyploidy (whole genomic duplication) can alter plant's genetic make –up, morphology, physiology and ecology within one or a few generations; and increase invasiveness through pre-adaptation, evolution of invasiveness, restoring sexual reproduction following hybridization or conversely and asexual reproduction in the absence of suitable mates (te Beest et al., 2011). As in hybridization, poploidy increases genetic diversity in which the haploid (2n) plants have lower genetic diversity than polyploidy (3n, 4n etc.) plants. *Prosopis juliflora* is polyploidy (Trenchard et al., 2008) and is the most invasive *Prosopis* species in the tropics (http://www.issg.org/database/welcome/).

Allelopathy

Allelopathy is the direct or indirect negative effect of biochemical compounds released to the soil by a plant species on another plant species (Callaway and Ridenour 2004, Inderjit et al., 2011). The "novel weapons hypothesis" (Callaway and Ridenour 2004) suggests that biochemicals from invasive aliens have more severe impacts on native species of invaded areas, than biochemical effects of native species that have co-evolved within a site. Severe biochemical effects of biochemical from invading species may arise from increased biochemical concentrations of as invasive species adapt to new environments or a lack defence mechanisms of native species in the invaded areas. For example, *Alliaria petiolata* Cavara & Grande is more limiting to soil mycorrhiza in introduced range in North America than in its native range in Europe (Callaway et al., 2008). Consequently, ecological benefits of plants- mycorrhizal association would be more adversely affected in North America than in Europe. Similarly, *Ageratina adenophora* (Spreng.) R.M.King & H.Rob. varieties that invaded areas in China and India had higher concentration of litter volatile chemicals than varieties in their native range in Mexico, and their chemicals are more lethal than those of varieties in the native range (Inderjit et al. 2011). Although *Prosopis* species are allelopathic to herbaceous species (Goel et al., 1989, Noor et al., 1995), their effects on trees are still not well understood.

Overview of *Prosopis* Species invasion in Kenya

Prosopis invasions are complex, because of the large variation in invasive traits amongst most species in the genus, and their hybrids. According to the global invasive database (http://www.issg.org/database/welcome/) *Prosopis glandulosa* Torr. and *Prosopis velutina* Wooton are most invasive in subtropics, whereas *P. juliflora* and *P. pallida* are most invasive in the tropics. Often, people perceive *Prosopis* species invasions with mixed reactions depending on what is affected by the invasion and the level of awareness of species management and utilization (Pasiecznik et al., 2001). For example, In Sudan and India the benefits and costs of *P. juliflora* differs amongst stakeholders (Laxen 2007, Walter 2011); pastoralists benefit most from fodder whereas farmers incur losses from clearing farmlands. Overall, the benefits have outweighed the costs in both countries, and *P. juliflora* is a significant livelihood component for the majority of rural people

as it provides fuelwood and fodder. Surprisingly, the species has even acquired sacred status in some parts of India.

Although the history of *Prosopis* species introduction in Kenya is rather unclear, dryland rehabilitation with *Prosopis*, occurred specially after the prolonged Sudano-Sahelian drought of 1970's (Pasiecznik et al., 2001, Ngunjiri and Choge 2004, Mwangi and Swallow 2008). Like other woodland resources in drylands, *Prosopis* species were unmanaged. Subsequently, unprecedented natural seed dispersal by livestock, wildlife and water lead to their spread to other areas (Mwangi and Swallow 2008, Mworia et al., 2011). Riverine forests and seasonal wetlands are the areas that are most invaded by *Prosopis* in Kenya (Stave et al., 2003, Mwangi and Swallow 2008, Mworia et al., 2011). For example, *Prosopis* invasion and decline of the previously dominant *Acacia tortilis* Hayne were first noted in the Turkwel riverine forest in 1998 (Stave et al., 2003). Since then, Turkwel riverine forest has become more invaded (Ngunjiri and Choge 2004).

Unlike in India and Sudan, the negative impacts of *Prosopis* invasion have outweighed benefits in Kenya (Ngunjiri and Choge 2004, Mwangi and Swallow 2008). Negative impacts of *Prosopis* invasion include irritable thorns, livestock deaths, loss of pastures and farmlands. The benefits include bee forage, fuelwood and environmental amelioration. Therefore, both negative and positive impacts may occur, and their relative importance and value is context dependent. To maximize benefits and reduce negative impacts, *Prosopis* management was included in government policy (GoK 2007) and the species were declared noxious weeds in 2008. Government policy recommends management through utilization, and this requires proper knowledge of the invading species, invasion trends, and the impacts of invasion.

Grey and published literature suggests that at least eight *Prosopis* species were introduced to Kenya; *Prosopis alba* Griseb., *Prosopis chilensis* Stuntz., *Prosopis cineraria* Druce, *Prosopis juliflora* (Sw.) D.C., *Prosopis pallida* Kunth, *Prosopis pubescens* Benth. *Prosopis nigra* Hieron. and *Prosopis tamarugo* Phil. (Barrow, 1980, Herlocker et al., 1980, Maghembe et al., 1983, Rosenschein et al., 1999, Otsamo et al., 1993, Stave et al., 2003, KFSC unpublished). In some sites, several species and their provenances were introduced (Maghembe et al., 1983, Otsamo et al., 1993, Rosenschein et al., 1999). The introduced species belong to sections; Agarobia (*Prosopis alba* Griseb., *Prosopis chilensis* Stuntz, *Prosopis juliflora* (Sw.) DC, *Prosopis nigra* Hieron, and *Prosopis pallida* Kunth),

Strombocarpa (*Prosopis pubescens* Benth. and *Prosopis tamarugo* Phil.) and Prosopis (*Prosopis cineraria* Druce) (Burkart 1976).

Prosopis chilensis, *P. pallida* and *P. juliflora* from Algarobia section were the most widely introduced species (Maghembe et al., 1983, Rosenschein et al., 1999, Otsamo et al., 1993). These species and their hybrids are difficult to differentiate morphologically (Saidman et al., 1996, Pasiecznik et al., 2001, Vega and Hernandez 2005). Although *P. chilensis* is not invasive in the tropics, it hybridizes readily with other species in Algarobia section (Hunziker et al., 1986, Landeras et al., 2006, Sherry et al., 2011) and hybridization is an acknowledged invasion stimulus (Shierenbeck and Ellstrand 2009, Pairon et al., 2010). Thus despite the tendency to attribute Kenyan invasions to *P. juliflora* (Pasiecznik et al., 2001, Ngunjiri and Choge 2004, GoK 2007, Mwangi and Swallow 2008, Mworia et al., 2011), invasion may also arise from *P. pallida* that is also present (Trenchard et al., 2008), and *P. chilenis* hybrids. This is more likely so in the invasion hotspots such Bura, Marigat and Turkwel where two or all the three species were introduced (Otsamo et al., 1993, Rosenschein et al., 1999, Oba et al., 2001). A conceptual framework on biological invasion with regard to Prosopis species invasion in Kenya is shown in Figure 1.1

Overview of invasibility of drylands riverine forests in Kenya

In Kenya, drylands are from an ecological and socio-economic point of view very vulnerable (Sietz et al., 2011). Ecological vulnerability is attributed to droughts, soil degradation and vegetation deterioration. Socio-economic vulnerability is attributed isolation, lack of infrastructure and poverty. Ecological vulnerability is exacerbated by resource overexploitation. For example, over 80% of charcoal, the main source of energy in Kenya is obtained from drylands (Kituyi 2004, Bailis 2009). According to UNEP (2000), charcoal production is almost the only viable livelihood option during prolonged droughts. During such period, charcoal production is a survival means that has little or no regard to environmental conservation. Because of the cyclic nature of droughts (Darkoh 1998, UNEP 2000) charcoal production has transformed into a permanent economic activity. Consequently, drylands have become charcoal mines with severe land degradation consequences (Kituyi 2004). Riverine forests have the highest wood resource (Adams 1989) and are not spared from charcoal mining.

Traditionally, the ecological resilience of drylands ecosystems was partly achieved through seasonal movements between pastures (Macpherson 1995, Sitters et al., 2009). This has been replaced by sedentarization and the tradition of keeping large stocks (previously sustained by seasonal movements) retained within settlements. Provisions of health care and veterinary services have accelerated human and livestock populations' growth thereby raising the demand for wood resources and pastures. This has in turn led to resource degradation that intensifies towards the settlement centres (Okoti et al, 2004, Kariuki et al., 2007). As settlements are normally located near water sources, the riverine forests have suffered tremendous resource degradation from overexploitation, shifting cultivation or irrigation abandonment (Oba et al., Mworia et al., 2011).

Description of study sites

Research was carried out in the Turkwel riverine forest that extends 0.5-3 km on either side of the river (Stave et al., 2005). The forest lies within the dry Turkana District which is characterized by low erratic rainfall, high temperatures and high potential evapotranspiration (Sombroek et al., 1980). Rainfall is bimodal, with peaks around April and November (Stave et al., 2007). Mean annual rainfall ranges from 500 mm upstream to less than 200 mm downstream, with large variations between years (Reid and Ellis 1995, Stave et al., 2007). Riverine forest soils are classified as calcaric fluvisols, are well drained and predominantly alluvial deposits (Sombroek et al., 1980, Van Bremen and Kinyanjui 1992). The riverine forest was dominated by *A.tortilis*, with *Faidherbia albida* (Delile) A.Chev*, F. sycomorus* and *Hyphaene compressa* H. Wendl. as sub dominants (Adams 1989, Stave et al., 2007), but *Prosopis* species occurrence has increased since 1998 (Stave et al., 2003, Muturi et al., 2010).

The riverine forest is intercepted by irrigation schemes such as Katilu and Turkwel irrigation schemes (Browne and Gans 1981). Other social economic activities along the riverine forest include pastoralism, shifting cultivation, charcoal burning and palm harvesting for basketry and thatch (Barrow 1990, Stave et al., 2001). Turkwel river was dammed in 1990 (Stave et al., 2005). All these anthropogenic factors have impacted on the forest ecology.

The studied *Prosopis* population along the Turkwel Riverine forest were located around Katilu (Latitude 2^{o}23' N, Longitude 35^{o}39'E), Nadapal (Latitude 3 ^{o}00'N 35^{o}30'E) and Turkwel delta (Latitude 3^{o}8'N, Longitude 36^{o}4'E).

In addition, *Prosopis* populations located around Bura (Latitude 1°14'N, Longitude 39°30'E), Bamburi (Latitude 4°1'N, Longitude 39°24'E), Marigat (Latitude 0°34'N, Longitude 35°58'E), Isiolo (Latitude 0°34'N, Longitude 37°45'E) and Taveta (Latitude 3°23'S, Longitude 35°50'E) were included for species identification and population genetic diversity studies. Populations at Bura and Marigat were also used in biomass prediction study. The geographical location of Turkwel River and representative samples for each sampled population is shown in Figure 1.2, and summary of environmental factors shown in Table 1.2. With the exception of Bamburi, all the study sites are within the drylands, where rainfall/potential evapotranspiration (r/E_o) is $\leq 50\%$.

Formulation of research objectives and questions

For *Prosopis* species, invasiveness could be invoked by adaptation, propagule pressure or colonization pressure, enemy escape, hybridization, allelopathy and competition (Hunziker et al., 1986, Goel et al., 1989, Zimmerman 1981, Shiferaw et al., 2004, Landeras et al., 2006, van Klinken et al., 2006). Invasibility of riverine ecosystems is caused by disturbance, fluvial erosion/ deposition, water table fluctuations, niche availability and low species diversity (Davis et al., 2000, Richardson et al., 2007). The objective this study is to evaluate trends and factors that predispose riverine habitats to *Prosopis* invasion, determine ecological invasion impacts and the underlying invasion mechanisms. We investigated *Prosopis* invasion by studying invasibility of riverine forest, mechanisms explaining the invasiveness of *Prosopis* species, and the species composition, genetic diversity, and genetic differentiation of naturally established *Prosopis* populations in Kenya. Finally, we investigated whether standing biomass can be predicted with tree diameter across sites, to guide woody resource exploitation as an invasion management strategy.

The thesis is structured into seven chapters. The current chapter (Chapter 1) provides the general introduction, Chapter 2 addresses habitat invasibility, Chapter 3 addresses with the ecological impacts of riverine invasion, Chapter 4 addresses the mechanisms that contribute to lack of *A. tortilis* regeneration under *Prosopis* canopies, Chapter 5 identifies the *Prosopis* species in populations of varying invasion ratings in Kenya and Chapter 6 addresses management interventions by developing volume equations to predict *Prosopis* tree biomass.

Chapter 7 provides a synthesis of the whole study, major recommendations and conclusions. The specific questions addressed in chapters 2-6 were:

(Chapter 2) What abiotic factors make riverine forests vulnerable to Prosopis invasion?

In this chapter, it is hypothesised that *Prosopis* species was colonizing forest gaps that were hitherto available to establishment of indigenous trees, thus altering the dominance of canopy trees. Geographical information systems techniques are combined with field surveys to describe vegetation changes and *Prosopis* invasion along the Turkwel riverine forest between 1986 and 2007.Occurence of indigenous species and *Prosopis* species in randomly selected plots with a positive vegetation change, a negative vegetation change or stable vegetation condition is used to evaluate *Prosopis* encroachment in the three vegetation status categories. Information on historical and prevailing plot condition is also obtained to evaluate factors that may have accelerated *Prosopis* invasion.

(Chapter 3) What are the ecological impacts of prosopis invasion on riverine forest herbaceous species and indigenous trees regeneration?

Prosopis invasion may have a large impact on the livelihood of pastoralists, because it affects the main livestock fodder resource in the region; the herbaceous vegetation and regeneration of indigenous trees. In chapter 3, the effect of a canopy of *Prosopis* species on herbaceous ground cover and diversity is compared with the canopy of a native *Acacia* stand, and a mixed canopy. Also the effect of *Prosopis* canopy on the regeneration of indigenous trees is evaluated, as this determines the future composition of the forest canopy regeneration.

(Chapter 4) What mechanisms underlie inhibition of A. tortilis regeneration by Prosopis species?

From the results of Chapter 3, it was hypothesized that *Prosopis* litter is more inhibitive to *A. tortilis* regeneration than to itself. The hypothesis is tested by three greenhouse studies. In the first study, effects of *Acacia* and *Prosopis* litter on seed germination are evaluated by assessing germination at increasing litter concentration in the soil. Then combined effects of each of the two litter

types concentration in the soil, and irradiance on seedling growth are evaluated. Finally, the two litter types are evaluated for nitrogen, phosphorous, potassium, soluble phenol content and soluble phenol leaching trends over time.

(Chapter 5) What is the species composition in Prosopis invaded areas of Kenya?

As several *Prosopis* species were introduced within some sites in Kenya and invasiveness vary across sites, it is hypothesized that invasion status at any site depends on the species composition. This hypothesis is tested by evaluating the relatedness of six Kenyan populations to *P. chilensis*, *P. juliflora* and *P. pallida* references, using Randomized Polymorphic DNA markers; as the three were the most widely introduced species. Also genetic diversity of Kenyan *Prosopis* populations is compared with three reference species and two *P. juliflora* populations from Middle East, to determine whether repeated introductions of species and provenances has increased the genetic diversity of *Prosopis* populations in Kenya.

(Chapter 6) Can basal diameter predict biomass in closed canopy Prosopis?

Since accurate measurement of height and crown in closed canopy *Prosopis* stands is not feasible, it is hypothesised that tree diameter can be used as a single biomass prediction variable across sites; despite variation of site conditions in Chapter 1 and the genetic diversity among populations found in Chapter 5. Using destructive sampling and water displacement method, biomass prediction models are developed with height, diameter and height * diameter at Nadapal, using regression methods. The models were validated at Bura and Marigat by regression analysis of measured and predicted biomass. After obtaining good validation results, data from all the three sites was pooled for further development of biomass prediction model for wider application.

Table 1.1 Comparison of global and Kenya's drylands statistics. Classes are delineated according to precipitation to evapotranspiration (P/ETp) ratio; hyper-arid (P/ETp <0.05), arid (0.05< P/ETp <0.20), semi-arid (0.20< P/ETp <0.5) and dry sub humid (0.50< P/ETp <0.65).

Country/ Continent	Hyper-arid	Semi-arid	Arid	Dry sub humid	National/ Continental (%)	Global (%)
Kenya*	45.6	21.7	15.0	4.9	87	-
Africa	34.3	25.7	35.6	13.7	66	32
Asia	14.2	32.1	35.6	18.1	46	32
Australia	0.0	45.7	46.6	7.7	75	11
Europe	0.0	3.7	35.0	61.3	32	5
North America	0.4	11.1	56.9	31.5	34	12
South America	4.8	8.3	48.8	38.1	31	9

Source: Sombroek et al., (1982) and Kassas (1995). * For Kenya, hyper-arid lands are classified as very arid and dry sub humid classified as semi humid to semi-arid.

Table 1.2: General description of sites where *Prosopis* populations for this study were sampled. r/E_o (%) refers to the percentage rainfall (r) over evapotranspiration (E_o).

Site Name	Natural vegetation	Average annual r/ E_o (%)	Common Land use	Soil (general description)	Rainfall (mm)	Mean temperature °C
Bura,	Riverine forest	25 - <15	Irrigated farming, shifting cultivation and seasonal grazing	Well drained to imperfectly drained, very deep, dark brown to yellowish brown, stratified, micaceous, strongly calcareous, predominantly loamy soils (calcalic fluvisols)	370	28
Katilu	”	15-25	”	”	350	24-36
Nadapal	”	< 15	”	”	200	28-40
Turkwel delta	”	< 15	”	”	200	28-40
Bamburi	Mangroves	50 - 65	Limestone mining and mine rehabilitation	Well drained, shallow, dark brown to dark reddish brown, friable rocky, sandy clay loam to sandy clay (Lithosols with ferralic cambisols)	>1200	-
Marigat	Bushland	25 -40	Grazing	Moderately well drained, very deep, dark brown to greyish brown, firm, strongly calcareous, moderately to strongly saline and sodic, fine sandy loam to clay loam with a stone surface (Orthic solonchaks)	500	24-34
Isiolo	Bushland to scrub land	15 - 40	Grazing	Complex of well drained, shallow to moderately deep, dark red to yellowish brown, non to moderately calcareous, friable to firm, stony sandy clay loam (Calcic cambisols)	-	-
Taveta	Bushland	25 - 40	Grazing	Well drained, deep to very deep, dusky red to dark red, friable sandy clay (Rhodic ferralsols)	-	-

Source: Sombroek et al., (1982), Ellis and Reid (1995), Stave et al., (2005), Maingi and Marsh (2006)

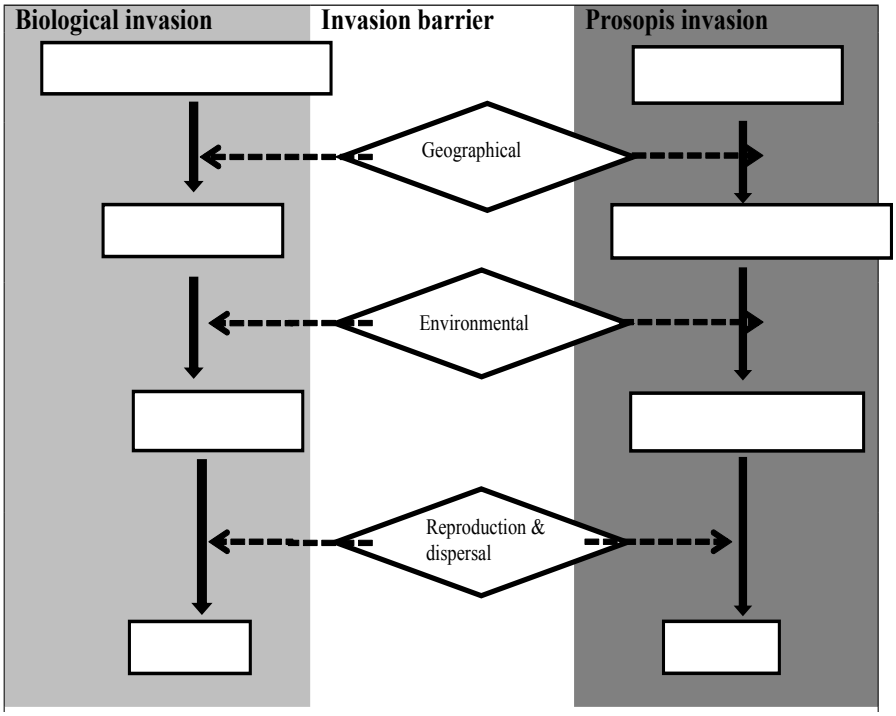


Figure 1.1: Conceptual framework for biological invasion with elaboration of *Prosopis* species invasion in Kenya. (Adapted from Blackburn et al., 2011).

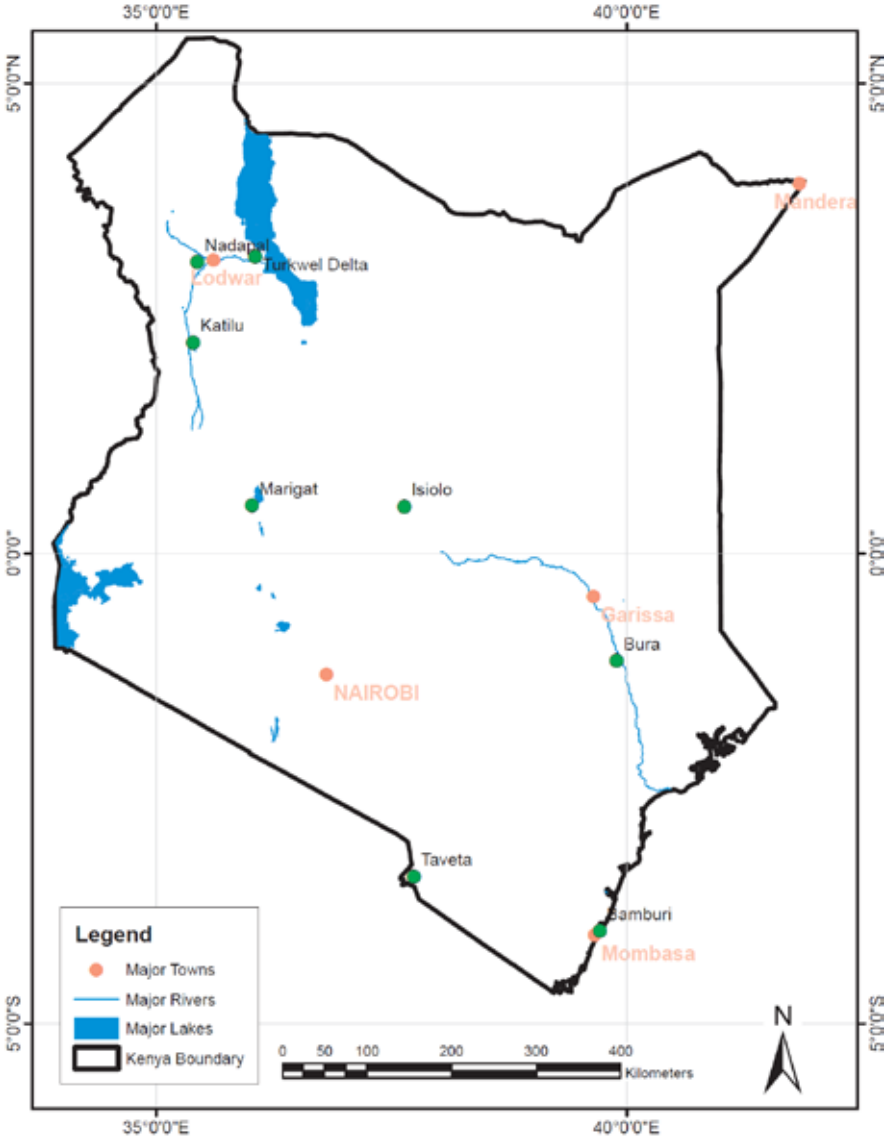


Figure 1.2: Geographical location of sample location from sites where *Prosopis* populations from this study were sampled. The sample locations were determined with a handheld global positioning system during sampling.

Chapter 2

Prediction of Prosopis Species invasion in Kenya using Geographical Information System (GIS) Techniques.

Gabriel M. Muturi, Godefridus M.J. Mohren and Jacob N. Kimani

Published in African Journal of Ecology 48:628-636 (2010)

Abstract

Tree species from *Prosopis* genus were widely planted for rehabilitation of degraded drylands of Kenya. However, they have invaded riverine ecosystems where they cause negative socio-economic and ecological impacts. GIS was used to estimate the reverine area threatened by *Prosopis* invasion in Kenya. Landsat satellite images, field surveys and past studies were also used to assess the resulting potential ecological impacts in the Turkwel ecosystem in Kenya. The study revealed that 3.0 to 27.7 million hectares are threatened by invasion, based on documented riverine forests width of 0.5-3 km. Image analysis showed that 34% of the sites under positive change were invaded, with most invasions occurring in natural forests and abandoned farms. *Prosopis* had overall occurrence of 39% in all the sampled sites in 2007, in contrast to 0% in 1990 that was reported in an earlier study. In these areas, *Acacia tortilis* occurrence dropped from 81% in 1990 to 43% in 2007, suggesting that *Prosopis* could be displacing it. Utilization of *Prosopis* for fodder, fuel wood and pods for animal feeds is recommended as a management tool to reverse the trend. The methods used in this study are also recommended for invasion prediction and management in other similar ecosystems.

Key-words: *Cadaba rotundifolia, Hyphaene compressa, Prosopis* and Turkwel

Introduction

Arid and semi-arid lands (drylands) are prone to desertification, a process that is attributed to combined effects of human and natural factors (Kassas, 1995), and leads to extensive vegetation loss. Overexploitation of resources, poor land husbandry, extreme climatic events and ecological fragility are among the main factors associated with desertification. In Kenya, climatic effects are manifested in cyclic droughts that cause devastating socio-economic and ecological impacts (UNEP, 2000, Speranza, Kiteme and Wiesmann, 2008). During prolonged droughts, traditional livelihoods like pastoralism and farming are unsustainable leading to an increased dependency on natural resources like charcoal burning (UNEP, 2000).

After the prolonged droughts of the 1970s, the drylands were severely degraded, leading to extensive vegetation loss. There was therefore an urgent need for rehabilitation, with tree planting given a high priority. This was constrained by the availability of drought tolerant species, so screening trials were a prerequisite. Trees from *Prosopis* genus were enlisted because they had shown potential in rehabilitation of degraded lands in Bamburi cement quarry mines in Mombasa (Maghembe, Kariuki and Haller*,* 1983) and are more drought tolerant than the indigenous species (Olukoye, Wamicha and Kinyamario*,* 2003). The introduced species included *Prosopis chilensis* Stuntz., *Prosopis juliflora* (Sw.) D.C*., Prosopis cineraria* Druce*, Prosopis pallida* Kunth and *Prosopis tamarugo* Phil. (Barrow, 1980, Herlocker, Barrow and Paetkau, 1980, Maghembe *et al.,* 1983). Unpublished data suggests that *Prosopis alba* Griseb*., Prosopis nigra* Hieron*.,* and *Prosopis pubescens* Benth. were also introduced. From these efforts, *P. chilensis* and *P. juliflora* emerged as the most promising species (Barrow, 1980, Herlocker *et al.,* 1980) and their seeds were freely exchanged across the country (Paetkau, 1980).

The introduced species may have hybridized, as this is known to occur among *Prosopis* (Pasiecznik *et al.,* 2001, Vega and Hernandez, 2005, Landeras *et al.,* 2006), leading to increased abundance of the *Prosopis* pool. This may be the cause of prevailing disagreement in *Prosopis* identification in Kenya. For example, populations in the Northern Kenya are often considered as *P. chilensis* (Olukoye *et al*., 2003, Stave *et al.,* 2003, 2005), while those from Coastal region are perceived as *P. juliflora* (Maghembe *et al*., 1983, Miettinen *et al*., 1988).

After successful introduction into the intended areas, livestock dispersed the seeds into the intermittent wetlands ecosystems in drylands (Otsamo *et al.,* 1993). This included the riverine ecosystems where they were originally not intended to extend (Ngunjiri and Choge, 2004, Anderson, 2005, Mwangi and Swallow, 2005). The species are therefore treated as invasive in the wetlands, a trend that is consistent with other global introductions of *Prosopis* (Pasiecznik *et al.,* 2001). The subsequent seed dispersal was random depending on the diverse areas from where livestock had browsed the pods. Because of this reason and the prevailing complexity of species identification in Kenya, this paper treats the invasion as a *Prosopis* species pool.

Based on the drylands rivers network (Figure 2.1) and riverine forest width of 0.5-3 km estimated from the literature (Maingi and Marsh 2002, Stave *et al.,* 2005), the spatial extent of areas threatened with *Prosopis* invasion is between 3.0 and 27.7 million hectares using buffers of 0.5 km to 3 km. These estimates are conservative because of the variability in woodlands widths along the rivers network. The current and increasing impediments of *Prosopis* invasion include loss of pastures, farms, fishing grounds and replacement of indigenous plants. This has elicited public outcry for eradication of the species and compensation for loss of land use.

Despite the potentially large area that is threatened with *Prosopis* invasion, methods for ascertaining the invaded areas and impacts are not yet developed. This study was conceived to address this important gap through the use of GIS. The Turkwel Riverine Forest ecosystem (Figure 2.2) was selected for this study because of its livelihood importance to the Turkana community and availability of relevant data for comparison from a past study that served as a baseline for assessment of trends in vegetation change (Stave *et al.,* 2003).

Methods

Evaluation of Prosopis invasion in the Turkwel Ecosystem

Landsat Thematic Mapper satellite images from Path 169, Row 058 and Path 170, Row 058 (69 and 170, hereafter) were obtained from the Regional Center for Mapping of Resources for Development in Nairobi, Kenya. The two image sets had a spatial resolution of 30 m and a complete coverage of the Turkwel Riverine ecosystem (Figure 2.2). Although images of exact date are desirable

to avoid seasonal effects in change detection analysis over several years (Jensen *et al.,* 1993, Im and Jensen, 2005), quality images were unavailable to meet this criterion. Images in 169 were available for 21/1/1995, 27/1/2000 and 25/1/2005, and those for 170 were available for 3/1/1986, 18/1/2000, 10/1/2003 and 3/2/2006.

The images were processed in ERDAS Imagine software (Leica Geosystems, Atlanta, Gerogia, USA) to produce color composites, using the 4-3-2 band combination for red, green and blue (RGB). After the processing of color composites, the 2005 and 2006 images were deemed positionally accurate for 169 and 170 respectively. Earlier images for each scene were registered onto the appropriate recent image for correction of image shifts. These were georeferenced using permanent features detectable in both the master (recent image) and the slave (earlier image).

After georeferencing all the images, a 3 km river buffer was calculated from the most recent image of each scene using ArcView software (ESRI, Redlands, California, USA) to estimate riverine forest width (Stave *et al.,* 2005). The buffer outline was used to clip an area of interest (AOI) from each of the georeferenced color composite image using ERDAS Imagine software. An example AOI clip is shown in Figure 2.2. The extracted AOI images were processed to obtain a Normalized Difference Vegetation Index (NDVI), which is the ratio of reflected spectrum over the incoming total radiation. NDVI is defined as

$$NDVI = (NIR-RED)/ (NIR+RED),$$

Where NIR (band 4) and RED (band 3) stand for the spectral reflectance measurements acquired in the near-infra red and red regions respectively with NDVI values ranging from -1.0 to +1.0.

ERDAS Imagine software was used to calculate the differences between consecutively dated images. The outputs for this analysis revealed changes that were classified as positive or negative and unchanged land use or land cover condition. The practical interpretations of the positive change is an increase of leaves or crown greenness (phenological change), increase in ground vegetation cover, flushing out of leaves in deciduous plants or forest improvement through regeneration, while the contrary applies for the negative change detection. Neutral status is associated with stable conditions in the examples already given

or unchanged condition in land use or land cover and in physical features such as ground soils and water bodies. These varied conditions of change detection analysis were ascertained through ground truthing.

Ground truthing

Forty random locations (plots) were selected from each of the areas under positive change, neutral condition and negative change for ground truthing, using the most recently detected change for each scene. The UTM coordinates for the plots were recorded and their locations in the field determined with a Global Positioning System (GPS). The coordinates were taken as the center of 50 m by 50 m plot as the area was large enough to enclose a pixel of 30 m by 30 m. A pixel is the smallest data unit from the images analysis outputs within which change detection had been sampled prior to fieldwork. At the delta, 4 pre-determined plot locations occurred in a waterlogged area and their UTM coordinates were adjusted around the original plots that were 50-100 m away from the original locations.

Stabilized GPS coordinates were marked as the plot center, and straight baseline extending 25 m on each side established using a tape measure. The baseline was used to locate and align the four plot corners that were marked using tagged posts. One of the team members remained stationery at the plot center to guide baseline establishment and plot delineation. This was particularly crucial under dense canopies where baselines were cleared under close guidance. After plot establishment, the presence or absence of *Prosopis* species was recorded followed by the listing of the entire indigenous tree species found in the plot. Land use and land cover was classified as riverine forest, riverbed, bare land, abandoned farms and active farms and plot the description entered as appropriate. Bare land was adopted for areas without indigenous plants and was characterized by bare sandy soils, except in areas of *Prosopis* invasion. Notes on plot description were then used in the comparison of *Prosopis* status under different land use and land cover scenarios. Field notes were also used to elucidate the factors associated with image analysis outputs.

Ground truthing data analysis

Ground truthing data was later transformed into a species presence or absence matrix and site descriptions summarized in a Microsoft Excel spreadsheet.

The data was analyzed to obtain case frequencies for species occurrence, land use and land cover. Because some tree species occurred in few plots, 10% occurrence frequency was adopted as the minimum for description of species distribution in the sampled areas.

Results

Vegetation change detection along the Turkwel River and factors attributed to detected change

NDVI calculations revealed a higher positive change at the delta than in other areas for scene 169 in all intervals (Figure 2.3a). This change was also higher in the long term between 1995 and 2005 than in the short term periods of between 1995 and 2000 and between 2000 and 2005. The short term change between 2000 and 2005 was higher than between 1995 and 2000, although the time intervals were equal. The overall change detected from this scene revealed positive change from 1995 and 2005.

In scene 170, we detected very dynamic changes between the shorter intervals, with no clear tends (Figure 2.3b). The change between 1986 and 2006 revealed a negative change that was intercepted by positive changes (Figure 2.3b). Unlike the first scene (169), the overall change from 1986 to 2006 was not a reflection of cumulative changes detected in the short term intervals of 1986 to 2000, 2000 to 2003 and 2003 to 2006 (Figure 2.3b).

Encroachment of the ecosystem by *Prosopis*, regeneration of *Hyphaene compressa* H. Wendl. and forest rejuvenation (flushing of new leaves) were the main factors associated with positive change (Figure 2.4a). Negative change was attributed to conversion of riverine forest to farmlands, destruction of forest by floods, and leaf fall (Figure 2.4b). Plots without change were mainly found along the riverine forest (Figure 2.4c). *Prosopis* invaded forest and farms were also stable over the assessment periods in the two scenes.

Occurrence of species in the sample plots

Of the one hundred and twenty plots sampled, the positive and neutral categories were represented by 41 plots each while the negative change category was represented by 38 plots (Table 2.1). The wood species with over 10% occurrence frequencies were *H. compressa* (45%), *Acacia tortilis* Hayne (43%),

Prosopis (39%), *Salvadora persica* L. (16%), *Cadaba rotundifolia* Forssk. (15%) and *Cordia sinesis* Lam. (11%) (Table 2.1). *Hyphaene compressa* and *Prosopis* species had higher occurrence in areas of positive change while their occurrences in areas under neutral and negative change were almost equal. *Cadaba rutondifolia* had highest occurrence in areas under neutral condition. *Acacia tortilis* and *Salvadora persica* had a nearly similar distribution pattern among the areas of positive change, neutral condition and negative change.

In plots under positive change, 21 plots were not invaded by *Prosopis*, while 20 plots were invaded. The distribution of *Prosopis* in the invaded areas was mainly in abandoned farms and riverine forest with an equal number for both land cover classes (n = 9), while each of the remaining two plots occurred in bare land (n = 1) and in active farms (n = 1). Plots without invasion were distributed among the riverine forest (n = 16), farms (n = 3) and in abandoned farms (n = 2).

For plots sampled under neutral condition 15 plots were invaded while remaining 26 plots were not invaded. The invaded plots were in riverine forests (n = 10), active farms (n = 4) and in abandoned farms (n = 1). Plots without invasion occurred on and in the riverine forest (n = 21), bare land (n = 2), active farms (n = 2) and in the river bed (n = 1).

In the negative change class, 12 plots were invaded while 26 plots were not invaded. The invaded plots occurred in the riverine forests (n = 6), abandoned farms (n = 4), in river bed (n = 1) and in an active farm (n = 1). The plots without encroachment were found in riverine forests (n = 14), river bed (n = 6), farms (n = 4) and in bare land (n = 2).

Status of Prosopis among the land use classes

Most sampled areas occurred within the riverine forest (n = 76) while the remaining 44 plots were distributed among abandoned farms (n = 16), active farms (n = 15), river bed (n = 8) and bare land (n = 5), with *Prosopis* species occurring in all the land use and land cover classes (Table 2.2). Based on the percentage of invaded plots within the five land use and land cover types, the decreasing order of invasion was abandoned farms, active farms, riverine forest, bare land and river bed (Table 2.2).

Discussion

A gradual positive change at the delta was mainly due to an intensified *Prosopis* invasion. This may be due to massive seed transportation by floods from the higher grounds to the low lying delta region, a trend that is consistent with flood plains seed dispersal (Sakai *et al.,* 1999, Hughes and Rood, 2003). The high occurrence frequency (39%) of *Prosopis* observed in this study is in contrast with 0% occurrence in 1990 and 5% occurrence in 1998 for *Prosopis chilensis* (Mol.) St. reported previously (Stave *et al.,* 2003). Therefore, the two studies portray an aggressive invasion trend into the riverine ecosystem that was hitherto dominated by *A. tortilis* and *H. compressa* (Stave *et al.,* 2006). The respective comparable occurrence for *A. tortilis*, *H. compressa and Prosopis* was 62%, 39% and 5% in 1998 (Stave *et al.,* 2003) and 43%, 45% and 39% in this study.

Although there was higher occurrence of *H.compressa* in plots under positive change than *Prosopis* (Table 2.1), the contribution of *Prosopis* in the change class was higher (Figure 2.4a) because contribution of *H. compressa* to positive change was only through the regenerating class. Contribution of *H. compressa* to the positive change is consistent with a previous study where its regenerative potential was higher than that of *A. tortilis* (Oba, Stenseth and Weladji*,* 2002). However, the higher incidence of *Prosopis* invasion in abandoned and active farms (Table 2.2), its contribution to the positive change in the ecosystem (Figure 2.4a) and the declining occurrence of *A. tortilis*, suggests that *Prosopis* invasion is potentially a greater threat to *A. tortilis* than any other species. Non-utilization of *Prosopis*, the contrasting intensive use of *A. tortilis* for charcoal production (UNEP 2000) and pods as fodder (Stave *et al.,* 2006) and the pioneering attributes of *Acacia* and *Prosopis* species are among underlying factors of shift in the dominance trends. This trend is continuously enhanced by the gradual forest degradation through natural and anthropogenic factors, hence the presence of *Prosopis* in plots within the two change categories and in plots under neutral condition (Table 2.1).

The circumstances for comparable long term changes detected from 1986 to 2006 and from 1986 to 2000, and a contrasting short term changes detected from 2000 to 2003 and from 2003 to 2006 under scene 170 (Figure 2.3d) could be a subject of further research. However, the stable or neutral conditions observed in the current study for both scenes were expected as they reflected maintenance of status quo in conditions of riverine forest, farms and bare ground.

Mature *A. tortilis* trees, the evergreen C. *rotundifolia* shrub and *S. persica* stands were conspicuously associated with forest stability, suggesting that they are good indicators of unchanged and undisturbed natural vegetation. The occurrence of *Prosopis* in plots under stable conditions suggests that *Prosopis* invasion has been continuous and that some stands have already stabilized.

As the images used for this study are from approximately the same date across the years and were of high quality for the area of interest, we assumed that detected change was not influenced by season. Furthermore, the riverine forest is normally evergreen, suggesting conditions of vegetation and land cover stability. Change detection using remote sensing is classified into simple or binary change detection and detection of detailed change information (Lu *et al.,* 2004). The image analysis of the current study was concerned with binary change detection which is basically confined to addressing whether a change has occurred or not, while ground truthing was an attempt to discern the detailed change information. Apparently, the objective of binary change detection was achieved by this study and preliminary details on change factors elucidated through ground truthing.

Conclusion

The study findings and those from an earlier study (Stave *et al.,* 2003) have demonstrated that the Turkwel riverine forest is undergoing an ecological shift from dominance by *A. tortilis* and *H. compressa* to dominance by *A. tortilis, H. compressa* and *Prosopis.* This change appears to be more detrimental to *A. tortilis* than *H. compressa*, although the ecological dominance of both species is affected. It is apparent therefore that concerns on ecological and socio – economic impacts of *Prosopis* invasion in the ecosystem are justified and intervention measures are required. At the community level, minimizing the rates of farm abandonment is the most appropriate strategy because of the high *Prosopis* invasion observed in abandoned farms. This should be complimented by enhanced utilization of *Prosopis* for fodder, fuel wood and pods in animal feeds rations, to reduce its ensuing dominance. At the landscape scale, ecosystem monitoring using the tools applied in the current study offers the best opportunity for identification of invasion hot spots for use and control management.

Table 2.1: Frequency of species occurrence under areas of positive change, neutral condition, negative change and overall occurrence percentage in surveyed areas in 2007.

Species	**Positive change**	**Neutral condition**	**Negative change**	**% Species occurrence**
Hyphaene compressa	23	15	16	45
Acacia tortilis	17	19	16	43
Prosopis spp	20	15	12	39
Salvadora persica	6	8	5	16
Cadaba rutondifolia	2	14	2	15
Cordia sinesis	3	5	5	11
Number of plots (n)	41	41	39	120

Table 2.2: Distribution of plots among the land use within the image analysis outputs and the status of *Prosopis* invasion among the land uses in 2007.

Land use/ Land cover	**Distribution of plots under**			**No of plots not invaded**	**No of invaded plots**	**Total**	**% Invasion**
	Positive	**Neutral**	**Negative**				
Riverine forest	25	31	20	51	25	**76**	**33**
Abandoned farms	11	1	4	2	14	**16**	**88**
Active farms	4	6	5	9	6	**15**	**40**
River bed	0	1	7	7	1	**8**	**13**
Bare land	1	2	2	4	1	**5**	**20**
Total	**41**	**41**	**38**	**73**	**47**	**120**	

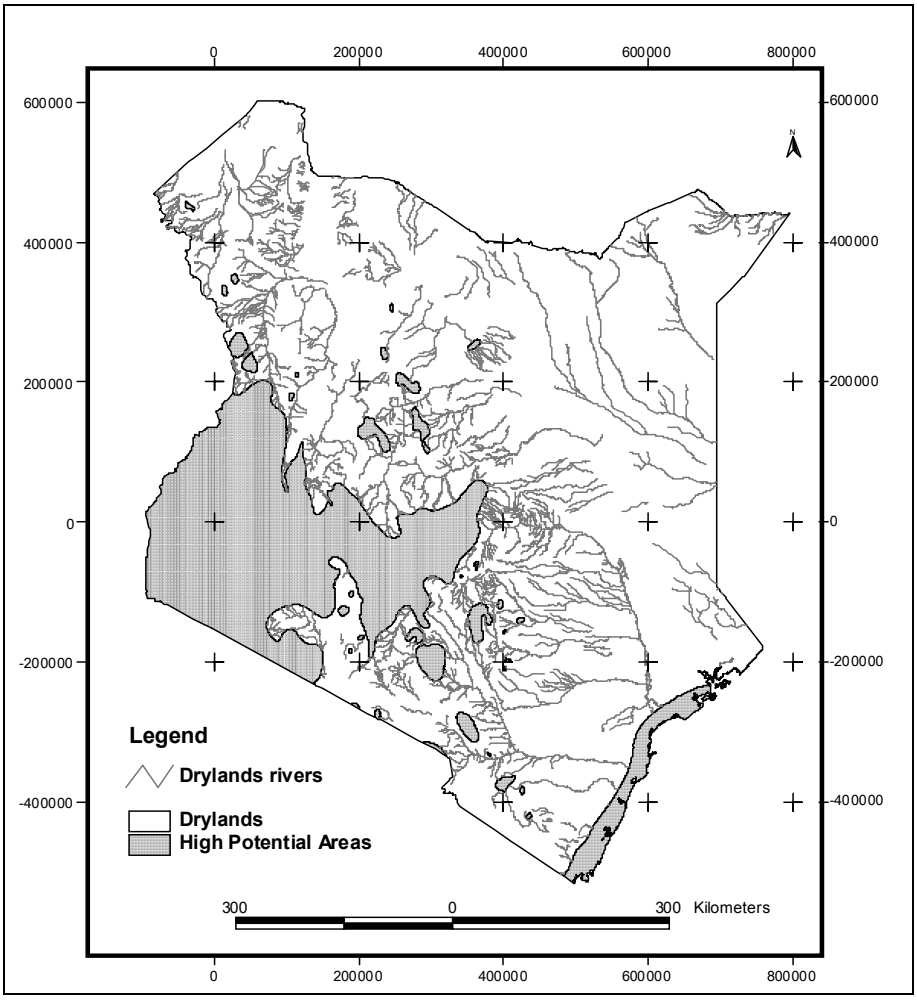


Figure 2.1: Kenya's drylands rivers network that was used to calculate the areas threatened with *Prosopis* invasion. It was estimated that 3.0 million hectares, 7.0 million hectares, 16.2 million hectares and 27.7 million hectares are potentially threatened with invasion, using buffers of 0.5 km, 1 km, 2 km and 3 km respectively, based on the documented riverine woodlands widths of 0.5 km to 3 km.

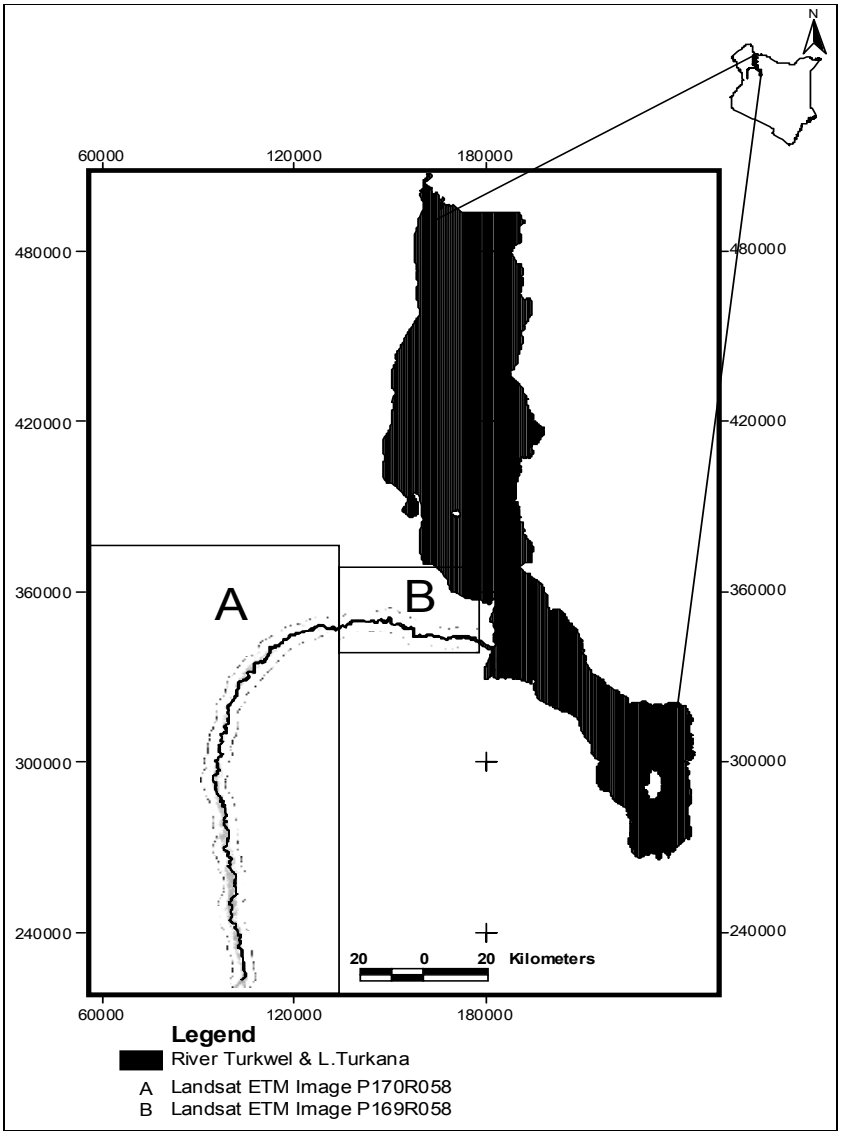


Figure 2.2: Location of Turkwel River in Kenya showing the areas covered by Landsat Thematic Mapper satellite images P169R058 (A) and P170R058 (B). The river is enclosed within a 3 km buffer. Shades outside the river course and buffer line show the data from the image that was used in delineating the buffer.

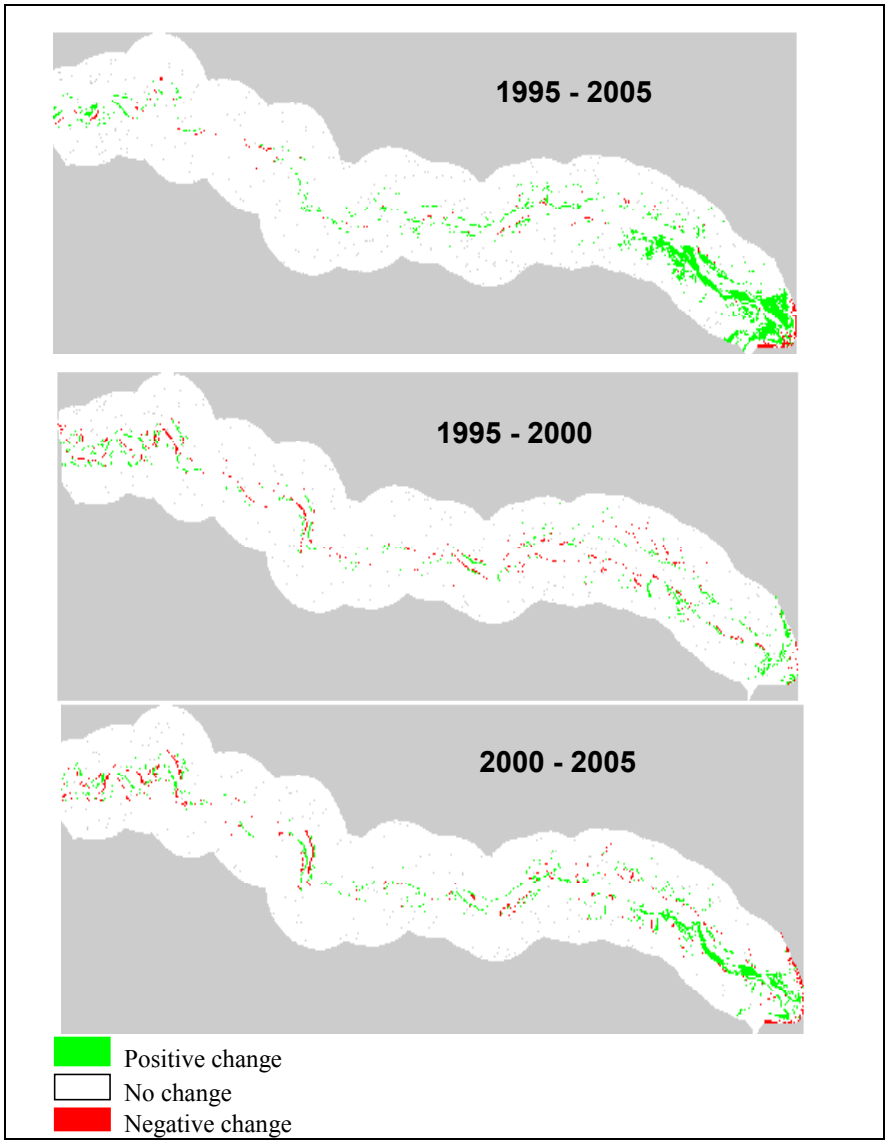


Figure 2.3a: Change detection between 1995 and 2000, between 2000 and 2005 and between 1995 and 2005 for Landsat Thematic Mapper satellite image P170R058. Green color indicates positive change, while the red color reflects negative change with reference to vegetation condition or ground cover. The light shade indicates stability in forest condition, farms or areas without vegetation.

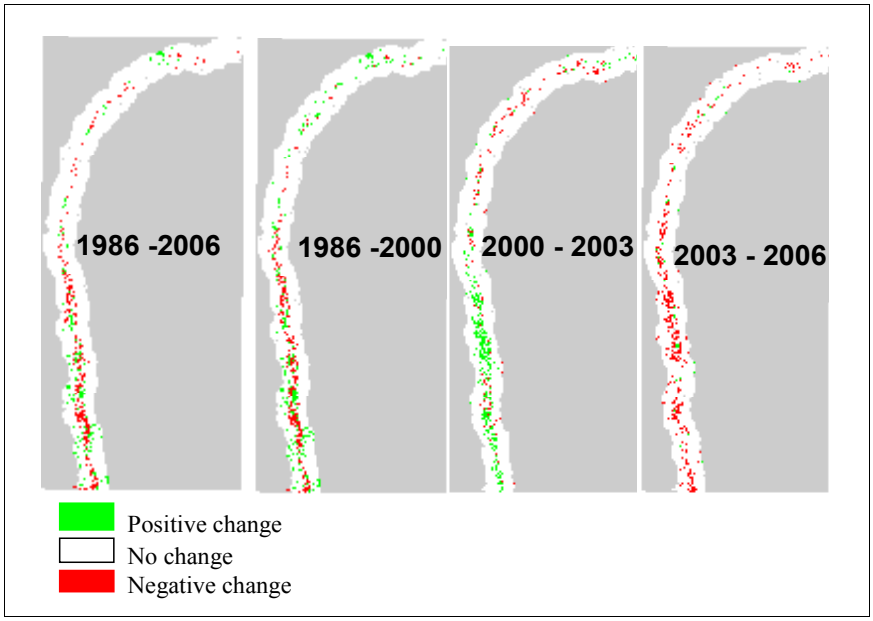


Figure 2.3b: Change detection between 1986 and 2006, 1986 and 2000, 2000 and 2003 and 2003 and 2006 for Landsat Thematic Mapper satellite images P169R058. Green color indicates positive change, while the red color reflects negative change with reference to vegetation condition or ground cover. The dominating light shade indicates stability in forest condition, farms or areas without vegetation.

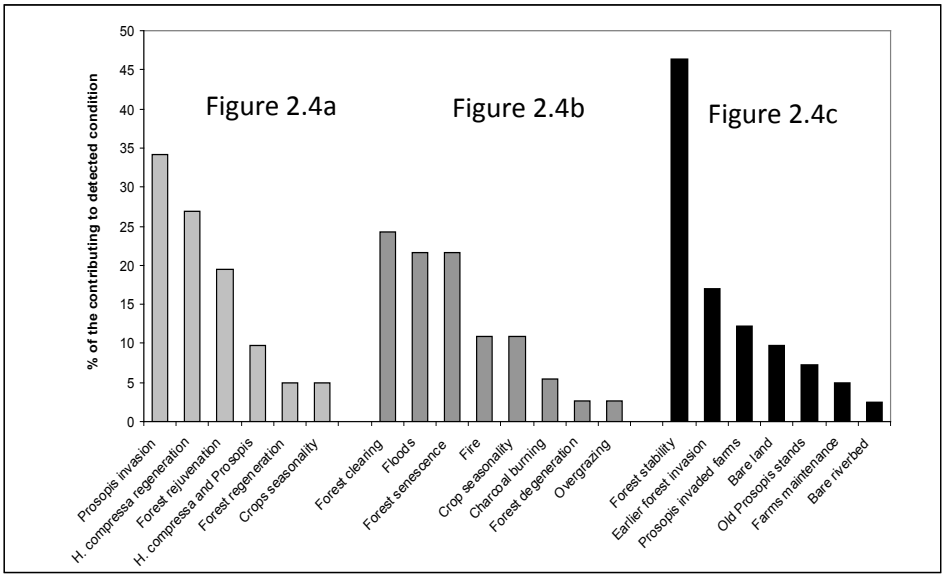


Figure 2.4: The factors associated with positive change (Figure 2.4a), neutral condition (Figure 2.4b) and negative change (Figure 2.4c) along the Turkwel River Ecosystem.

Chapter 3

Ecological impact of Prosopis species invasion in Turkwel Riverine Forest, Kenya

Gabriel M. Muturi, Lourens Poorter, Godefridus M.J. Mohren and Bernard N. Kigomo

Submitted

Abstract

The impact of Prosopis species invasion in the Turkwel riverine forest in Kenya was investigated under three contrasting: Acacia, Prosopis and Mixed species canopies. Variation amongst canopies was assessed through soils nutrients and physical properties, tree characteristics and crown canopy closure. Invasion impact was evaluated by comparing herbaceous species ground cover, density, diversity, and tree regeneration. Soils under Acacia canopy had higher silt, carbon and calcium, and lower sand content than soils under other two canopies. Tree density and multistems were higher under Prosopis than Acacia canopies. Low tree diameter classes were found in Prosopis trees, in contrast to high diameter classes in Acacia trees. Diameter distribution in Mixed species canopy revealed invasion of Prosopis into mature Acacia stands. Canopy closure was insignificant because of the high inter-plots variations. Herbaceous species cover, diversity and density were lower under Prosopis than under other two canopies. Seedlings density was higher under Prosopis than under Acacia and mixed canopies but Acacia tortilis seedlings were confined to Acacia canopy whereas Prosopis and Ficus sycomorus seedlings were distributed in all three canopies. We recommend Prosopis invasion management to mitigate loss of herbaceous species biodiversity and productivity; and to improve regeneration of *A. tortilis.*

Keywords: *Acacia tortilis*, ground cover, herbs diversity, soil nutrients

Introduction

The genus *Prosopis* has 44 tree and shrub species found in the hot dry tropics of Africa, America, Asia and Australia although 90% of all *Prosopis* species are native to North and South America (Burkat 1976). American species such as *Prosopis chilensis* Stunz, *Prosopis juliflora* (Sw.) D.C. and *Prosopis pallida* Kunth have been extensively introduced to Asia, Africa and Australia where they have become naturalized (Pasiecznik et al., 2001). Introduced *Prosopis* species have played a significant ecological role in land rehabilitation and contributed economically through provision of fodder, food and forestry products (Rosenschein et al., 1999, Pasiecznik et al., 2001, Gallaher and Merlin 2010). However, the species have spread from their areas of intended introductions and have become invasive as a result of seed dispersal by livestock, wildlife, and water (Shiferaw et al., 2004, Mworia et al., 2011).

Low-lying riverine forests are more prone to invasion than other areas as they are convergent zones for most waterborne and animal dispersed seeds (Richardson et al., 2007, Robinson et al., 2008). Riverine forests in dryland landscapes are characterized by a rich biodiversity, including herbaceous plants (Richardson et al., 2007, Stave et al., 2007), which are highly valued for fodder (Morgan 1981, Timberlake 1994). Yet, in Kenya, about 27 million hectares of riverine forests are threatened with *Prosopis* invasion (Muturi et al., 2010). The negative consequences of *Prosopis* invasions include injuries to livestock and humans, restriction of movement, livestock deaths, and pasture loss (Mwangi and Swallow 2008). The dense, impenetrable and thorny *Prosopis* thickets may lead to injuries and restriction of movement and excessive pod consumption may lead to livestock deaths. The mechanisms behind pasture loss are less well understood, but it seems likely that trees affect the productivity and diversity of the herbaceous layer (Kahii et al 2009, Mworia et al., 2011).

Tree canopies may have positive effects on the herbaceous layer by improving the microclimate below the canopy in dry environments, by enhancing soil moisture through hydraulic lift, and by increasing nutrient availability through nitrogen fixation and deposition of faeces by animals sheltering under the canopy. Trees can also have negative impacts on the herbaceous layer through competition for water, light and nutrients, and possibly through negative allelopathic effects. Whether tree canopies have positive, neutral, or negative impacts on the herbaceous layer depend on the prevailing environmental conditions, the type

of canopy species and extent of canopy closure. In the semi-arid savannah, herbaceous biomass production is for example higher under isolated *Acacia tortilis* Hayne trees than in adjacent open areas (Belsky et., al., 1989, 1993). By contrast, at a more arid site, herbaceous biomass production was lower below tree canopies than in adjacent open areas, but this effect varied with the type of species; *P. juliflora* canopies were found to be more inhibitive than *A. tortilis* canopies (Kahii et al., 2009). *Prosopis juliflora* canopy has also been found to have adversely affected the richness and diversity of the native herbaceous flora of the United Arab Emirates: the magnitude of this effect increased with canopy size and tree density (El-Keblawy and Al-Rawai 2007). Although the negative impacts of the invasive *Prosopis* species on the herbaceous layer have been the focus of many studies (van Klinken et al., 2006, El-Keblawy and Al-Rawai 2007, Teague et al, 2008, Kahii et al.2009, Mworia et al., 2011), to date there have been no comparative studies of impacts caused by indigenous and invading exotics and therefore the relative impacts of the invading exotics cannot be easily ascertained.

The Turkwel riverine forest has recently been found to have discrete canopies of *A.tortilis*, *Prosopis*, and a Mixture of *A. tortilis* and *Prosopis*. (Muturi et al., 2010), thus providing an opportunity to evaluate the impacts of *Prosopis* invasion on the herbaceous understory. Before *Prosopis* invasion, the most common dryland species in Kenya, including the riverine forests was *A. tortilis* (Adams 1989, Reid and Ellis 1995, Patten and Ellis 1995). Populations of *A. tortilis* tend to be formed by cohorts of different ages that establish sporadically, mostly outside the *A. tortilis* canopy (Mwalyosi 1990, Loth et al., 2005), when environmental conditions are favorable for germination and seedling growth (Reid and Ellis 1995, Wilson and Witkowski 1998, Loth et al., 2005). *Acacia tortilis* provides dry season fodder supplement and coexists naturally with diverse herbaceous species that are also a significant pasture resource (Morgan 1980, Timberlake 1994, Stave et al., 2007). The species therefore provides a good yardstick against which to evaluate the impacts of *Prosopis* species invasion on herbaceous species, fodder and the regeneration of indigenous species.

In this study we compared the effect of three different tree canopies (*Acacia,* Mixed *Acacia* and *Prosopis* species) on 1) the abiotic conditions, 2) the regeneration of woody species, and 3) the productivity, richness and composition of the herbaceous layer. It was hypothesized that: 1) soil conditions were similar amongst canopies, but that the canopy closure was highest in *Prosopis* stands due

to higher tree densities that characterize invading *Prosopis* species; 2) the dense shade in *Prosopis* stands inhibits the regeneration of the pioneer *A. tortilis* and that of other indigenous trees; 3) herbaceous ground cover, density and diversity is high under the relatively open *Acacia* stands and low in closed *Prosopis* stands.

Materials and methods

Species

Acacia tortilis is an easily identifiable tree, common in African savannah and dryland riverine forests. *Prosopis chilensis*, *P. juliflora* and *P. pallida* are among the *Prosopis* species introduced in Kenya (Maghembe et al., 1983, Rosenschein et al., 1999, Stave et al., 2003). The species are difficult to distinguish because they are morphologically similar and hybridize, creating hybrids with intermediate phenotypes (Saidman et al., 1996, Pasiecznik et al., 2001, Landeras et al., 2006). Here, as in a related study (Muturi et al., 2010), naturally established stands of *Prosopis* species are simply referred to as *Prosopis*. *Acacia tortilis* and the *Prosopis* species in the study area are pioneer, shade-intolerant nitrogen-fixing trees.

Study sites

The fieldwork was done in the Turkwel Riverine Forest, in Kenya, at sites located near Katilu (Latitude 2°23' N, Longitude 35°39'E) and Nadapal (Latitude 3 °00'N 35°30'E). The forest lies within the dry Turkana District which is characterized by low erratic rainfall, high temperatures and high potential evapotranspiration (Sombroek et al., 1980). Rainfall is bimodal, with peaks around April and November (Stave et al., 2007). Mean annual rainfall along the Turkwel riverine forest ranges from 500 mm upstream to less than 200 mm downstream, with large variations between years (Reid and Ellis 1995, Stave et al., 2007). Rainfall is higher at Katilu (≈ 350 mm/yr) than at Nadapal (≈ 200 mm/yr), as Katilu is near the highlands and Nadapal in the middle of the dry areas. The soils are predominantly developed on alluvial deposits and are deep sandy or silty loams classified as calcaric fluvisols (Sombroek et al., 1980, Van Bremen and Kinyanjui 1992). The riverine forest used to be dominated by *A.tortilis*, with *Faidherbia albida* (Delile) A.Chev*, F. sycomorus* and *Hyphaene compressa*

H. Wendl. as sub dominants (Adams 1989, Stave et al., 2007), but since 1998, *Prosopis* species have become common (Stave et al.,2003, Muturi et al., 2010).

Study design

Three distinct canopies of *A. tortilis*, *Prosopis* species and a mixture of *A. tortilis* and *Prosopis* species (henceforth referred to as respectively *Acacia, Prosopis* and Mixed stands) were identified in the Turkwel riverine forest during a recent study (Muturi et al., 2010). To minimize site variation between the canopy sites (El-Keblawy and Al- Rawai 2006), the canopy types selected for study were approximately within 0.3-9.0 km from each other, within each of the two sampling sites. The distance between canopies was subjective and depended on both availability and proximity of the different canopy types, but was within the distance used in a similar study (El-Keblawy and Al- Rawai 2006). Plots were then randomly established under each canopy type in the field.

Forty intensive sample plots (Barnett and Stohlgren 2003) were established in the two sites (21 in Katilu and 19 in Nadapal): 15 were under *Acacia*, 16 under *Prosopis* and nine under Mixed species. All the nine Mixed canopies were established at Katilu as no Mixed canopy stands were found at Nadapal. The plots under *Acacia* and *Prosopis* were located at both Katilu and Nadapal. Intensive sample plots have a nested design consisting of a main plot of 100m^2, one subplot of 10 m^2 at the center of the main plot, and four subplots of 1 m^2 near the plot corners. The plots were at least 100 m apart, to avoid spatial autocorrelation (Tiegs et al., 2005, de Knegt et al., 2010). The location of each plot was recorded using GPS coordinates and/ or by painting reference trees.

Soil sampling and analysis

In each plot, soil samples were taken from three random sampling points, at depths of 0-10, 10-20 and 20-30 cm. These depths are commonly used because most of the root mass and root activity are concentrated there (Belsky et al., 1989, El-Keblawy and Al- Rawai 2007). The soil samples were pooled into a single sample per depth, and transferred to the laboratory for analysis. They were air-dried at room temperature, sieved with a 2 mm sieve to remove litter and debris, and homogenized (El-Keblawy and Al- Rawai 2007). Overall, 13 soil variables were evaluated. Soil texture was determined using hydrometer method, soil pH using calcium chloride method, organic carbon using Waldey Black method,

total nitrogen using Kjeldhal procedure and phosphorus using Olsen method. Exchangeable cations (calcium, potassium and magnesium) were extracted with ammonium acetate. The concentration of potassium in the extract was determined using a flame photometer and that of calcium and magnesium determined with an atomic absorption spectrophotometer. Micronutrients (copper, manganese, iron and zinc) were extracted with ethylenediaminetetraacetic acid (EDTA) and their concentration was determined using an atomic absorption spectrophotometer.

Canopy cover, ground vegetation cover and light availability

Canopy closure is the proportion of the sky hemisphere obstructed by vegetation when viewed from a single point; ground vegetation cover is the proportion of the ground covered by vegetation when viewed from above (Jennings et al. 1999, Paletto and Tosi 2009). Canopy closure and ground vegetation cover were estimated visually by three persons independently of each other (Jennings et al., 1999, Murphy and Lodge 2002) and then averaged. The canopy closure was estimated by standing in the center of the plot and looking upwards. Herbaceous ground cover was estimated from the 1 m^2 subplots corners by looking down. To account for seasonal variation in canopy phenology, four canopy closure estimates were made per plot during the rainy season in November 2008, October 2009, January 2010 and May 2010, and averaged.

Additional data on canopy closure were collected using two Minolta light meters. Before data collection the two meters were counterchecked for parity each day, by taking simultaneous sample measurements in an open area and recording their readings. Thereafter, the two meters designated for measuring light inside and outside the forest were used simultaneously to collect data. Light data was collected at the center of the four 1 m^2 subplots and, using a sisal twine on which seven light measurement points had been marked, along the diagonals of the main plot. All data was collected around noon when the sun's rays were nearly perpendicular to the canopy. After the light measurement, canopy closure was estimated visually, as described above. At the end of each day, parity countercheck was repeated for the two light meters. The parity check revealed that the reading for the meter designated for use in the forest gave 103.3% of the reading obtained from the meter designated for the open area. Percentage light penetration in the forest canopy was therefore calculated as: (100/103.3)*(Light measured in the

forest/ light measured in the open)*100.Canopy closure was calculated as 100 minus the canopy light penetration.

Plant data collection

High inter-annual climate fluctuations in the study sites (Reid and Ellis 1995, Stave et al., 2007) can affect tree seedlings and herbaceous species, therefore the data on the herbaceous layer was collected twice, during two wet seasons: November 2008 (year 1) and January 2010 (year 2). Herbaceous species and tree seedling data were collected from the 1 m^2 subplots, tree sapling data were collected from the 10 m^2 subplots, and data on the trees and merchantable stems were collected from the 100 m^2 plots.

In year 1, the regeneration of herbaceous species was abundant, but in year 2 it was poor. Therefore in year 2, the data collection from the four 1 m^2 subplots was modified. In year 1, percentage ground cover for each herbaceous species was used as a surrogate for productivity, and tree seedlings per species were counted. In year 2, both the herbaceous species and tree seedlings were counted according to species. The species were identified in the field, following Beentje (1994) and Dharani (2006). If the species could not be identified, its vernacular name was used, a specimen was collected for later identification at the national herbarium, and the name was cross-referenced with previous checklists (Morgan 1981, Timberlake 1994). The nomenclature of the resultant species list was checked against the international plant names index website (www.ipni.org.).

In the 10 m^2 subplots, all saplings (trees with < 2.5 cm diameter at breast height [dbh]) were identified and counted. In the 100 m^2 plots all trees or merchantable stems (dbh > 2.5 cm) per stump were identified and their dbh was measured with a diameter tape. Tree densities were recorded as stem density which classified any stem as a single tree irrespective of the number of merchantable stems per stump, and merchantable stems density, which was the cumulative sum for single stem trees and the total number of merchantable stems per stump in all the multistemmed trees.

Data analysis

One-way analysis of variance (ANOVA) was used to determine whether the three canopy types differed in abiotic, vegetation characteristics and diversity index. Prior to statistical analyses, variables were tested for normality using Levene's test in order to decide on the appropriate post hoc tests. Means for variables with equal variance were separated by Tukey post hoc test and those with unequal variance separated with Tamhane post hoc test. A t-test was used to check whether biotic and abiotic variables that differed amongst canopies also differed between Katilu and Nadapal. Chi-square test was used to evaluate the seedling abundance of tree species (*A. tortilis, F. sycomorus* and *Prosopis*) amongst canopies. T-test was also used to determine whether tree dbh, occurrence of multistems and densities differed between the *A.tortilis* trees in *Acacia* and Mixed stands, and between *Prosopis* trees found in *Prosopis* and Mixed stands.

Herbaceous species diversity was calculated for each plots with Shannon-Wiener diversity index ($H^{'}$) as $\Sigma\ (p_i)/\ln p_i)$ where p_i is the proportion of each species in a sample (Krebs 1999).

To evaluate how abiotic variables affect the regeneration of woody and herbaceous species, a forward multiple regression was done, in which the dependent variables were number of seedlings, number of herbaceous species, their ground vegetation cover and their density, and the independent variables were the density of merchantable stems, % sand, % silt, % carbon, pH, and dummies for *Prosopis* stands and Mixed species stands. With the exception of the dummy variables, all other variables were selected from ANOVA results based on their significant differences amongst canopies. Stem density and basal area were excluded from regression analysis because tree density was a sub component of the merchantable stems density, while basal area was derived from merchantable stem density. All statistical analyses were performed with Predictive Analysis Software (PASW) for Windows version 18, (formerly SPSS).

Finally, a canonical correspondence analysis (CCA) was done with CANOCO (Ter Braak 1997) to evaluate whether composition of herbaceous species differed amongst the three canopy types. The cumulative species presence / absence data was used for species variable and dummies for *Acacia,* Mixed and *Prosopis* canopies used as environmental variables. To avoid rare species distorting the results, only species that occurred in at least 10% of the plots were included in the analysis.

Results

Variation in abiotic factors amongst the three canopy types

Five out of the13 soil variables evaluated differed significantly with soil depth (data not shown), but the absolute differences were small, hence the values of the three soil horizons were pooled for subsequent analyses. Five soil variables differed significantly amongst the canopy types (Table 3.1). Soils under *Acacia* canopy had significantly higher silt, carbon and calcium concentrations and lower sand content than soils under *Prosopis* canopy (Table 3.1). Soil pH was slightly lower in the Mixed canopy plots than under the other two canopies (Table 3.1). Zinc was a trace element in many plots and could not be statistically compared amongst canopies.

Variation of tree characteristics amongst the three canopy types

Mean canopy closure did not differ significantly amongst canopy types ($F = 0.5$, $P = 0.6$). However, the range of canopy closure was narrow under *A. tortilis*, intermediate in Mixed species and wide under *Prosopis* canopies (Fig. 3.1a). The densities of trees, merchantable stems and seedlings were high under *Prosopis* species, intermediate in Mixed species and low under *Acacia* canopies (Table 3.2). The diameter structure among the three canopies revealed a near-normal distribution curve for *A. tortilis* trees under *Acacia* canopy (Fig. 3.1b), *Prosopis* species tree encroachment under mature *A. tortilis* in the Mixed species canopy (Fig. 3.1c) and a negative exponential structure of *Prosopis* species trees under *Prosopis* canopy (Fig. 3.1d). For *A. tortilis*, the characteristics of trees growing under *Acacia* canopies were similar to those of trees growing under Mixed species canopies (Fig. 3.2). In contrast, *Prosopis* species had more merchantable stems per stump and higher dbh, tree and merchantable stem densities under *Prosopis* canopy than under Mixed species canopy (Fig. 3.2).

The seedlings found in the plots were of six woody species and one palm species (Table 3.3). *Acacia tortilis, F. sycomorous* and *Prosopis* had a sufficient number of seedlings to be statistically tested, and their relative abundance varied significantly amongst canopy types (Table 3.3). *Ficus sycomorous* and *Prosopis* species seedlings were found in the three canopy types but *A. tortilis* seedlings were found only under *Acacia* canopy. Seedlings of the three species accounted

for 98.4% of the total seedlings: the vast majority (83.4%) was *Prosopis*, followed by *F. sycomorous* (7.3% and *A. tortilis* (6.7%).

Only *Prosopis* was found in the sapling category, and the saplings were mainly found under *Prosopis* canopy. Except for the soil pH, there was no difference between the plots established at Katilu and Nadapal in terms of any of the biotic and abiotic variables that differed amongst canopies (data not shown).

Herbaceous species under the three canopy types

The ground cover and number of herbaceous species was significantly higher under *A. tortilis* and Mixed species canopies than under *Prosopis* (Table 3.2). Similarly, the number of species and diversity ($H^{'}$) were higher under *Acacia* and Mixed species than under *Prosopis* canopies. Forty-six herbaceous species were recorded under the three canopy types in 2008, compared with fifty in 2010. The cumulative total species over the two years was sixty (Table 3.4). According to the previously mentioned checklists (Morgan 1981, Timberlake 1994), 72% of the species encountered are used as fodder, and 12% have potential fodder utility. *Achyranthes aspera* L.*,* was the most abundant herbaceous species (83% occurrence), followed by *Crotalaria deflersii* Schweinf. (78%), *Corchorus olitorius* L. (60%), *Commelina benghalensis* Forssk. (58%), *Setaria verticillata* (L.) P. Beauv. (55%), *Chenopodium pumilio* R.Br. (53%) and *Justicia caerulea* Blume (53%).

Effects of tree and soil variables on the herbaceous layer

Multiple regressions were used to evaluate the effects of abiotic conditions and canopy type on tree seedlings and the herbaceous layer. The dummy variable for *Prosopis* canopy had significant negative effects on all herbaceous characteristics and a positive significant effect on seedlings. Soil variables (e.g., sand or carbon or pH) had positive effects on herbs (Table 3.5a). *Prosopis* species merchantable stem density had positive effects on seedlings and negative effects on herbs ground vegetation cover and number, but no effects were found between *Acacia* merchantable stems density and the herbaceous layer (Table 3.5b). When the soil and tree variables were considered individually, their effects on seedlings and herbs were found to depend on the canopy type (Fig. 3.3a, b and c). For example herbaceous ground vegetation cover increased with silt content under

Acacia ($R^2 = 0.29$, $P < 0.05$, Fig.3.3a), herb number increased with carbon content under *Prosopis* ($R^2 = 0.63$, $P < 0.01$, Fig.3.3b) and seedling density increased with *Prosopis* species merchantable density under *Prosopis* ($R^2 = 0.28$, $P < 0.05$, Fig.3c) canopies, but no significant relationships were found in the other two canopy types for any of the aforementioned variables.

The canonical correspondence analysis indicated that canopy type alone explained 13.8% of the variation in species composition on the first two canonical axes. There was more clustering of herbaceous species near *Acacia* canopies than near the other two canopy types (Fig. 3.4). The typical herbaceous species for the *Acacia* canopy were *Amaranthus hybridus* L., *Brachiaria deflexa* (Schumach.) Robyns, *Chenopodium pumilio* R.Br. *Digitaria horizontalis* Willd. and *Justicia caerulea* Blume, for the Mixed species canopy they were *Commelina benghalensis* Forssk.and *Evolvulus alsinoides* (l.) L. Plate and for the *Prosopis* canopy they were *Amaranthus graecizens* Desf. and *Glycine wightii* (Wight & Arn.) Verdc.

Discussion

In this study we hypothesized that *Prosopis* canopies have negative effects on regeneration of indigenous trees and both productivity and both the productivity and diversity of herbaceous species. Study hypotheses were formulated under the assumption that edaphic factors were uniform and canopy closure different among the three canopy types. We found that soil under *Prosopis* and Mixed canopies differed in calcium, carbon sand and silt contents from soils under *Acacia* canopy but that herb ground cover, density and species number were similar under *Acacia* and Mixed canopies and higher than under *Prosopis* canopies. Seedling regeneration, tree densities and diameter structures differed among canopies but the canopy closure was homogenous. The characteristics of *A. tortilis* trees were similar under Acacia and Mixed stands, in contrast to the differences found between *Prosopis* tree characteristic under *Prosopis* and Mixed canopies. The density of merchantable *Prosopis* stems had negative impacts on herbaceous species characteristics, as evident from multiple regressions and the clustering patterns of herbaceous species in the *Acacia*, Mixed and *Prosopis* dummy variables.

Variation of soil conditions among canopies, past tree establishment and current regeneration

We predicted that soil conditions would be similar amongst canopies, as the plots were close to each other. Nevertheless, *Acacia* canopies turned out to have significantly high silt, carbon and calcium concentrations (Table 3.1). Such soil variation is not exceptional to this study as our findings were consistent with previous studies in the ecosystem (Coughenour and Ellis 1993, Patten and Ellis 1995, Stave et al 2003). However, soil variation appeared not to have influenced the past establishment of *A. tortilis*, as the tree characteristics in *Acacia* and Mixed canopies were similar, despite the variation in soil properties between the two canopies.

Previous studies have also demonstrated that *A. tortilis* can establish in a wide variety of soil types (Patten and Ellis 1995, Stave et al 2003) if environmental conditions favor its seed germination and seedling growth (Reid and Ellis 1995, Wilson and Witkowski 1998, Loth et al., 2005, Stave et al., 2006). Therefore, the notable absence of *A. tortilis* seedlings in Mixed and *Prosopis* canopies was probably due to *Prosopis* somehow inhibiting its seed germination. *Acacia tortilis* tree seeds were equally present in *Acacia* and Mixed canopies, and therefore seeds were unlikely to have been a limiting factor. Moreover, *A. tortilis* seeds are easily dispersed by livestock (Reid and Ellis 1995) and germinate readily shortly after rains, as previously demonstrated in the study area (Stave et al 2006). From the results, it can be concluded that the lack of *A. tortilis* seedlings in canopies with *Prosopis* was not limited by soils or seed availability. Although not quantified, litter accumulation was higher under Prosopis and Mixed canopies than under Acacia canopy (Muturi –field observations). Therefore, litter was the most likely constraint to the germination of *A. tortilis* seed as *Prosopis* species can be selectively allelopathic (Nakano et al., 2002, Iponga et al., 2009)

The finding that unlike *A. tortilis*, seeds of *F. sycomorus* germinated under all the canopies is consistent with a recent finding that *Prosopis* extracts stimulated root growth in *Ziziphus spina-christi* Willd. (Thoyabet et al., 2009), and that the invasive *Prosopis* species had no effect on the establishment of *Schinus molle* L. in the field (Iponga et al., 2009). The adverse effect of *Prosopis* canopy on *A. tortilis* and lack of such effects on *F. scymorous* indicate that the effect of *Prosopis* invasion on the regeneration of indigenous trees is species-specific.

The occurrence of *Prosopis* seedlings under *Prosopis* canopy and mixed canopies is consistent with recent research on *Prosopis juliflora* (El-Keblawy and Al- Rawai 2007) but contrary to a previous finding on autotoxicity (Warrag 1995). The most likely factors influencing the occurrence of *Prosopis* seedlings under *Acacia* canopy are the previously reported *Prosopis* seed dispersal mechanism (Shiferaw et al., 2004, Mworia et al., 2011), and the probable wide range of environmental conditions favorable for *Prosopis* species establishment. Our findings suggest that the sites invaded by *Prosopis* species were edaphically appropriate for *A. tortilis* establishment, but that *Prosopis* species are more environmentally opportunistic than *A. tortilis*. The fact that *Prosopis* species seedlings occurred in all three canopies whereas *A. tortilis* seedlings were found only under the *Acacia* canopy indicates that *A. tortilis* is losing out in areas that until now were available for its establishment.

Variation of tree characteristics among the canopies

We hypothesized that canopy closure should be highest in *Prosopis* stands because the tree densities were higher there. The *Prosopis* stands did indeed have higher tree densities, but mean canopy closure did not differ significantly amongst canopies because the plots varied greatly in their canopy closure (Fig. 3.1a). Although the density of *Prosopis* was high, most trees were in the lower diameter class (Fig. 3.1d) and tree canopies overlapped. An earlier study also reported a wide range of canopy closure in *A. tortilis* (Coughenour and Ellis 1993). In our study, the uniformity of canopies under *Acacia*, Mixed species and *Prosopis* canopies has two implications. First, the invading Prosopis species were gradually filling a previously more open *Acacia* canopies in mixed stands. Secondly, *Prosopis* species are gaining a canopy tree status similar to that exhibited by *A. tortilis* in this ecosystem.

The *A. tortilis* trees in the *Acacia* stands were mature, with near normal diameter distribution (Fig.1b), in contrast to the regenerating characteristic revealed by the negative exponential curve of the *Prosopis* species under *Prosopis* canopy (Fig. 3.1d). The density of *A. tortilis* trees found in this study is common for mature stands in the region (Oba 1990), but young stands can have a high

density that decreases with stand age (Reid and Ellis 1995). Similarly, the high density of *Prosopis* species under the *Prosopis* species canopy is consistent with the high densities found in areas newly invaded by *Prosopis* (van Klinken et al. 2006). Despite the high densities, the basal area under *Prosopis* species canopy was lower than in the other two canopies because the dbh in the *Prosopis* stand tended to be low (Fig. 3.1d). It remains to be seen whether in the long term self-thinning in the dense *Prosopis* stands will lead to a stand structure similar to that of the indigenous *A. tortilis* stands.

Effects of tree and soil variables on herbaceous species

We had predicted that herbaceous ground cover, density and diversity would be high under the relatively open *Acacia* stands and low in closed *Prosopis* stands. Herbaceous ground cover, density and diversity were high under *Acacia* stands and low in *Prosopis* stands (Table 3.2), supporting our third hypothesis. Our results are consistent with other studies that have found that herbaceous species productivity and diversity is reduced by *Prosopis* species (Schade et al., 2003, van Kilnken et al., 2006, El-Keblawy and Al-Rawai 2007, Kahii et al 2009).

Regression analysis revealed that herbaceous species were affected by soil conditions and by tree characteristics. Ground cover increased with silt content, whereas the number of herbaceous species increased with carbon content (Table 3.5a). Similarly, herbaceous species number increased with an increase in carbon (Table 3.5a). However, the effects of these soil variables on ground vegetation are canopy-dependent; the correlation between ground vegetation cover and silt content observed under the *Acacia* canopy was not found under the other two canopies (Fig. 3.3a). Whereas the positive effects of carbon and silt content on moisture content and nutrients are conceivable (Gicheru et al., 2003), the mechanisms behind contrasting trends of soil variables amongst canopies are not yet clear and can be a subject of further research.

Although edaphic factors varied amongst canopies and affected the herbaceous layer, they are unlikely to be the main driver of variation amongst canopies because of three reasons. First, *Acacia* and Mixed species canopies had different soil properties but the characteristics of the herbaceous layer were similar. Second, *Prosopis* and Mixed species canopies had similar soil properties but the characteristics of the herbaceous layer differed. Third, the two regression

analyses revealed that *Prosopis* dummy and merchantable stems adversely affected the herbaceous layer variables, but no such effects occurred for the mixed species dummy and *A. tortilis* trees and merchantable stems.

Including *Prosopis* stands as a dummy variable in the analysis, had a consistent independent and negative effect on herbaceous ground cover, species number and their density. This indicates that environmental factors other than, those studied underlie the inhibiting impact of *Prosopis* canopies. As already suggested for *A. tortilis* germination, a high litter accumulation under *Prosopis* species canopies may have inhibited the germination of herbaceous species through allelopathic or physical effects. This merits further research.

Whereas some past studies have attributed the negative impacts of *Prosopis* species on herbaceous layer to their canopies (Schade et al. 2003, El-Keblawy and Al-Rawai 2007, Teague et al., Kahii et al., 2009) the current study did not reveal a direct effect of canopy on the herbaceous species characteristics measured. Instead, reduction of productivity and biodiversity of herbs can be attributed to the high stem density in *Prosopis* (Table 3.2), as reported previously in Australia (van Klinken et al., 2006). Nevertheless, it is conceivable that tree density may not have direct effects on herbs, and that associated factors such as surface litter accumulation could be more plausible. Litter hampers seed germination physically and chemically, but can also improve seed germination by ameliorating temperature and moisture availability (Donath and Eckstein 2008, Hata et al., 2010). The greater litter accumulation noticed under the *Prosopis* canopy is the most likely possible cause of the observed negative impacts of *Prosopis* on herbs.

Conclusion

Prosopis is invading the riverine forest, with negative impacts on the regeneration of native *A. tortilis*, and the productivity and diversity of the herbaceous layer. The negative impact is not due to dense shading or changed soil conditions, but seems rather to be the result of negative allelopathic effects. *Prosopis* has the potential to substantially modify ecosystem structure and functioning in these riverine systems, and the loss of biodiversity and of the productivity of the herbaceous layer may have negative consequences for subsistence grazing in the region. More periodic assessments are recommended, in order to understand the

processes and rates of loss in herbaceous species diversity and productivity that is brought about by *Prosopis* species. To avoid further negative impacts in this riverine ecosystem, *Prosopis* should be controlled.

Table 3.1. Soil characteristics under three tree canopy types (*Acacia*, Mixed species and *Prosopis* species). Analysis of variance results are shown by F and corresponding P values if significantly different amongst canopies or Ns if not significant. Means and standard errors are shown; values in the same row followed by a different letter are significantly different at P<0.05 (Tukey post-hoc test).

Soil variable	F	P	Acacia	Mixed	Prosopis
Sand (%)	4.9	0.013	47.6±5.19 b	72.6±4.94 a	64.4±5.74 a
Silt (%)	9.5	0.000	27.2±3.30 a	11.1±2.11 b	14.1±2.19 b
Clay (%)	Ns		25.2±4.14	16.3±3.54	21.6±3.98
pH	15.3	0.000	7.4±0.05 a	7.1±0.08 b	7.5±0.03 a
Carbon (%)	6.0	0.006	0.68±0.058 a	0.49±0.059 b	0.39±0.068 b
Calcium (meq)	4.9	0.013	10.5±0.70 a	6.3±1.40 b	8.3±0.78a b
Nitrogen (%)	Ns	-	0.10±0.007	0.09±0.008	0.08±0.008
Phosphorus (meq)	Ns	-	1.2±0.06	1.0±0.10	1.1±0.08
Potassium (meq)	Ns	-	1.9±0.20	1.5±0.28	1.5±0.26
Magnesium (meq)	Ns	-	2.1±0.28	1.7±0.51	1.6±0.28
Manganese (meq)	Ns	-	0.85±0.118	0.69±0.216	0.62±0.120
Iron (meq)	Ns	-	0.37±0.040	0.41±0.062	0.35±0.029
Copper (meq)	Ns	-	0.009±0.001	0.007±0.001	0.006±0.001

Table 3.2. Characteristics of trees and herbaceous plants in three canopy types (*Acacia*, Mixed species and *Prosopis*). Analysis of variance results are shown by F and corresponding P values. Means and standard errors are shown; values in the same row followed by a different letter are significantly different at P<0.05 (Tamhane or Tukey post-hoc tests).

Plant variable	**F**	**P**	**Acacia**	**Mixed**	**Prosopis**
Stem density (#/ha)	9.9	0.000	333±61 b	756±138 b	1225±198 a
Merchantable stems (#/ha)	57.2	0.000	387±60 b	889±190 b	3031±254 a
Basal area (m^2/ha)	15.7	0.000	37.6±4.09 a	36.3±3.24 a	15.5±2.04 b
Seedling density (#/ha)	8.6	0.001	9464±3024 ab	19722±3760 b	71093±16294 a
Herb cover (%)	24.9	0.000	33.5±3.90 a	29.3±3.93 a	5.3±1.84 b
Herb density (#/m^2)	6.3	0.004	41±7.8 a	38±13.2 a	7±4.6 b
Species number (#/ 4 m^2)	20.5	0.000	15±1 a	14±3 a	6±1 b
Herb diversity ($H^{'}$)	3.6	0.042	1.75±0.11 a	1.40±0.20 ab	1.18±0.13 b

Table 3.3. Mean tree seedlings density (No. / ha) found under each canopy type (*Acacia*, Mixed species and *Prosopis*). The mean is based on the two years but Chi square test was based on mean for plot counts. Chi square and P-values are shown for the three species with a sufficient number of individuals.

Species	*Acacia*	Mixed	*Prosopis*	X^2	P
Acacia tortilis	6167	0	0	61.7	<0.001
Prosopis spp.	4500	14444	58594	351.1	<0.001
Ficus sycomorus	833	4167	1719	13.2	<0.01
Grewia bicolar	167	0	0	-	-
Hyphaene compressa	167	0	313	-	-
Ricinus communis	0	0	156	-	-
Ziziphus mauritiana	333	278	0	-	-

Table 3.4: Herbaceous species found under each canopy type and the cumulative number of species under each canopy. Most species are used as fodder (✓) or have fodder potential (*). Occurrence of a species under each canopy is denoted by X and the absence shown by -:

No.	Species	% Occurrence	Family	Fodder use	Occurrence of species under canopies of:		
					A. tortilis	Prosopis	Mixed species
1	*Abution hirtum* (Lam.) Sweet	10	Malvaceae	✓	X	X	X
2	Abutilon mauritianum (Jacq.) Medik.	22.5	Malvaceae	✓	X	X	X
3	*Acalypha fruticosa* Forssk.	27.5	Euphorbiaceae	✓	X	X	X
4	*Achyranthes aspera* L.	82.5	Amaranthaceae	*	X	X	X
5	*Aerva lanata* (L.) Schult	15	Amaranthaceae	*	X	X	-
6	*Amaranthus graecizens* Desf.	15	Amaranthaceae	✓	X	-	-
7	*Amaranthus hybridus* L.	35	Amaranthaceae	✓	X	X	X
8	Aristida mutabilis Trin. & Rupr.	10	Poaceae	✓	X	-	X
9	*Asparagus falcatus* L.	2.5	Asparagaceae	-	-	X	-
10	*Barleria acanthoides* Vahl	10	Acanthaceae	✓	X	-	-
11	*Bidens hildebrandtii* O. Hoffm	2.5	Asteraceae	*	-	-	X
12	*Bidens pilosa* L.	10	Asteraceae	*	X	X	X
13	*Brachiaria deflexa* (Schumach.) Robyns	27.5	Poaceae	✓	X	X	X
14	*Calotropis procera* (Ait.) Ait. f.	2.5	Asclepiadaceae	✓	X	-	-
15	*Cenchrus cilliaris* L.	40	Poaceae	✓	X	X	X
16	*Chenopodium pumilio* R.Br.	52.5	Chenopodiaceae	-	X	X	X
17	*Chloris virgata* Sw.	2.5	Gramineae	✓	X	-	-
18	*Coccinia grandis* (L.) Voigt	32.5	Cucurbitaceae	✓	X	X	X
19	*Combretum aculeatum* Vent.	10	Combretaceae	✓	X	X	X

Table 3.4: Herbaceous species found under each canopy type and the cumulative number of species under each canopy. Most species are used as fodder (✓) or have fodder potential (*). Occurrence of a species under each canopy is denoted by X and the absence shown by -.

20	*Commelina benghalensis* Forssk.	57.5	Commelinaceae	✓	X	X	X
21	*Corchorus olitorius* L.	60	Tiliaceae	-	X	X	X
22	*Crotalaria deflersii* Schweinf.	77.5	Papilionaceae		X	X	X
23	*Cucumis dipsaceus* Spach	15	Cucurbitaceae	✓	X	X	-
24	*Cucumis prophetarum* L.	20	Cucurbitaceae	✓	X	X	X
25	*Cynodon dactylon* (L.) Pers.	2.5	Poaceae	✓	X	-	-
26	*Cyphostemma manieriense* (Th. Fr. jr) Desc	5	Vitaceae	✓	X	-	-
27	*Cyperus articulatus* L.	2.5	Cyperaceae	-	-	X	-
28	*Digitaria gayana* (Kunth) A. Chev	45	Poaceae	*	X	X	X
29	*Digitaria horizontalis* Willd.	2.5	Poaceae	*	X	-	-
30	*Euphorbia granulata* Forssk.	5	Euphorbiaceae	✓	X	-	-
31	*Evolvulus alsinoides* (l.) L. Plate	25	Convolvulaceae	✓	X	X	X
32	*Geigeria acaulis* Oliv. & Hiern	2.5	Compositae	✓	X	-	-
33	*Glycine wightii* (Wight & Arn.) Verdc	17.5	Fabaceae	✓	X	X	X
34	*Gynandropsis gynandra* Briq.	2.5	Capparaceae	✓	X	-	-
35	*Hibiscus fuscus* Garcke	7.5	Malvaceae	-	X	-	-
36	*Hibiscus ovalifolius* Forssk.	2.5	Malvaceae	✓	X	-	-
37	*Indigofera errecta* Thunb.	5	Leguminosae	-	X	-	-
38	*Ipomoea wightii* Choisy	47.5	Convolvulaceae	-	X	X	X
39	*Justicia caerulea* Blume	52.5	Acanthaceae	✓	X	X	X

40	*Justicia odora* Vahl	2.5	Acanthaceae	✓	X	-	-
41	*Leucas glabrata* (Vahr) R. Br	12.5	Labiatae	✓	X	X	X
42	*Maerua subcordata* (Gilg) DeWolf	2.5	Capparaceae	✓	X	-	-
43	*Maerua triphylla* T. Durand & Schinz	7.5	Capparaceae	✓	X	X	X
44	*Momordica trifoliolata* Hook. f. Mathew	7.5	Cucurbitaceae	✓	X	-	X
45	*Ocimum staminosum* Baker	20	Lamiaceae	✓	X	-	X
46	*Plectranthus ignarius* (Schweinf.) Agnew	2.5	Labiatae	✓	-	-	X
47	*Portulaca oleracea* L.	15	Portulacaceae	✓	X	X	-
48	*Portulaca quadrifida* L.	17.5	Portulacaceae	✓	X	X	-
49	*Seddera hirsuta* Damm. ex Hallier f.	5	Convolvulaceae	✓	X	-	-
50	Senna Spp	2.5	Caesalpiniaceae	-	-	X	-
51	*Setaria verticillata* (L.) P. Beauv.	55	Gramineae	✓	X	X	X
52	*Sida ovata* Forssk.	45	Malvaceae	✓	X	X	X
53	*Solanum coagulans* Forsk	5	Solanaceae	✓	X	-	-
54	*Solanum incanum* L.	10	Solanaceae	✓	X	X	-
55	*Solanum nigrum* L.	2.5	Solanaceae	✓	-	-	X
56	*Sorghum bicolor* (L.) Moench	2.5	Poaceae	✓	X	-	-
57	*Sonchus oleraceus* L.	2.5	Asteraceae	*	-	-	X
58	*Tephrosia uniflora* Pers	20	Leguminosae	✓	X	X	X
59	*Withania sommifera* (L.) Dunal	2.5	Solanaceae	✓	-	X	-
60	*Zehneria scabra* Sond.	2.5	Cucurbitaceae		-	-	X
Total number of species					**51**	**34**	**33**

Table 3.5a. Results of multiple regressions of tree seedlings and herbaceous characteristics against biotic stand characteristics. Only those characteristics that differed significantly amongst canopies were included (see Tables 3.2 and 3.3). *Prosopis* canopy and Mixed species canopy were included as dummy variables. Standardized regression coefficients (β), significance levels (P), F value and coefficient of determination (R^2) are shown.

Variable	Seedlings		Ground cover		Herb density		Herb diversity	
	β	P	β	P	β	P	β	P
Calcium (meq)	-		-		-		-	
Sand (%)	-		-		0.65	0.003	-	
Silt (%)	-		0.28	0.010	-		-	
Carbon (%)	-		-		0.87	0.000	0.40	0.001
pH	-		-		0.36	0.016		
Merchantable stems density (#/ha)	-		-		-		-	
Dummy Mixed	-		-		-		-	
Dummy Prosopis	0.57	0.000	-0.67	0.000	-0.45	0.005	-0.55	0.000
R^2	0.33		0.64		0.53		0.65	

Table 3.5b. Results of a repeat of multiple regressions of [5a], but with substitution of dummy variables with *Acacia tortilis* and *Prosopis* species merchantable stem densities.

Test variable	Seedlings		Ground cover		Herbs density		Species number	
	β	P	β	P	β	P	β	P
Calcium (meq)			-		0.41	0.028	-	
Sand (%)	-		-		0.88	0.000	-	
Silt (%)	-		0.70	0.000	-		-	
Carbon (%)	-0.31	0.020	-0.32	0.047	0.86	0.000	0.43	0.000
pH			-0.57	0.000			-0.25	0.026
Merchantable *Acacia* stems density (#/ha)	-		-		-		-	
Merchantable *Prosopis* stems density (#/ha)	0.40	0.003	-0.35	0.003	-		-0.35	0.004
R^2	0.34		0.61		0.44		0.57	

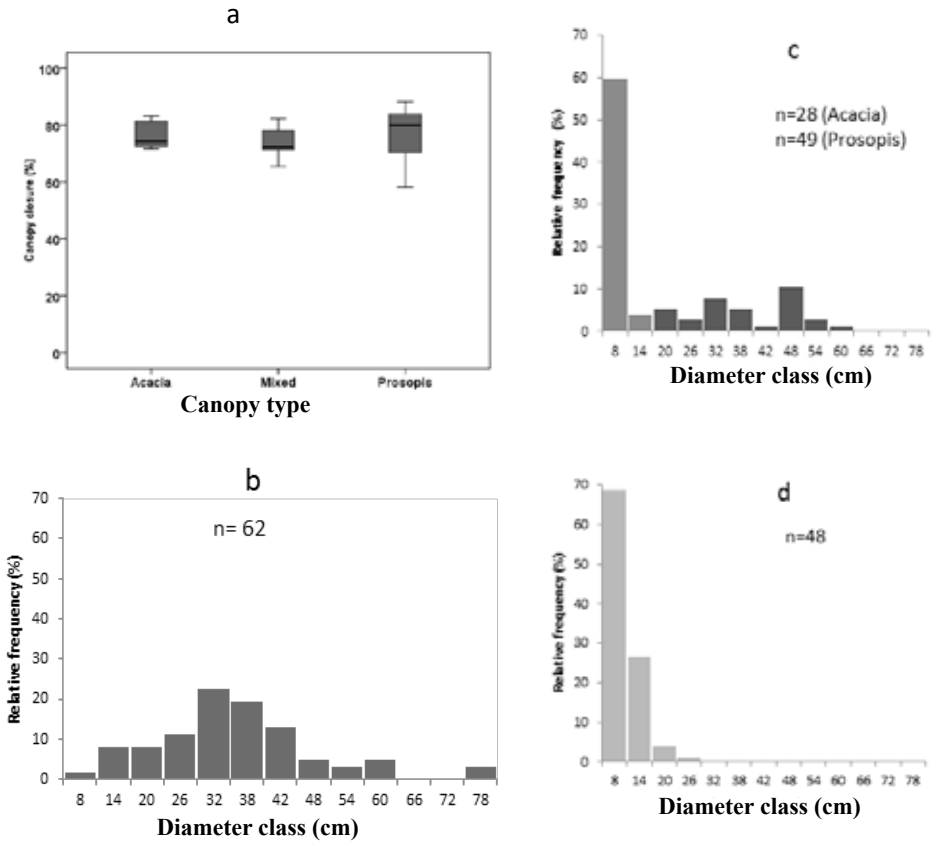


Figure 3.1: Canopy closure among the canopy types (a), relative frequency of diameter at breast height (dbh) for trees found under *Acacia* (b), Mixed species (c) and *Prosopis* (d) canopies. For figures b-d, diameter classes have a width of 6cm, starting from 2.5 (2) cm onward. For each class the upper limit is shown. All trees per canopy type were pooled and their total number is shown in each graph. The dark bars are *Acacia tortilis*, the pale bars are *Prosopis* spp.

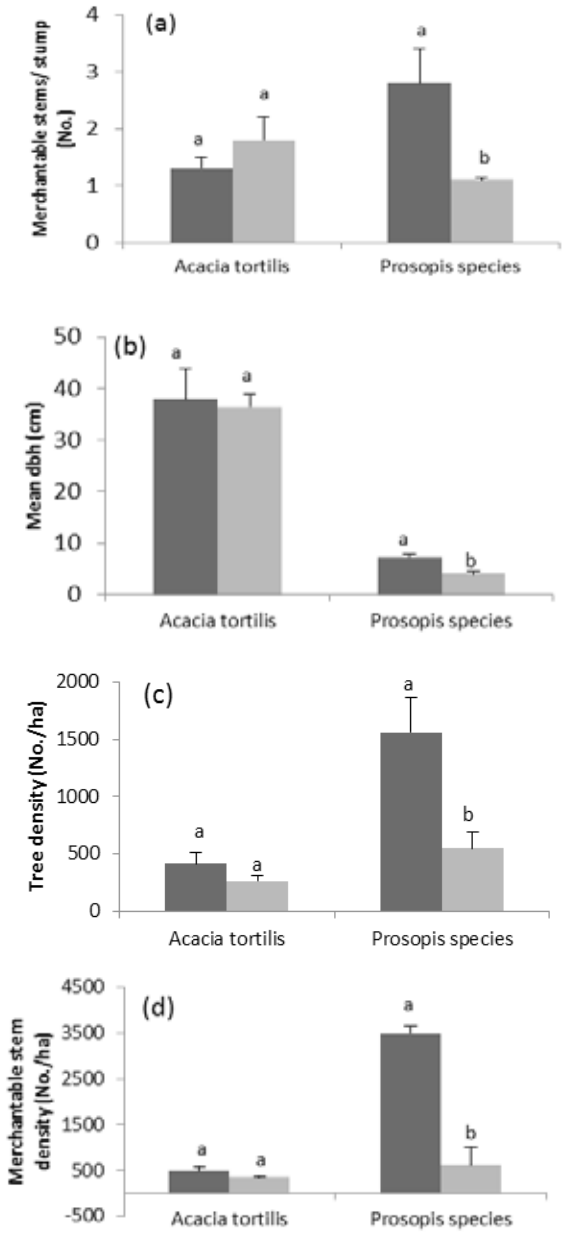


Figure 3.2: Merchantable stems per stump (a) diameter at breast height (b), tree density (c) and merchantable stems density (d) of *Acacia* and *Prosopis* trees growing in *Acacia* or *Prosopis* canopies (dark bars) and Mixed species canopies (grey bars). Means and standard errors are shown. Bars within species, accompanied by different letters are significantly different at $P<0.05$ t-test).

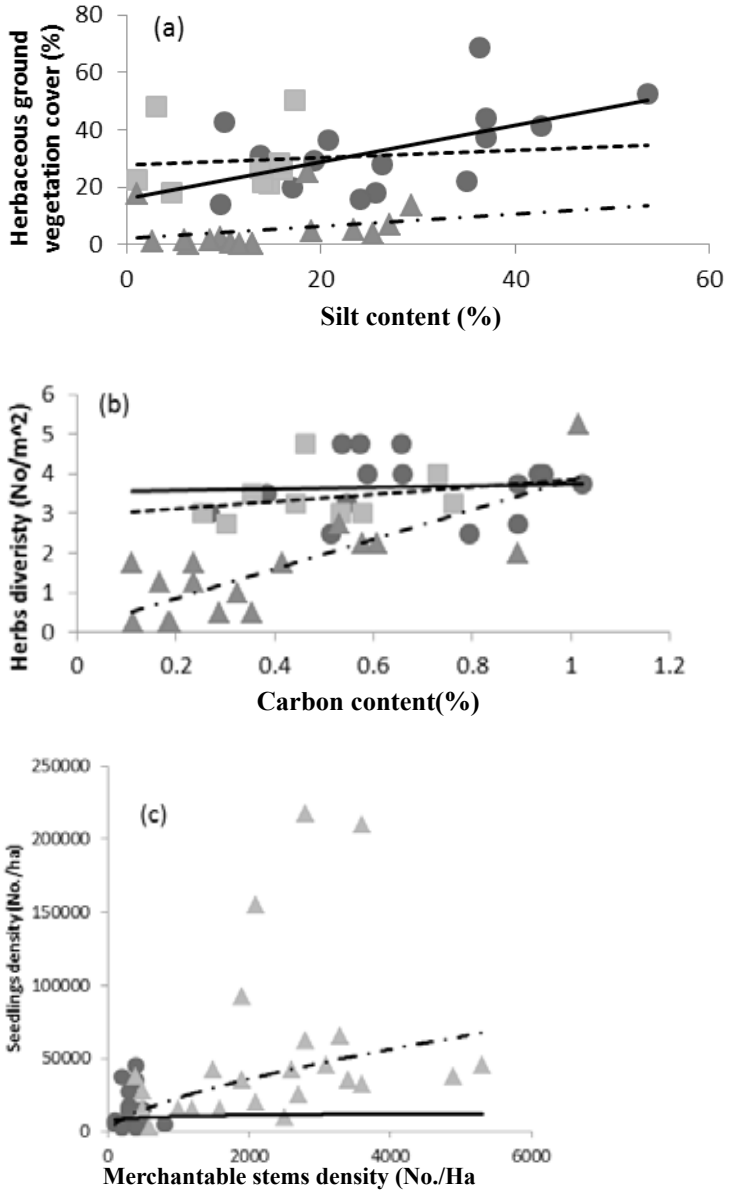


Figure 3.3: Herbaceous species ground vegetation cover plotted against silt content (a), herbaceous species diversity plotted against carbon content (b) and seedling density plotted against merchantable stem density (c). The canopy types are shown with different symbols and lines; Acacia (circles and unbroken line, Mixed (squares and dashed lines), and *Prosopis* (triangles and dashed-and-dotted line). Regression lines were significant for *Acacia* (a) and *Prosopis* (b and c) canopies.

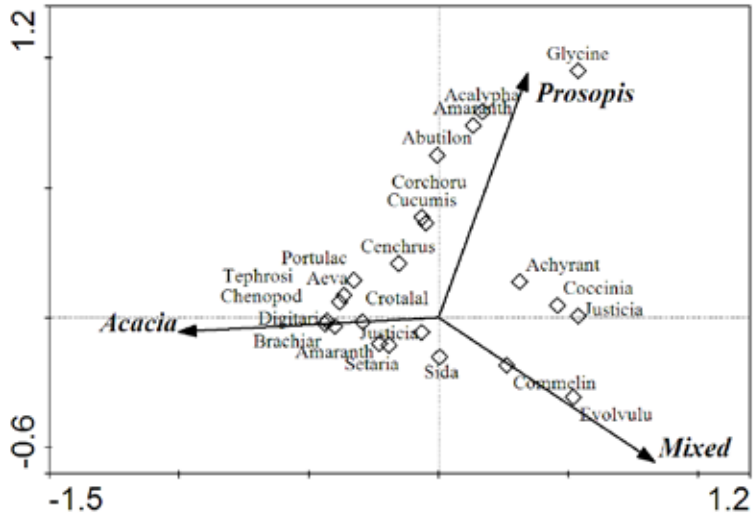


Figure 3.4: Canonical Correspondence Analysis (CCA) of herbaceous species with canopy type (Acacia, Mixed, and Prosopis) as dummy variables. Cummulative species presence / absence for two years was used. The first and second canonical axes together accounted for13.8% of the variation in herbacuous species composition. Species are shown by the first eight letters of their genus names (full species names are shown in Table 3.4).

Chapter 4

Prosopis litter inhibits germination and stimulates seedling growth of dry woodland species

Gabriel M. Muturi, Lourens Poorter, Godefridus M.J. Mohren and Pauline Bala

Submitted

Abstract

Prosopis species invade arid woodlands in Kenya, and have been found to replace indigenous *Acacia* stands. We performed a number of greenhouse studies to test the hypothesis that dense shade and allelopathic effects may reduce the germination and growth of *Acacia* more strongly than that of *Prosopis*. We first evaluated the germination of *Acacia* and *Prosopis* seeds with increasing concentration of unleached and leached *Acacia* and *Prosopis* litter in soil. We then evaluated the performance of *Acacia* and *Prosopis* seedling in response to concentration of *Acacia* and *Prosopis* litter and different irradiance. Phenols in unleached *Prosopis* litter inhibited germination of *Acacia* and *Prosopis* seeds more strongly than phenols in unleached *Acacia* litter. Leached litter had no effect on seed germination and enhanced the growth and shoot nutrient concentrations of *Acacia* and *Prosopis* seedlings. The findings suggest that the lack *Acacia* seedlings under *Prosopis* canopies in the field may be partially explained by *Prosopis* allelopathy on *Acacia* seed germination. However, leached litter may accelerate seedling growth as could be the case during heavy prolonged rains.

Keywords: *Acacia tortilis*; Phenols; Unleached litter; Leached litter

Introduction

Prosopis species have become invasive in many regions of the world after naturalization (Pasiecznik et al. 2001). Enemy escape, hybridization (Zimmerman 1991), prolific seeding and subsequent seed dispersal by livestock and wildlife and water (Shiferaw et al. 2004; Mworia et al. 2011) are among the factors that contribute to their invasiveness. The invading species or their hybrids have higher tree densities and more closed canopies than that found in their natural range (Sharifi et al. 1982; Dussart et al. 1998; van Klinken et al. 2006) or that of indigenous tree species commonly found in the invaded landscapes (Legesse and Eddy 1990; Oba 1998). Additionally, *Prosopis* have higher litter production than other dryland species (Garg 1992; Garg and Jain 1992); resulting in a thick litter layer below *Prosopis* canopies (van Klinken et al. 2006). Litter can affect seed germination and seedling growth by both physical and chemical mechanisms depending on species, thickness and decomposition rates (Hata et al. 2010; Ruprecht et al. 2010). Physically, litter prevents radicle-soil contact for root establishment and inhibits shoot emergence to access photosynthetic light. Allelochemicals released from fresh and decomposing litter are responsible for chemical inhibition mechanisms on seed germination and seedling growth (Goel et al. 1989; Inderjit et al. 2011).

In those areas where *Prosopis* invade, it tends to have a negative impact on the understory vegetation. Diversity, density and productivity of herbaceous species is reportedly lower under closed canopies and isolated trees of *Prosopis* species, than under native tree species canopies (Kahii et al. 2009; Muturi et al. in prep.) or in more open areas (Schade et al. 2003; El-Keblawy and Al-Rawai 2007). The negative impacts of *Prosopis* on herbaceous species are widely studied and fairly understood. For example, in Australia a decrease in ground grass cover is attributed to thick surface litter layer under *Prosopis* canopies (van Klinken et al. 2006). Other studies have related decrease of herbaceous species diversity, density and productivity to the deep shade under *Prosopis* crowns (Schade et al. 2003; El-Keblawy and Al-Rawai 2007; Kahii et al. 2009). Moreover, allelopathy and autotoxicity of *Prosopis* species have also been demonstrated (Goel et al. 1989; Warrag 1995).

Studies on impacts of *Prosopis* species on tree regeneration are scarce and effects are therefore not yet well understood. In some cases, *Prosopis juliflora*

DC. regenerates well below its own canopy (El-Keblawy and Al-Rawai 2007), despite reputed autotoxicity (Warrag 1995). *Prosopis* hybrid also regenerate below own canopy (van Klinken et al. 2006). Other studies found no effects of *Prosopis* canopy on growth of *Schinus molle* L. seedlings under savannah conditions (Iponga et al. 2009) or *P. juliflora* leaf-leachate on root growth of *Ziziphus spina-christi Willd.* in greenhouse experiments (Thobayet et al. 2008). Recently, *Prosopis* species and *Ficus sycomorus L.* were found to regenerate below *Prosopis* and *A. tortilis* canopies (Muturi et al. submitted.). In contrast, no *A. tortilis* regeneration was found below *Prosopis* species canopy which was thought to be caused by the inhibiting effect of *Prosopis* litter. Both *Acacia* and *Prosopis* species are shade intolerant (Smith and Shackleton1988; Vilela and Ravetta 2000), although their comparative growth response to light has not yet been investigated. Phenotypically*, Prosopis* species are highly plastic (Hunziker et al. 1986; Guevara et al. 2010) and growth is therefore expected under a range of light environments.

The objective of this study was to determine the effects of *A. tortilis* and *Prosopis* species litter on seed germination, and seedling performance of *A. tortilis* and *Prosopis* species. Additionally, the effect of irradiance on seedling performance was evaluated. It was hypothesized that; 1) *Prosopis* would inhibit seed germination and seedling growth of *A. tortilis* but not of itself, 2) inhibition of germination and growth is caused by allelopathy and not by physical mechanisms and 3) *Prosopis* species realize faster growth than *A.tortilis* under similar litter and irradiance treatments.

Materials and methods

Study species and research site

This study focuses on *Prosopis* species and *A. tortilis* from the Turkwell riverine forest, in Northern Kenya. In Kenya, *Prosopis* is thought to consist of a complex of interbreeding species, and identification of *Prosopis* germplasm is discussed by Muturi et al. (submitted). Henceforth, *Prosopis* species and *A. tortilis* will be referred to as *Prosopis* and *Acacia* respectively. To evaluate the effect of litter leachate, *Acaci*a and *Prosopis* leaves were collected from trees growing naturally along the Turkwel Riverine Forest near Nadapal (Latitude 3^{o}00'N Longitude 35^{o}30'E). The leaves were sundried at air temperature and transported to the laboratory at Kenya Forestry Research Institute's Kitui Regional

Centre near Kitui Town (Latitude 1°23'S Longitude 38°00'E). Three experiments were carried out in the greenhouse at Kitui Regional Research Centre. A first experiment was carried out to determine effects of unleached and leached litter on seed germination, a second experiment carried out to evaluate the effect of litter and irradiance on seedling growth, and a third experiment was carried out to determine leaching trend of soluble phenols from Acacia and Prosopis litter.

Preparation of potting media and seed pretreatment

Dry *Acacia* and *Prosopis* leaves were ground separately with a Willey mill to pass through a 2 mm sieve (Warrag 1995). Freshly collected woodland soil was mixed with sand using sand: soil volume ratio of 80:20. Subsequently, the three media types are referred to as *Acacia* litter, *Prosopis* litter and soil. The three media types were used to prepare potting media,. When litter and soil are mixed, they are referred to as soil with *Acacia* litter or soil with *Prosopis* litter, and the litter ratio used to define volumetric percentage of litter concentration. Pure soil was used as control.

To test effect of *Acacia* and *Prosopis* litter on seed germination and seedling growth each litter was thoroughly mixed with soil using predetermined litter: soil ratios based on similar studies (Warrag1995; Diallo et al. 2006). For the germination experiment, volumetric litter: soil ratios of 1:10, 1:8, 1:6, 1:4, 1:2 and 1:1 were used, which corresponds to a volumetric litter concentration of 9.1, 11.1, 14.3, 20.0, 33.3 and 50.0 %. In seedling growth experiment litter: soil ratios of 1:20, 1:15 and 1:10 were used, corresponding to a volumetric litter concentration of 4.8, 6.3 and 9.1%. In both cases, soil without litter added was used as a control.

To stimulate germination, *Acacia* seeds were pretreated by soaking for 20 minutes in concentrated sulphuric acid and rinsed with tap water (Masamba 1994). Acid pretreated *Acacia* seeds and fresh *Prosopis* seeds were then soaked in tap water in a growth chamber at 30°C overnight. The overnight soaking achieved uniform water imbibition in both species and facilitated selection of good experimental seeds. Such seeds had intact seed coats and a visibly expanded radicle.

Germination experiment

To evaluate the effect of litter concentration on seed germination, two germination experiments were carried out; first seeds were germinated in unleached litter, and subsequently seeds were germinated in leached litter. Pretreated *Acacia* and *Prosopis* seeds were germinated in two unleached litter types (*Acacia* or *Prosopis*), six percentages of litter concentrations (9.1, 11.1, 14.3, 20.0, 33.3 and 50.0) and a soil control, for each species. Two pretreated seeds were sown in a pot and replicated 10 times per litter concentration for each litter type and the control. Hence, in total 260 pots were used; 2 species x ([2 litter types x 6 litter concentrations] + a soil control) x 10 replicates). After completion of this unleached litter germination experiment, the litter was leached daily for 14 days, using 100ml tap water per pot. Subsequently, the germination experiment was repeated, but this time with the leached litter. In both experiments germination was assessed daily, and pots were watered if needed.

Growth experiment

To evaluate the effect of irradiance and litter on seedling growth, a growth experiment was carried out, in which *Acacia* and *Prosopis* seedlings were grown at four irradiance levels (10, 25, 46 and 55%) in two litter types (*Acacia* or *Prosopis*) with four litter concentrations (0, 4.8, 6.3 and 9.1). The 0% litter concentration refers to pure soil control. Each treatment combination was replicated in three blocks, and with three pots. Hence, in total 576 pots were used; 2 species x 4 irradiance levels x ([2 litter types x 4 litter concentrations] x 3 blocks x 3 pots. The blocks were for testing uniformity within a shade treatment. At harvest, there were a total of 564 seedlings, which was achieved by a repeated sowing after poor germination in the initial sowing. Repeated sowing was undertaken 3 weeks after the initial sowing, using four pretreated seeds and thinning the germinants to one seedling after three weeks.

Four irradiance treatments were created in the greenhouse using three different types of shade netting and a fourth control treatment consisted of greenhouse conditions without any shading. The corresponding irradiance levels were determined with Minolta light meters following Muturi et al. (submitted), and corresponded to 10, 25, 46 and 55% of total irradiance outside the greenhouse. These irradiance levels reflect the range of light condition found under *Acacia* and *Prosopis* canopies in the field (Muturi et al. submitted).

Litter treatments were randomized within the four light treatments, using three blocks within each light treatment. The experiment was concluded after three months. Seedlings were harvested, presence of nodulation recorded, the seedlings oven-dried at 40^{o} C until constant weight, their dry weights determined and shoots analyzed for nutrient concentration. Because of cost implications, nutrients were only analyzed for control, 4.8 and 9.1 litter concentrations for each litter type. Also the two extreme irradiance (10% and 55%) treatments were sampled for nutrient concentration analysis. This facilitated testing of effect of potting media (soil, soil with *Acacia* and soil with *Prosopis*), litter concentration (0, 4.8 and 9.1), irradiance (10% and 55%) and species (*Acacia* and *Prosopis*) on seedling shoot nutrient concentrations. Procedures for nutrient extraction and determination of their concentration in the leaves are described later.

At the beginning of germination and seedling growth experiments, 600ml of potting medium was potted in ≈ 800 ml pots, each pot was placed on a leachate trap and all the pots were uniformly watered to field capacity. A leachate trap is an impervious plastic plate used to trap and retain litter leachate from the pot, and prevents inter-pot contamination in the event of leachate spillover on greenhouse floor. Watering frequency differed amongst treatments, as the water holding capacity varies with litter concentration, and the evapotranspiration varied with irradiance. Depending on assessed needs, pots for each treatment unit were watered with 50ml of tap water to moisten the upper surface layer while the trapped leachate could moisten the medium in the pot through capillary activity.

Litter leaching experiment

Temporal effects of water leaching on concentration of soluble phenols in each litter type were tested over a period of five weeks. 600ml of each litter type was potted in ≈ 800 ml pots and a leachate trap used for each pot as previously described. The litter was watered to saturation with tap water at the beginning of the experiment. Subsequently, all pots were uniformly watered with 100ml of tap water every day. Four pots per leached litter type were sampled at weekly intervals over five weeks. Surface litter was then sampled from each pot and air dried in the laboratory. At the end of the leaching experiment, each of the two fresh litter types were analyzed for nitrogen, phosphorus, potassium and soluble phenols; and leached litter samples analyzed for soluble phenol concentrations, as described later .

Extraction of litter phenols and litter and leaf nutrients

Litter and seedling samples were ground and oven dried at 40°C until constant weights (Palm and Rowland 1997). All the litter samples were assayed for soluble phenols by Folin – Denis Method (Waterman and Mole 1994). Thereafter, absorbance was measured at 760nm and phenol concentrations calculated using a calibration curve standard with known concentration of tannic acid whose absorbance was also measured at 760nm. Nitrogen, phosphorus and potassium were extracted from control litter and seedlings samples following the Kjeldahl wet digestion. Concentration of nitrogen in the digest of each sample was calculated, phosphorus concentration determined calorimetrically and potassium concentration measured by flame photometry.

Statistical analysis

To evaluate the effect of litter concentration on seed germination a linear regression was performed per species, using the average percentage of seed germination per litter treatment as dependent variables. To evaluate the effect of species, light, potting medium (soil, soil mixed with *Acacia* litter and soil mixed with *Prosopis* litter) and litter concentration (0 [soil], 4.8, 6.3 and 9.1 volumetric percent of litter) on seedling growth, a four-way analysis of variance (ANOVA) was used. A Tukey, Tamhane or t-test post hoc test was used to evaluate differences amongst treatment levels. A multiple logistic forward regression was used to evaluate effect of potting media, litter concentration, light and species on seedling nodulation. All statistical analyses were performed with Predictive Analysis Software (PASW) for Windows version 18, (formerly SPSS) and GenStat version 13.

Results

Effects of litter type and litter leaching on seed germination

Germination of both species decreased significantly with increase of unleached litter concentration in the potting media, but more strongly so for *Prosopis* litter than for *Acacia* litter (Fig. 4.1a, b). Surprisingly, *Prosopis* litter had a stronger inhibiting effect on its own germination than on *Acacia* germination, as indicated by the steeper slope (Fig. 4.1a). Yet, as *Prosopis* seeds germinated more readily (90% germination at zero litter content, compared to ca 50% for *Acacia*),

Prosopis germinated better at the same *Prosopis* litter concentration compared to *Acacia*. Leached *Prosopis* litter had no effect on seed germination (Fig. 4.1c), whereas leached *Acacia* litter negatively affected *Prosopis* germination only at high concentrations (Fig. 4.1d).

Effect of litter type, species and irradiance on seedling biomass

Seedling biomass production was significantly influenced by irradiance, potting medium, litter concentration and the interaction between species and potting medium (Table 4.1). On the contrary, species, and their interactions with litter concentration, and with irradiance had no effects on seedling biomass production (Table 4.1). Therefore, we focused further analyses on the soil control and highest (9.1%) litter concentration in each litter type at the four light treatments for each species. For all irradiance treatments, biomass was significantly higher in seedlings grown in soil with litter than in seedlings grown in soil without litter (Figs. 4.2 and 4.3). *Acacia* had higher biomass than *Prosopis* in the soil control, but biomass of the two species was similar when grown in soil with either *Acacia* or *Prosopis* litter (Fig. 4.3). This is also indicated by the significant interaction effect between species and potting medium on biomass (Table 4.1). Biomass of *Acacia* and *Prosopis* seedlings increased in a similar curvilinear way with irradiance (Figs. 4.2a & b).

Effect of litter type, species and irradiance on seedling nutrient concentrations

Shoot nutrient (N, P, K) concentrations differed significantly with species and irradiance Table 4.2). Species' effect on shoot nutrient concentration depended on irradiance, potting media, litter concentration and the specific nutrient, whereas nutrient concentrations tended to be lower at high irradiance (Table 4.3). Potting media and litter concentration had little or no effect on nitrogen and potassium concentrations, but strong effects on phosphorus concentrations. Shoot phosphorus concentrations were highest in soil without litter, intermediate for soil with *Acacia* litter, and lowest for soil with *Prosopis* litter. For *Prosopis*, shoot phosphorus concentration also decreased with an increase in *Prosopis* litter concentration.

Effects of potting medium, irradiance and litter concentration on seedling nodulation

The two species did not differ in nodulation probability (P =0.502). Addition of litter to the soil decreased seedling nodulation, with *Prosopis* litter being more inhibitive than *Acacia* litter (Table 4.4). There was a significant inhibition of seedling nodulation in *Prosopis* litter of 9.1% compared to 4.8% litter, but there was no such concentration effect for *Acacia* litter (Table 4.4). In addition, seedling nodulation increased with an increase in irradiance (Table 4.4).

Litter characterization

Acacia litter had initially a higher concentration of soluble phenols than *Prosopis* litter (Fig. 4.4), but leaching of phenols over time was more drastic in *Acacia* (Fig. 4.5). The concentration of soluble phenols in the two litter types was nearly equal after two weeks of leaching, after which phenol concentration was higher in *Prosopis* than in *Acacia* (Fig. 4.5). Statistically, *Prosopis* litter had higher potassium concentration than *Acacia* litter but concentration of nitrogen and phosphorus were similar in the two litter types (Fig. 4.4).

Discussion

Effect of Acacia and Prosopis litter on seed germination

It was hypothesized *Prosopis* litter would inhibit germination of *Acacia* but not of itself. In fact, litter types of both species inhibited germination, but *Prosopis* litter had a stronger effect than *Acacia* litter, and surprisingly, *Prosopis* litter had a stronger inhibiting effect on its own germination than on *Acacia* germination. It was also hypothesized that inhibition was caused by allelopathy, and not by physical factors. For *Prosopis* litter this certainly seems the case, as leached *Prosopis* litter had no effects seed germination. Though the germination function of *Prosopis* seed in leached *Acacia* litter was insignificant (R^2 = 0.57, P =0.049), the litter still had some negative impact at higher concentrations. As phenol leaching was very drastic in *Acacia* litter, the result suggests that inhibition of *Prosopis* germination by *Acacia* litter might not only be caused by allelopathic effects, but also by physical effects (Hata et al. 2010). Our findings are consistent with germination inhibition by phenolic compounds of *P. juliflora* leachate in *Cassia occidentalis L.* and own seeds (Goel et al. 1989; Warrag 1995).

The negative impacts of *Acacia* litter on germination of *Acacia* and *Prosopis* seed is in line with findings of other studies revealing presence of potentially allelopathic phenolic compounds in *A. tortilis* litter (Diallo et al. 2006; Nakafeero et al. 2007).

From our study, it appears that *Prosopis* phenols are allelopathicaly more potent in germination inhibition than *Acacia*. This was evident from the stronger decline in germination with litter concentration (i.e., stronger slopes). Although studies on phenol assay for *Acacia* and *Prosopis* are scarce, the phenol concentrations found in this study are within the range of concentrations found in *A. tortilis* (Bryant et al. 1991) and *Prosopis caldenia* (Pisani et al. 2001). Also the leaching of *A. tortilis* phenol was consistent with high solubility of *Acacia* phenols (Chou et al. 1998), whereas resistance of Prosopis phenols to leaching imitated slow decomposition of *P. juliflora* litter found by Goel et al. (1989).

Despite the inhibiting effect of *Prosopis* on its own germination, *Prosopis* seedlings are still found below their own canopy (El-Keblawy and Al-Rawai 2007; Muturi et al. submitted). This can possibly be attributed to prolific seeding (Zimmerman 1991; Shiferaw et al., 2004) and the high germination rates, as has also been found in this study. Moreover, there is strong spatial variation in litter distribution in the field, which may allow *Prosopis* to establish in patches with low litter accumulation. The lack of *Acacia* seedlings under *Prosopis* canopies in the field (Muturi et al. submitted) may be explained by its relatively low germination rate as found in the experiment, dispersal limitation because of a lack of mature *Acacia* trees s in dense *Prosopis* stands, and the notable allelopathic effects of *Prosopis* on *Acacia* seed germination.

Effects of litter on seedlings biomass production, nutrient concentration and nodulation

It was hypothesized that high litter concentration should result in growth inhibition through allelopathic effects. Yet, seedling biomass was actually higher in soil mixed with *Acacia* and *Prosopis* litter than in pure soil. Similar results were obtained in *C. occidentalis* that realized faster growth when grown in soil with decomposed *P. juliflora* and *Prosopis cineraria Druce* litter (Goel et al. 1989) and in onions, that grew faster when grown at 1% A. *tortilis* litter (Dilallo et al. 2006). However, other studies found inhibitory growth effects of *P. juliflora* litter on its own seedling growth (Warrag 1995) and that of 5% *A. tortilis* litter

on onions (Diallo et al. 2006). Litter can either increase or decrease biomass production depending on decomposition stage or concentration, as they both influence the release of litter nutrients and phenolic compounds (Goel et al. 1989; Diallo et al. 2006). In our study, it appears that the litter concentration used may not have been inhibitive to seedling growth but were initially inhibitive to seed germination. We attribute stimulation of biomass production by litter addition to a possibility of adequate and stable seedlings nutrients supply by gradual litter decomposition, which matches steady state seedling nutrition (Timmer 1996; Zabek and Prescott 2007); evident from simultaneous high biomass production (Fig. 4.3) and retention of high nutrient concentration, for example nitrogen (Table 4.3).

Although litter stimulated seedling growth of *Acacia* and *Prosopis,* it also decreased simultaneously the nodulation probability. Nodulation is an indicator of a symbiotic relationship with nitrogen fixing bacteria, when nitrogen supply is limited. At high soil nitrogen levels, nitrogen is readily available and nodulation is reduced (Thomas et al. 2000, Indieka and Odee 2005), as found in our study. The lower nodulation in litter treatments was probably a result of increased nitrogen supply from the decomposing litter. Decrease of nodulation with litter concentration may also be attributed to phenol concentration watering (Sayed et al. 2002).

Effects of light on seedling growth, nutrients and nodulation

Seedling biomass and nodulation probability increased with irradiance, whereas shoot nutrient concentrations tended to decline with irradiance. Other studies have also shown increase of biomass with irradiance in *A. tortilis* (Smith and Shackleton 1988) and in *Prosopis* (Bush and van Auken 1987, Vilela and Ravetta 2000). We anticipated that, because of its high plasticity, *Prosopis* may produce more biomass than *Acacia* under similar irradiance, but there was no significant species and species x irradiance effect on seedling biomass (Table 4.1). The results indicate that both *Acacia* and *Prosopis* have comparable growth characteristics, and shading is not a factor that explains the lack of *Acacia* regeneration under *Prosopis* canopies. Nodulation probability increased with irradiance, which may be attributed to two factors. First, with increased growth at higher irradiance, the demand for plants nutrients, including nitrogen increases.

Second, increased watering at high light intensities may have reduced phenol concentration in the potting media and triggered nodulation.

Compared to *Prosopis*, *Acacia* litter may not be allelopathic, and neither can it deter nodulation under natural conditions because of three factors. First, the density of *A. tortilis* trees is generally low (Legesse and Eddy 1990; Oba 1998). Second, *A. tortilis* litter is readily consumed by livestock and wildlife, thus litter accumulation is unlikely in contrast to what is commonly found in *Prosopis* species. Third, our experiments show that phenols are rapidly leached; hence phenols are adequately leached during rains. Because of lack of those allelopathic effects, herbaceous layer productivity and diversity might be higher under *A. tortilis* than under *Prosopis* canopies (cf. Muturi et al. submitted).

Acacia and *Prosopis* did not differ in biomass production, nodulation, and in 58% of all the nutrients concentration cases tested in (Table 4.3). Similar biomass production contrasted with our hypothesis that *Prosopis* may produce more biomass particularly in response to light treatments. Results suggests similar growth characteristics on both species and do not support the idea that the exotic *Prosopis* species are faster growing than indigenous *Acacia*, at least in the seedlings stage. As two species responded similarly to several treatments, this may imply overlapping ecological characteristics, but contrasting allelopathy traits was implied by seed germination results.

Conclusion

Soluble phenols in *Prosopis* litter inhibited germination of *Acacia* and *Prosopis* seeds more strongly than the phenols in *Acacia* litter, as *Prosopis* phenols were resistant to water leaching. Once leached, both litter types enhanced seedling growth and shoot nutrient concentrations but they inhibited nodulation, probably because of an enhanced nitrogen supply. Our findings do not support the common view that *Prosopis* species are faster growing than indigenous *Acacia*, at least in the seedlings stage. Instead, *Acacia* and *Prosopis* show rather similar responses to litter and irradiance treatments. Overall, this study suggests that the combined effects of high litter accumulation and the leaching resistance of soluble *Prosopis* litter phenols may inhibit *Acacia* germination, and explain the lack of *Acacia* regeneration under *Prosopis* canopies.

Table 4.1: Results of analysis of variance for seedling dry weight as influenced by species, irradiance, potting media, litter concentration and interactions between species and the other factors. Statistical outputs shown are degrees of freedom (df), F values (F) and significance levels (P).

Source of variation	df	F	P
Species	1	3.0	0.082
Irradiance	3	542.9	<0.001
Potting medium	2	445.2	<0.001
Litter concentration	3	5.6	<0.001
Species * Potting medium	2	56.0	<0.001
Species * Litter concentration	3	1.9	0.136
Species * Irradiance	3	1.6	0.188

Table 4.2: Results of analysis of variance for shoot nutrient concentration (nitrogen, phosphorus and potassium) as influenced by the main factors (species, irradiance, potting medium, and litter concentration) and their interactions. Degrees of freedom (df), F values (F) and significance levels (P) are shown for each factor. The degrees of freedom differ from those Table 4.1 as the analysis was based sub-sampling from the main experiment.

Source of variation	df	Nitrogen (%)		Phosphorus (%)		Potassium (%)	
		F	P	F	P	F	P
Species	1	4.6	0.035	34.6	<0.001	67.1	<0.001
Irradiance	1	10.6	0.002	239.7	<0.001	11.2	0.001
Potting medium	2	1.7	0.197	126.3	<0.001	0.3	0.723
Litter concentration	2	3.1	0.050	143.8	<0.001	0.3	0.765
Species * Potting medium	2	2.8	0.067	1.5	0.238	0.9	0.417
Species * Litter concentration	2	1.2	0.300	12.8	<0.001	0.6	0.564
Species * Irradiance	1	11.2	0.001	60.4	<0.001	1.9	0.178

Table 4.3: Mean seedling shoot nitrogen, phosphorus and potassium concentration in *Acacia* and *Prosopis* seedlings depending on irradiance, potting medium and concentration of *Acacia* or *Prosopis* litter in the soil. Variation of shoot nutrient concentration between irradiance levels and among other treatments for *Acacia* or *Prosopis* is denoted by different letters (P<0.05), down the column for each factor. Variation between species within a treatment level (across the rows) is shown by ** (P<0.01), * (P<0.05) and Ns if insignificant.

Factor/ Variable	Nitrogen (%)			Phosphorus (%)			Potassium (%)		
	Acacia	*Prosopis*	Species	*Acacia*	*Prosopis*	*Species*	*Acacia*	*Prosopis*	Species
Irradiance									
10% Irradiance	3.2a	3.3a	Ns	0.31a	0.36a	**	1.4a	2.1a	**
55% Irradiance	3.2a	2.7b	**	0.29b	0.28b	Ns	1.3b	1.8b	**
Potting medium									
Soil without litter	2.9b	2.8a	Ns	0.35a	0.39a	**	1.4a	2.0a	Ns
Soil & *Acacia*	3.5a	3.0a	**	0.32b	0.34b	Ns	1.4a	1.9a	**
Soil & *Prosopis*	3.0b	3.0a	Ns	0.26c	0.27c	Ns	1.3b	1.9a	**
Concentration of Acacia litter									
Soil without litter	2.9c	2.8a	Ns	0.35a	0.39a	**	1.4a	2.0a	Ns
Soil & 4.8 *Acacia*	3.7a	3.2a	*	0.32a	0.34b	Ns	1.4a	2.0a	**
Soil & 9.1 *Acacia*	3.3b	2.8a	NS	0.32a	0.34b	Ns	1.4a	1.8a	Ns
Concentration of Prosopis litter									
Soil without litter	2.9b	2.8a	Ns	0.35a	0.39a	**	1.4a	2.0a	Ns
Soil & 4.8 *Prosopis*	2.7b	3.0a	Ns	0.26b	0.30b	Ns	1.2b	1.9a	**
Soil & 9.1 *Prosopis*	3.3a	3.0a	Ns	0.26b	0.24b	Ns	1.3ab	1.9a	*

Table 4.4: Logistic regression coefficients (β), Wald values (Wald) and significance level (P) for seedling nodulation at three potting media, three *Acacia* or *Prosopis* litter concentrations and four irradiance levels. The reference for each case is defined as the constant.

Factor	β	Wald	P
Potting medium			
Soil & *Prosopis*	-3.09	30.4	0.000
Soil & *Acacia*	-1.84	10.6	0.001
Constant (Soil)	2.64	26.0	0.000
Acacia litter concentration			
9.1 *Acacia* litter	-	-	-
6.3 *Acacia* litter	-	-	-
Constant (4.8 *Acacia* litter)	0.80	12.19	0.000
Prosopis litter concentration			
9.1 *Prosopis* litter	-2.74	14.7	0.000
6.3 *Prosopis* litter	-0.82	2.4	0.123
Constant (4.8 *Prosopis* litter)	0.55	2.1	0.149
Irradiance			
10% Irradiance	-3.38	48.8	0.000
25 % Irradiance	-1.68	17.0	0.000
45 % Irradiance	-0.43	0.9	0.345
Constant (55% Irradiance)	1.77	37.4	0.000

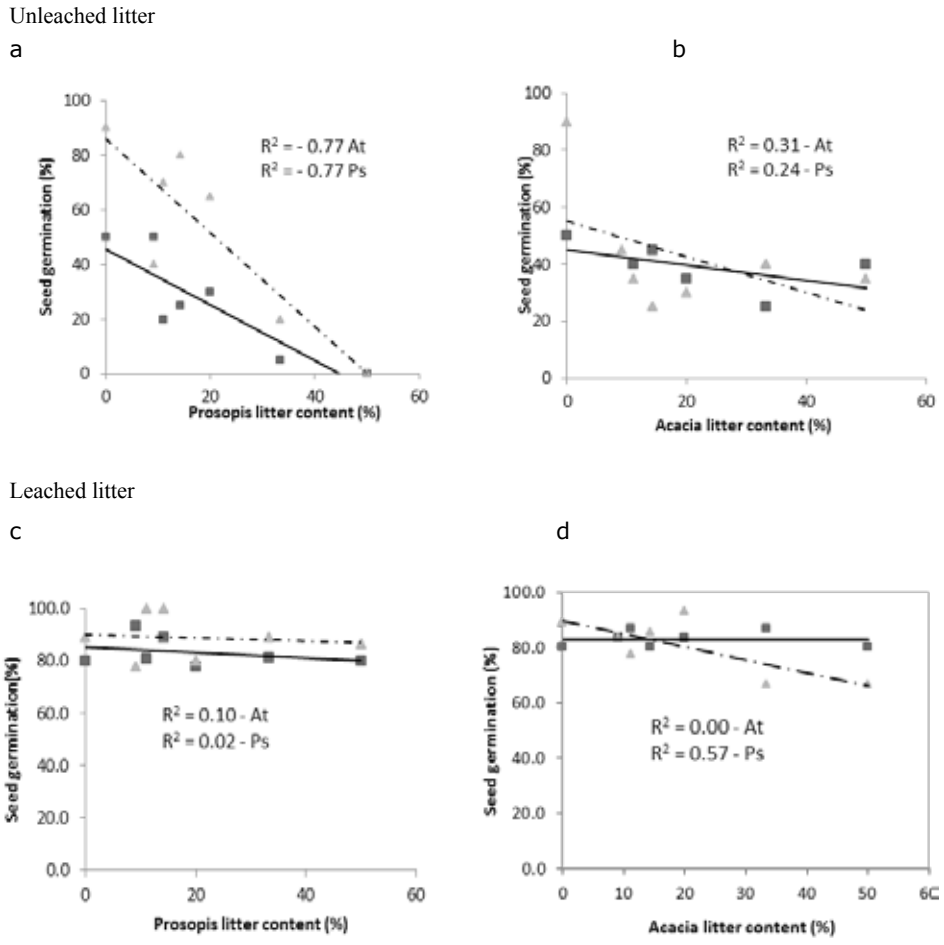


Figure 4.1: Germination of *Acacia tortilis* (At, square symbol, continuous linear regression line) and *Prosopis* species (Ps, triangle symbol, dotted regression line) seeds as a function of concentration of unleached *Prosopis* litter (a), unleached *Acacia* litter (b), leached *Prosopis* litter (c) and leached *Acacia* litter (d). Unleached *Prosopis* reduced seed germination significantly ($R^2 = 0.77$, $P < 0.05$), whereas litter effect on germination was insignificant in all other cases.

Acacia tortilis *Prosopis* species

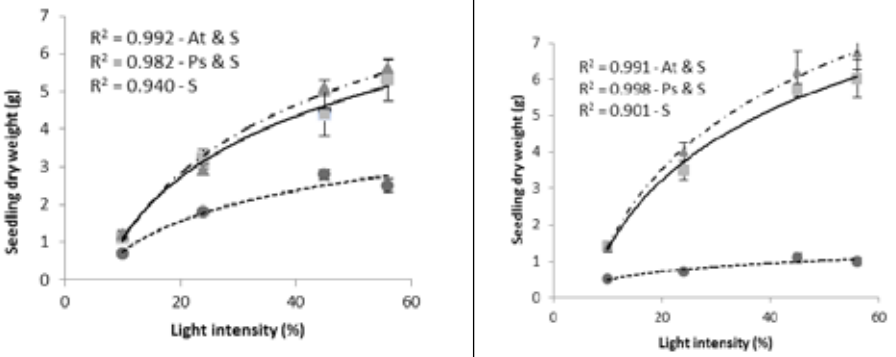


Figure 4.2: Logarithmic relationship between seedling biomass and irradiance for *Acacia tortilis* and *Prosopis* species grown at soil with *Acacia* litter with soil (At & S, squares and continuous line), soil with *Prosopis* litter with soil (Ps & S triangles with broken-dotted line) and with soil alone (S, circles with broken line). The used litter concentration is 1volumetric unit of litter to 10 volumetric units of soil. Averages and standard error of the mean are shown by bar errors and R^2 for each case described.

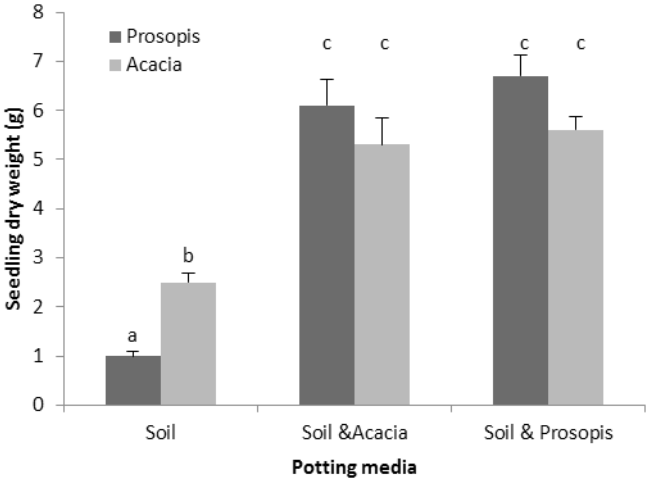


Figure 4.3: *Prosopis* (black bars) and *Acacia* (grey bars) seedling biomass for seedlings grown in soil alone and seedlings grown with 9.1 volumetric % of *Acacia* and *Prosopis* litter in the soil. Bar denote standard error of the means. Bars accompanied by a different letter are significantly different ($P<0.05$).

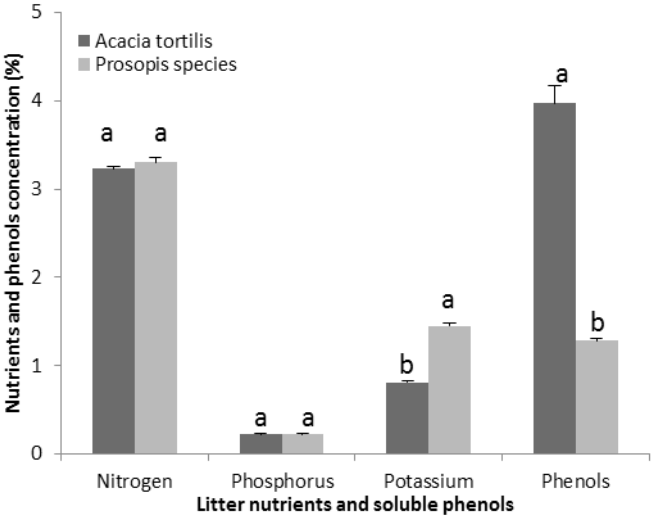


Figure 4.4: Nitrogen, phosphorus, potassium and soluble phenols concentration in fresh *Acacia* litter (dark shading) and *Prosopis* species litter (light shading). Bars accompanied by a different letter are significantly different at P<0.05.. The bars are standard error of the means.

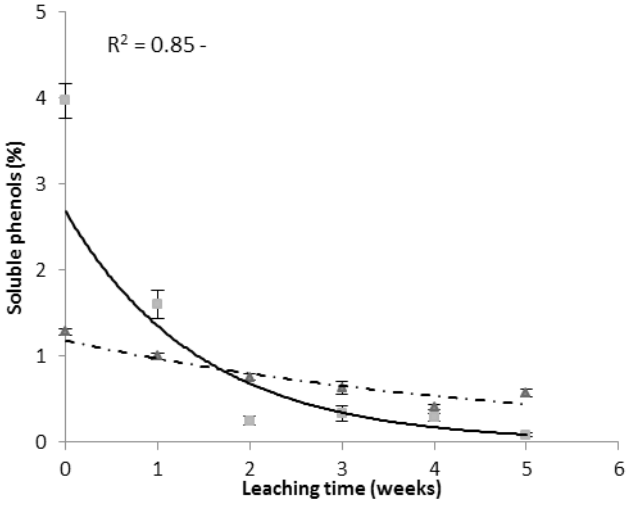


Figure 4.5: Exponential time-dependent decline in soluble phenols in *Acacia* litter (square symbol, continuous line) and *Prosopis* litter (triangles, dotted line). The bars show the standard errors of the mean.

Chapter 5

Genetic diversity of Kenyan Prosopis populations based on Random Amplified Polymorphic DNA markers

Gabriel M. Muturi, Joseph M. Machua, Godefridus M.J. Mohren, Lourens Poorter, John M. Gicheru and Lorna W. Maina

Submitted

Abstract

Several *Prosopis* species and provenances were introduced in Kenya, either as a single event or repeatedly. To date, naturally established *Prosopis* populations are described as pure species depending on site, despite the aforementioned introduction of several species within some sites. To determine whether naturally established stands consist of a single or mixture of species, six populations from Bamburi, Bura, Isiolo, Marigat, Taveta and Turkwel were compared for relatedness with reference *Prosopis chilensis*, *Prosopis juliflora* and *Prosopis pallida* using Random Amplified Polymorphic DNA markers. Cluster analysis based on Nei's genetic distance clustered Kenyan populations as follows: Marigat, Bura and Isiolo with *P. juliflora,* Bamburi with *P. pallida* and Taveta with *P. chilensis,* whereas the Turkwel population is likely to be a hybrid between *P. chileneis* and *P. juliflora*. Four populations had private markers, revealing germplasm uniqueness. Expected heterozygosity tended to be larger for Kenyan populations (ranging from 0.091 to 0.191) than in the three reference (ranging from 0.065 to 0.144). For the six Kenyan populations and two *P. juliflora* provenances from the Middle East, molecular variation was larger within populations than between population. Higher molecular variance among populations is attributed to their geographical separation and the low variation within populations is due to gene flow between individuals within a population. Overall this study shows that 1) the Kenyan *Prosopis* populations are genetically isolated, 2) multiple introductions enhanced genetic diversity within sites; and 3) *P. juliflora* and its hybrid are the most aggressive invaders.

Keywords: *Prosopis chilensis, Prosopis juliflora, Prosopis pallida* multiple introduction, genetic diversity

Introduction

The genus *Prosopis* Linnaeus emend. Burkart has 44 species of trees and shrubs found in the hot dry tropics of America, Africa and Asia (Burkart 1976). About 90% of all *Prosopis* species are native to North and South America. Taxonomically, the genus is classified into Algorobia (30 species), Anonychium (1 species), Monilicarpa (1 species), Strombocarpa (9 species) and Prosopis (3 species) sections (Burkart 1976). Some species within a section (Burkart 1976), and their hybrids are morphologically indistinguishable (Saidman et al., 1996, Vega and Hernandez 2005). Consequently, species misidentification is common, particularly in areas of *Prosopis* species introductions (Harris et al., 2003, Landeras et al., 2006). Proper identification of species is required for species-specific invasion management, for example through biological control (Zimmerman et al., 1991, van Klinken et al., 1999).

In Kenya, eight *Prosopis* species were periodically introduced to various sites (Maghembe et al., 1983, Rosenschein et al., 1999, Stave et al., 2003, unpublished data from the Kenya Forestry Seed Centre). Introduced species are from the sections Algarobia (*Prosopis alba* Griseb., *Prosopis chilensis* Stuntz, *Prosopis juliflora* (Sw.) DC*, Prosopis nigra* Hieron, and *Prosopis pallida* Kunth), Strombocarpa (*Prosopis pubescens* Benth. and *Prosopis tamarugo* Phil.) and Prosopis (*Prosopis cineraria* Druce). *Prosopis* species and provenances have been introduced sometimes in a single event, but often by multiple introductions (Kaarakka et al., 1990, Otsamo et al., 1993, Oba et al., 2001). The introduced species have adapted and become invasive (Stave et al., 2003, Muturi et al., 2010), causing negative socio economic and ecological impacts (Mwangi and Swallow 2008, Muturi et al. in prep).

Multiple introductions can enhance species invasiveness in four ways: through propagule pressure, colonization pressure (Lockwood et al., 2009, Blackburn et al., 2011), hybridization, and genetic diversity (Shierenbeck and Ellstrand 2009, Pairon et al., 2010). Propagule pressure is an inclusive term for frequency, size, spatial and temporal patterns of propagules arrival when dealing with a single species. On the other hand, colonization pressure is commonly used in reference to the frequency, size, spatial and temporal patterns of propagules arrival in reference to several species. For a species, the probability to establish a viable population increases with propagule pressure, whereas that of species increases with colonization pressure (Lockwood et al 2009; Simberloff 2009).

When the barrier between geographically separated species or provenances is removed through introduction of species and provenances, hybridization and subsequent gene introgression may occur, thus increasing genetic diversity and enhancing the adaptability of progenies (Parsons et al., 2011). For example, hybrids have, compared to their progenitors, an expanded habitat range in the case of sunflower (Rieseberg et al., 2007), higher growth rate in the case of *Mahonia* species (Ross and Auge 2008), and higher seed germination and seedling growth rates in the case of *Schinus terebinthifolius* Raddi (Geiger et al., 2011). In combination, these traits may enhance the invasiveness of plant hybrids.

The introduction of *Prosopis* species in Kenya was characterized by both propagule pressure through multiple introduction of *P. chilensis, P. juliflora* and *P. pallida* provenances in sites such as Bura (Kaarakka et al., 1990, Otsamo et al., 1993), and colonization pressure by multiple introduction of several species within specific sites (Maghembe et al., 1983, Oba et al 2001, Rosenschein et al., 1999, unpublished data from the Kenya Forestry Seed Centre). The pooling of germplasm at introduction, their subsequent exchange between sites (Kaarakka et al., 1990, Otsamo et al., 1993) and random seed dispersal by livestock, wildlife and water (Mwangi and Swallow 2008, Mworia et al., 2011) could have enhanced hybridization and gene introgression, which are known to occur among the *Prosopis* species (Bassega et al., 2000, Vega and Hernandez 2005, Landeras et al., 2006). To date, the composition and diversity of introduced *Prosopis* species in Kenya is largely unknown. There is a general tendency to classify populations of invaded areas as *P. juliflora* (Pasiecznik et al., 2001, Ngunjiri and Choge 2004, GoK 2007, Trenchard et al., 2008). Populations have also been classified as either *P. chilensis* (Stave et al., 2003, Olukoye et al., 2003) or *P. juliflora* (Maghembe et al., 1983, Mwangi and Swallow 2008) depending on site; whereas other introduced species are occasionally mentioned (Maghembe et al., 1983, Rosenschein et al., 1999).

Molecular techniques have been successfully used for *Prosopis* species to resolve species identity and progenitors (Vega and Hernandez 2005, Landeras et al., 2006, Sherry et al., 2011). Such techniques are handy when morphological species identification is problematic (Harris et al., 2003, Landeras et al., 2006). Random Amplified Polymorphic DNA (RAPD) is most widely used molecular technique. The genetic diversity of the species is described by heterozygosity, polymorphism and molecular variance (Juarez-Munoz et al., 2002, Ferreyra

et al., 2010). The objectives of this study were to quantify genetic diversity of various *Prosopis* populations in Kenya, and identify to what species they belong. We hypothesized that: a) Kenyan *Prosopis* populations are genetically diversified because of multiple introductions; b) within sites, populations consist of a mixture of introduced species or species and their hybrids.

Material and Methods

Description of sample populations, plant sampling and reference species

Six naturally established *Prosopis* populations (Bamburi, Bura, Isiolo, Marigat Taveta and Turkwel) were selected for sampling (Table 5.1, Fig. 5.1), based on the literature (Ngunjiri and Choge, 2004, Anderson, 2005, Mwangi and Swallow, 2008) and our knowledge on *Prosopis* distribution in Kenya. Bura, Marigat and Turkwel are heavily invaded areas (Ngunjiri and Choge 2004). Isiolo is encroached by *Prosopis* species but the encroachment is not yet problematic (Mwangi and Swallow 2008). During sampling, Taveta was found to be under intermediate invasion threat, whereas Bamburi had mixed exotic and indigenous species used to rehabilitate abandoned limestone quarry mines (Maghembe et al., 1983). Thus this study ranked the invasion status in the sampled populations as heavy (Bura, Marigat and Turkwel), intermediate (Taveta), low (Isiolo) and no invasion (Bamburi).

Thirty trees were sampled per site and a distance of $\geq$ 500m between trees used to maximize genetic diversity within a population. The distance between trees was determined with a global positioning system. Young tender healthy leaves were collected from each tree and preserved in polythene bags containing silica gel. All samples were stored in a cool box before being transferred to the laboratory where they were preserved in a deep freezer at –40 ^{o}C until further analysis to isolate DNA.

Seeds of known provenances of *P. chilensis* (batch number FAO 01590/86, provenance Agua Chica), *P. juliflora* (batch numbers 0101594 (Oman –Muscat), 0103738 (Yemen-Abyan) and 0109132 **(**Venezuela, Nueva Esparta - Isla de Margarita) and *P. pallida* (batch number FAO 01353/84, provenance Zana) were also included in the analysis. With the exception of the *P. juliflora* provenances from Oman and Yemen (Middle East), the reference materials originated from the natural range of the three *Prosopis* species (Burkart 1976). *Prosopis chilensis* and *P. pallida* seeds were obtained from University of Copenhagen, Denmark and

P. juliflora seeds were obtained from Kew Botanical Gardens, UK. Seedlings for the three species were raised at KEFRI greenhouse and their leaves were sampled for DNA analysis. The three known species were used as reference materials. Reference materials are briefly described in Table 5.1 and their approximate geographical location is shown in Figure 5.1. Subsequently, all reference provenances and the Kenyan samples are treated as population.

DNA isolation

DNA isolation was carried out using a modified SDS method with RnaseA addition (Edwards et al., 1991; Machua et al., 2011). About 0.1g of leave tissue was obtained from the tree leaves by shutting an eppendolf (1.5ml) lid on the leaf to obtain equal leaf discs. Some sterile sand, polyvinylypyrollidone (pvp), 200µl of SDS extraction buffer [1M Tris (pH 7.5), 5M NaCl, 0.5M EDTA, 10% SDS and 7µl of mercaptol ethanol] were added and the samples ground in liquid nitrogen using a sterile plastic micro pestle. An extra 500µl of the SDS extraction buffer was added and samples were vortexed for 10 seconds and then left at room temperature for about 45 minutes. The samples were centrifuged at 10,000 rpm for 10 minutes and 500µl of the supernatant was transferred into a fresh eppendolf tube and an equal volume of chilled chloroform: isoamyl alcohol (24:1) was added. The samples were mixed well by inversion to emulsify and then centrifuged at 10,000 rpm for 10 minutes after which 400µl of the supernatant was transferred into a fresh eppendolf tube and an equal volume of chilled isopropanol added. The samples were then mixed well by inversion and then left at room temperature for about 2 minutes followed by centrifuging at 10,000 rpm for about 8 minutes to pellet the nucleic acids while the supernatant was poured off.

The DNA pellet was washed with 0.4ml of chilled 70% ethanol by centrifuging at 10,000 rpm for 1 minute. Ethanol was then drained by inverting the tubes and the DNA pellet re-suspended in 200µl of TE buffer [10mM Tris (pH 7.5), 1mM EDTA]. Thereafter, 2µl of RNAseA (10 mg ml^{-1}) was added into each sample and the samples incubated at 37^0 C for about 30 minutes. A further 2 volumes (400µl) of 99% chilled ethanol was added into each sample and then centrifuged at 10,000 rpm for 10 minutes to re-precipitate the DNA pellets dried under vacuum before re-suspending in 1ml of TE buffer [10mM Tris (pH 7.5), 1mM EDTA] and stored at $–20^0$ C before use.

RAPD assay

A total of 40 decamer primers were screened for polymerase chain reaction (PCR) on a batch of *Prosopis* DNA samples. Ten primers revealed clear, reproducible bands and these were selected for amplification of all the samples (Table 5.2). DNA amplification was carried out in a 25µl volume reaction mix containing 200mM of each of the dNTPs (Invitrogen), 1 µl *Taq* polymerase buffer (Invitrogen), 3mM $MgCl_2$ (Invitrogen), 0.2 M primer (Invitrogen), 2.5 ng I^{-1} DNA and 0.75 units of *Taq* polymerase (Invitrogen). Amplification program included 1 cycle at 15 min at 94°C (denaturation), 1 min at 36°C (annealing) and 2 min at 72°C (Extension). A final 5 min extension (72°C) was allowed to ensure full extension of all amplified products. Amplification products were mixed with 6× gel loading dye (0.25 % bromothymol blue, 25% xylene cyanol and 30% glycerol) and separated on a 2% agarose gel. To either side of the gel 5µl of 100 bp molecular marker ladder (Invitrogen Ltd) was added, to size up the amplified loci. Gels were stained in ethidium bromide and visualized under ultra violet light and photographed using Kodak ID 3.5 gel imaging system (Kodak).

Data analysis

Amplified products were scored for presence (1) or absence (0) of a band using Kodak ID 3.5 application program (Pizzonia, 2001). Data were subjected to genetic analysis using POPGENE 3.2 (Yeh et al., 1999) and GenAlEx 6 (Peakall and Smouse, 2006), assuming diploid inheritance and Hardy-Weinberg equilibrium (Wright 1976). Genetic distances between populations were calculated according to Nei (1978). Cluster analysis based on Nei's genetic distance was carried out using unweighted pair-wise group arithmetic averaging (UPGMA) method (Sneath and Sokal, 1973) using TFPGA Software (Miller, 1997). Cluster analysis was complimented by Principal Component Analysis (PCA) on all populations to obtain more insight on distances among populations (Sneath and Sokal 1973, Hauser and Crovello, 1982).

Analysis of molecular variance (AMOVA) was carried out to partition genotypic variance among the 3 regions (Kenya, Middle East and South America). The AMOVA was carried out three times; 1) within and among the Kenyan *Prosopis* populations alongside the reference species, 2) within and among the Kenyan *Prosopis* populations, and 3) within and among the *P. juliflora* reference populations. AMOVA was used to estimate population differentiation

directly from the RAPD molecular data. AMOVA and PCA were performed using GenAlEx 6.4 software (Peakall and Smouse, 2006).

Results

All the six Kenyan populations and the reference species showed variation in polymorphism and mean expected heterozygosity (H_e) over the 10 primers (Table 5.3). Polymorphism was higher amongst the Kenyan populations (ranging from 31.0% in Bura to 59.8% in Isiolo) than that of the reference species (ranging from 15.5% in *P. juliflora* (0103738) to 46.6% in *P. chilensis*). Similarly, H_e range was higher in the Kenyan populations (ranging from 0.091 in Bura to 0.191 in Isiolo) than in the reference species (ranging from 0.065 in *P. juliflora* (0103738) to 0.144 in *P. chilensis*). The results for polymorphism and H_e (Table 5.3) were consistent with those of a PCA in which more genetically diverse populations had higher multidimensional spread than populations with low genetic diversity (Fig. 5.2). The PCA results separated the three references as *P. chilensis, P. juliflora* and *P. pallida* (Fig. 5.2). For Kenyan populations, Bamburi and Taveta were differentiated as separate populations but the other four populations were closely interlinked (Fig. 5.2). The PCA multidimensional spread revealed that Bamburi was closer to *P. pallida*, Taveta closer to *P. chilensis* and the other populations closer to both *P. chilensis and P. juliflora*. Cumulatively, the first three principal axes accounted for 64.9% of the genetic diversity found in the entire study material, for which the first axis contributed 28.5%, second axis contributed 20.5% and third axis contributed 15.9%.

Analysis of molecular variance (Table 5.4) revealed a higher variation (62%, $p < 0.001$) between the Kenyan *Prosopis* populations than within (38%, $p < 0.001$). A similar trend was also observed in *P. juliflora* reference material where molecular variation was higher between (74%, $p < 0.001$) than within (26%, $p < 0.001$) populations.

Three primers (KFP1, KFP3, KFP 4 and KFP5) generated molecular markers that were only found in four Kenyan populations and *P. chilensis* (Table 5.5). The specific molecular markers for Bamburi at 450bp and 750bp and contrasting absence of similar markers in Isiolo population are shown in Figure 5.3. Other primers showing specific markers were: KFP-1 for Turkwel population at 200bp and for *P. chilensis* at 1300bp, KFP-3 for Taveta population at 1400bp, and KFP-5 for Isiolo population at 230bp (Table 5.5).

According to Nei's unbiased genetic distance matrix (Table 5.6), the most genetically close Kenyan populations were Isiolo and Marigat (0.172) whereas the most genetically distant materials were *P. pallida* and *P. juliflora*-0103738 (0.463). Results also indicated that the three *P. juliflora* populations were genetically closer to each other than to the other two reference species (Table 5.6). A dendogram based on Nei's unbiased genetic distance (Fig. 5.4) revealed clustering of *P. chilensis* with Taveta, *P. juliflora* with Bura, Isiolo and Marigat, *P. pallida* with Bamburi, whereas the Turkwel population was between *P. chilensis* and *P. juliflora* (Fig. 5.4).

Five out of six Kenyan populations clustered with reference species (Fig. 5.4), thus facilitating comparison of genetic diversity of local populations with the corresponding reference species from the natural range. The Kenyan *P. juliflora* populations in Isiolo and Marigat had a higher genetic diversity than the reference *P. juliflora* with which they clustered. Similarly the Kenyan Bamburi population had a higher genetic diversity than *P. pallida* with which it clustered. In contrast, genetic diversity of Bura population was lower than the reference *P. juliflora* with which it clustered and that of Taveta population lower than *P. chilensis* with which it clustered.

Discussion

The aim of this study was to determine genetic diversity and species composition of six *Prosopis* populations in Kenya. Results show that genetic variation was larger amongst populations than within populations. The relative genetic isolation of these populations is also supported by the presence of unique genetic markers for some populations generated by the four primers (Table 5.5).

Genetic diversity of Prosopis populations in Kenya

Our first hypothesis was that the naturally established *Prosopis* populations in Kenya had a high genetic diversity because of multiple introductions of species and provenances within sites. Five out of six Kenyan populations clustered with reference species (Fig. 5.4), thus facilitating comparison of genetic diversity between local populations with their corresponding references from the natural range. For three out of these five populations, genetic diversity was indeed higher than populations of the species from the native range. Moreover, genetic diversity for all *P. juliflora* populations from Kenya was higher than populations introduced

to the Middle East (Oman, Yemen). These findings support our hypothesis that *Prosopis* populations in Kenya have a high genetic diversity, as a result of multiple introductions. Our findings are also consistent with increase of genetic diversity with multiple species introductions (Pairon et al., 2010), as formerly separated genotypes mix and hybridize (Schierenbeck and Ellstrand 2009, Parsons et al., 2011). The high genetic diversity found in *P. juliflora* populations can be explained by the introduction of several *P. juliflora* provenances to Kenya and subsequent seed exchange in the country (Maghembe et al., 1983, Otsamo et al., 1993).

Partitioning of genetic variation in the studied *Prosopis* germplasm was based on two population genetics assumptions (Wright 1976), as origin of *Prosopis* germplasm introduced to Kenya and Middle East was unknown; some materials may have originated from the reference provenances from the natural range. First that each of the study material had population characteristics, such a free random mating of individuals within a population but minimal or no inter-population gene flow. Second, there existed three distinct (geographically isolated) regions for *P. juliflora* (Kenya, South America and Middle East). The assumption was based on the expectation that further genetic differentiation or evolution occurs after the materials were introduced to Kenya and Middle East, thus leading to genetic variation from their progenitors. Comparisons of genetic variation partitioning across the three regions (Kenya, Middle East and South America) revealed a higher genetic variation among *Prosopis* populations (61%) than within *Prosopis* populations (32%). The trend was also found for Kenyan population where genetic variation among populations was higher (62%) than genetic variation within populations (38%). Our results were consistent with genetic variation partitioning among *Prosopis* species in their natural range (Juarez-Munoz et al., 2002). The genetic variation of 7% attributed to geographical regions in this study was higher than 3% attributed to the geographical regions within the natural range of *Prosopis* species (Ferreyra et al., 2010). This may be relegated to a further environmentally driven genetic differentiation of introduced germplasm (Ferreyra et al., 2010), hybridization (Vega and Hernandez 2005, Landeras et al., 2006) and ploidy (Trenchard et al., 2008) that may infer higher genetic variability between introduced genotypes and their progenitors.

The higher genetic variation found among *P. juliflora* populations (74%) than genetic variation within *P. juliflora* populations (26%) contrasts with genetic variation of *P. juliflora* populations introduced to Sudan (Hamza 2010) where

genetic variation among populations (33%) was lower than genetic variation within populations (67%). The most likely reason for the contrast between our study and that of Sudan is that populations sampled in Sudan were closer to each other than those sampled in Kenya. Geographical proximity may facilitate inter-population gene flow thus reducing the genetic diversity among populations.

Both the larger genetic variation amongst populations than within populations and the occurrence of private markers in some study populations indicate genetic differentiation amongst the Kenyan populations. Such genetic differentiation can be either as a result of genetic variation of germplasm at introduction, or a gradual adaptation of populations to site-specific environmental conditions.

Do Prosopis populations consist of several species?

We also hypothesized that naturally established stands consist of a mixture of species and/or hybrids, as several species were introduced within sites, and subsequent seed dispersal was random among sites. The distribution of Kenyan populations and reference species along the first two PCA axes and their clustering in UPGMA Dendogram did not reveal any evidence of establishment of a mixture of species or species and hybrids within any one site. Therefore our hypothesis was rejected. Instead, the results suggest that only *P. juliflora* was present at Bura and Marigat, despite the fact that also *P. chilensis* and *P. pallida* were introduced in Bura and Marigat (Otsamo et al., 1993, Rosenschein et al., 1999). Similarly, only *P. pallida* successfully established at Bamburi, although also *P. juliflora* was also introduced at this site (Maghembe et al., 1983). In Turkwel, neither *P. chilensis* nor *P. juliflora* had successfully established despite the introduction of the two species in this site (Oba et al., 2001).

Our study confirms past description of populations at Bura, Isiolo and Marigat as *P. juliflora*, (Ngunjiri and Choge 2004, Mwangi and Swallow 2008) and Bamburi as *P. pallida* (Trenchard et al., 2008). However, the results suggests that the Taveta population is not *P. juliflora* (as proposed by Ngunjiri and Choge 2004), but is likely to be *P. chilensis.* The Turkwel population seems to be neither *P. chilensis* (as proposed by Stave et al., 2003) nor *P. juliflora* (as proposed by Trenchard et al., 2008), but instead we demonstrated that it could be a *P. chilensis - P juliflora* hybrid, as both species were indeed introduced into the area (Oba et al., 2001) and hybridization between *P. chilensis* and other species in Algarobia

section is quite common (Hunziker et al., 1986, Landeras et al., 2006, Sherry et al., 2011). Besides the clustering of Kenyan populations with reference species, our findings also corroborate differentiation of *P. juliflora* and *P. pallida* by RAPD markers (Landeras et al., 2006, Sherry et al. 2011). Our study has contributed to increasing evidence for molecular differentiation of *P. juliflora* and *P. pallida* which are morphologically described as a complex (Pasiecznik et al 2001).

Several species were introduced to the Bamburi, Bura, Marigat and Turkwel sites but surprisingly, our study revealed the occurrence of a single species or a single hybrid at each site. Four populations (Bamburi, Isiolo, Taveta and Turkwel) had a specific private marker each, suggesting their unique genetic differentiation. Three inferences can be made from these results. First, not all introduced species were adapted, as species mixtures were not found at any one site where mixture of species were introduced. Second, natural random seed dispersal (Mwangi and Swallow 2008, Mworia et al., 2011) or exchange of germplasm between sites (Kaarakka et al., 1990, Otsamo et al., 1993) did not seem to induce genetic homogenization, as implied by the genetic uniqueness in four of the studied populations. Third, adaptation of the successfully established germplasm from the introduced pool was site specific, probably because of variation of environmental factors among sites. *Prosopis juliflora* was a common species in two sites (Bura and Marigat) and a parent of the hybrid in Turkwel, yet the three sites are within the most *Prosopis* invaded areas of Kenya (Stave et al., 2003, Ngunjiri and Choge 2004, Mwangi and Swallow 2008). Therefore, we opine that *P. juliflora* and its hybrids are among the most aggressive invaders.

Conclusion

The multiple introductions of species and provenances within sites in Kenya has led to high genetic *Prosopis* diversity and hybridization. Although several species were introduced to some sites, only a single species or a hybrid has successfully adapted in any given site. Whereas it is generally assumed that naturally established *Prosopis* populations in Kenya consist almost entirely of *P. juliflora* we revealed the presence of *P. chilensis, P. pallida* and a likely hybrid between *P. chilensis* and *P. juliflora*. Our study classifies the Kenyan *Prosopis* populations as *P. chilensis* for Taveta, *P. juliflora* for Bura, Isiolo and Marigat, *P. pallida* for Bura and a likely *P. chilensis – P. juliflora* hybrid for Turkwel.

We have further revealed genetic differentiation of Kenyan *Prosopis* populations as evident from specific molecular markers.

Table 5.1: The source of study materials in Kenya and that of reference species as stated by seed supplier (site), number of species introduced to sampled site or reference species description (Species), representative geographical location of a sample tree within a site in Kenya (Location) and corresponding elevation (altitude). Sample references are included in the species column describing the species introduced to Kenya sites, whereas reference seed batch numbers for reference species were provided by the seed suppliers.

Site	**Species**	**Location**	**Altitude (m.a.s.l)**
Bamburi	*Prosopis juliflora* and *Prosopis pallida* (Maghembe et al., 1983)	4.02° S, 39.72° E	13
Bura	*Prosopis chilensis*, *Prosopis juliflora* and *Prosopis pallida* (Kaarakka et al., 1990)	1.17° S, 39.85° E	101
Isiolo	*Prosopis juliflora*	0.39° N, 37.67° E	1047
Turkwel	*Prosopis chilensis* and *Prosopis juliflora* (Oba et al., 2001)	3.04° N, 35.50° E	526
Marigat	*Prosopis chilensis, Prosopis juliflora* and *Prosopis pallida* (Rosenschein et al., 1999)	0.47° N, 36.07° E	985
Taveta	*Prosopis juliflora* (Ngunjiri and Choge 2004)	3.42° S, 37.72° E	727
Chile	*Prosopis chilensis* - FAO 01590/86	-	-
Peru	*Prosopis juliflora* - 0101594 , KEW	-	-
Oman: Muscat	*Prosopis juliflora* - 0109132, KEW	-	-
Yemen: Abyan	*Prosopis juliflora* - 0103738, KEW	-	-
Venezuela: Nueva Esparta - Isla de Margarita	*Prosopis pallida* - FAO 01353/84	-	-

Table 5.2.Random Amplified Polymorphic DNA (RAPD) primers (primer code) used in the polymerase chain reaction (PCR), oligonucleotide primers base sequence (primer sequence), percentage content of guanine and cytosine bases in the primer (GC content (%)) and melting temperature (Tm ^{o}C) for each primer.

Primer Code	**Primer sequence**	**GC content (%)**	**Tm (^{o}C)**
KFP-1	GGC TCG TAC C	70	34
KFP-2	CGT CCG TCA G	70	34
KFP-3	GTT AGC GGC G	70	34
KFP-4	CGG AGA GTA C	60	32
KFP-5	CCT GGC GAG C	80	36
KFP-6	TCC CGA CCT C	70	34
KFP-7	CCA GGC GCA A	70	34
KFP-8	AGC CGC TGG T	70	34
KFP-9	GAC TGG AGC T	60	32
KFP-10	ACG GTG CGC C	80	36

Table 5.3: Sample size (N), number of loci per sample (L), percentage polymorphism in the sampled population (%P), number of population specific loci (PSL) and Nei's mean diversity estimates (H_e) of eleven *Prosopis* species populations based on the ten RAPD markers.

Provenance/ Species	N	L	% P	PSL	H_e
Isiolo	30	135	59.8	1	0.191
Marigat	30	114	47.0	0	0.140
Bamburi	30	113	46.6	2	0.127
Turkwel	18	98	41.6	1	0.148
Taveta	30	106	42.0	1	0.132
Bura	30	92	31.0	0	0.091
P. chilensis	30	112	46.6	1	0.144
P. pallida	*30*	*92*	*22.1*	*0*	*0.069*
P. juliflora 0101594	25	73	28.3	0	0.110
P. juliflora 0109132	27	66	21.0	0	0.077
P .juliflora 0103738	20	65	15.5	0	0.065

Table 5.4: Results of analysis of molecular variance (AMOVA) of six Kenyan *Prosopis* populations and three reference species (a), three *Prosopis juliflora* provenances (b) and six Kenyan *Prosopis* populations (c). Probability (P) values are based on 1000 random permutations of individuals across populations. DF= degrees of freedom.

Source of variation	df	Sumof squares	Mean sum of squares	Variance components	Variance (%)	*P*
(a) AMOVA results for six Kenyan *Prosopis* Population and three Prosopis reference species						
Among regions*	2	1753.747	876.874	2.725	7	<0.001
Among populations**	8	5006.386	625.798	22.641	61	<0.001
Within all population	289	3429.080	11.865	11.865	32	<0.001
Total	299	10189.213		37.232	100	
(b) AMOVA results for *Prosopis juliflora*						
Among provenances	2	981.456	490.728	20.297	74	<0.001
Within provenances	69	500.891	7.259	7.259	26	<0.001
Total	71	1482.347		27.557	100	
(c) AMOVA results for six Kenyan *Prosopis* populations						
Among populations	5	3191.747	638.349	22.418	62	<0.001
Within populations	162	2241.289	13.835	13.835	38	<0.001
Total	167	5433.036		36.254	100	

* signifies three distinct regions as Kenya (1), South America (2) and Middle East (3) where *Prosopis* material was sourced from. ** implies the pooling of all three *P. juliflora* provenances into a single population and treating all the other *Prosopis* samples as discrete populations.

Table 5.5: Private marker (specific locus) only amplified in four Kenyan population and *P. chilensis* (Population / Reference) using Random Amplified Polymorphic DNA (RAPD) markers (RAPD marker sequence). Marker code is the lab description of the primers used in the study.

Population/ Reference	**RAPD marker sequence**	**Marker code**	**Specific locus**
Turkwel	GGCTCGTACC	KFP-1	200 bp
P. chilensis	GGCTCGTACC	KFP-1	1300 bp
Taveta	GTTAGCGGCG	KFP-3	1400 bp
Bamburi	CGGAGAGTAC	KFP-4	750 bp
Bamburi	CGGAGAGTAC	KFP-4	450 bp
Isiolo	CCTGGCGAGC	KFP-5	230 bp

Table 5.6: Pairwise population matrix of Nei's unbiased genetic distance (Nei, 1978) of six Kenyan *Prosopis* populations and five *Prosopis* references (population/ reference). The Kenyan populations are described by their location names, whereas references are denoted as Pp (*P. pallida*), Pc (*P. chilensis*), Pj1 (*Prosopis juliflora*- 0101594), Pj2 (*P. juliflora*–0109132) and Pj3 (*P. juliflora* - 0103738).

Population/ Reference	Isiolo	Marigat	Bamburi	Turkwel	Taveta	Bura	Pp	Pc	Pj1	Pj2	Pj3
Isiolo	0.000										
Marigat	0.172	0.000									
Bamburi	0.248	0.233	0.000								
Turkwel	0.266	0.282	0.315	0.000							
Taveta	0.262	0.287	0.367	0.354	0.000						
Bura	0.223	0.149	0.310	0.323	0.290	0.000					
Pp	0.337	0.314	0.217	0.385	0.425	0.398	0.000				
Pc	0.217	0.197	0.251	0.318	0.234	0.221	0.328	0.000			
Pj1	0.229	0.181	0.309	0.335	0.312	0.273	0.379	0.267	0.000		
Pj2	0.230	0.210	0.328	0.309	0.317	0.260	0.429	0.287	0.187	0.000	
Pj3	0.300	0.253	0.421	0.378	0.367	0.322	0.463	0.341	0.222	0.262	0.000

Figure 5.1: Geographical distribution of the six Kenyan *Prosopis* populations and five *Prosopis* species references used in this study.

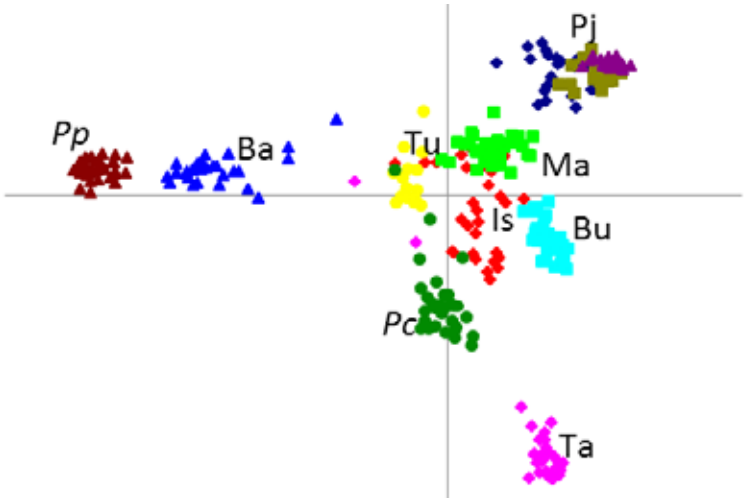
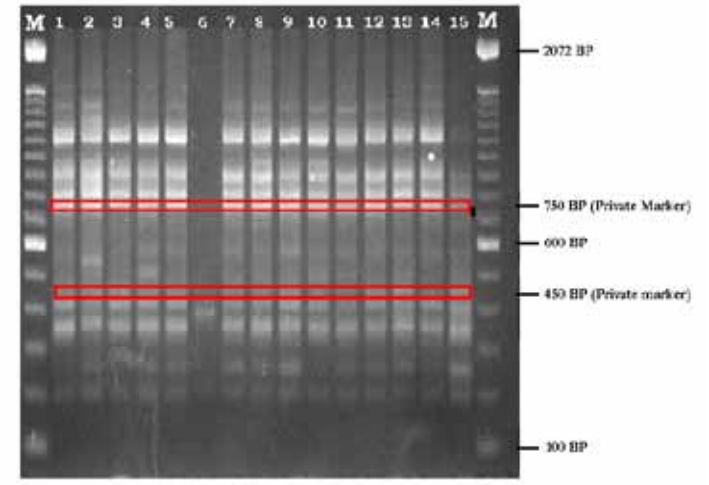


Figure 5.2: Principal component analysis six Kenyan *Prosopis* populations; Bamburi (Ba, blue triangles), Bura (Bu, turquoise squares), Isiolo (Is, red diamonds), Marigat (Ma, green squares), Taveta (Ta, pink diamonds) and Turkwel (Tu, yellow circles); and reference specie; *Prosopis chilensis* (Pc green circles), *Prosopis juliflora* (Pj, blue diamonds, purple triangles and grey squares) and *Prosopis pallida* (Pp, brown triangles). *Prosopis juliflora* had three reference provenances. PCA was based on Orloci (1978) algorithm of distance matrix. The first axis accounted for 28.5% of genetic diversity and the second axis accounted 20.5% genetic diversity.

a



b

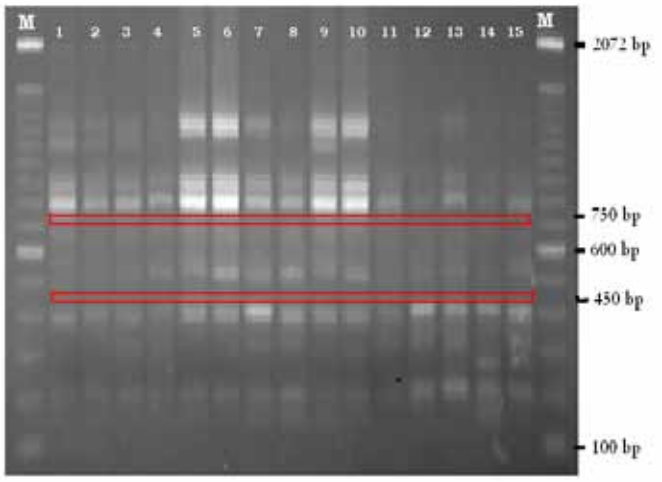


Figure 5.3: A 1.4% Agarose gel stained in Ethidium bromide showing two private bands (Markers) at loci 750bp and 450bp in Bamburi population and (a) and Isiolo population where the private marker are missing in the same loci (b). M is 100bp molecular weight marker (Invitrogen, UK) whereas 1-15 are the tree samples.

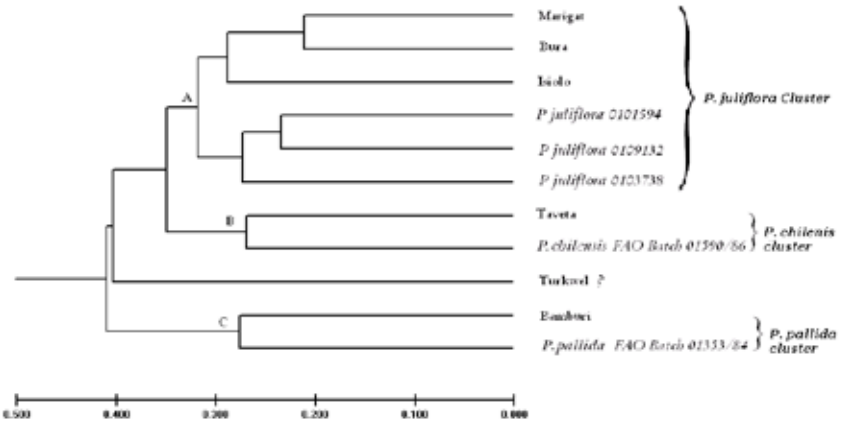


Figure 5.4: Dendrogram of unweighted pair-wise group arithmetic averaging (UPGMA) cluster analysis of three *Prosopis* reference species (*P. chilensis, P. juliflora* and *P. pallida*) and six Kenyan *Prosopis* species populations based on Nei's (1978) unbiased genetic distance. *Prosopis juliflora* is supported by node A, *P. chilensis* by node B and *P. pallida* by node C. The Kenyan populations clustered with *P. juliflora* (Marigat, Bura and Isiolo), *P. chilensis* (Taveta) and *P. pallida* (Bamburi). Turkwel population appeared to be a *P. chilenis – P. juliflora* hybrid.

Chapter 6

Allometric equations for estimating biomass in naturally established Prosopis stands in Kenya

Gabriel M. Muturi, Jason G. Kariuki, Lourens Poorter and Godefridus M.J. Mohren

Published in Journal of Horticulture and Forestry 4:69-77 (2012)

Abstract

Forty five *Prosopis* stems of 2.5-18.0 cm diameter at breast height (DBH) were sampled at Nadapal along the Turkwel riverine forest for development of biomass and volume prediction equations for naturally established stands. Tree basal diameter (D_{30}), DBH and heights were measured, felled trees and their volumes, fresh and dry weights determined. Linear and power models were evaluated for volume and biomass prediction through regression analysis of measured tree parameters. Power models yielded better results than linear models in volume and biomass prediction, with D_{30} and DBH being more reliable than height. Validation of models at two sites in Marigat and Bura, revealed strong significant correlations between predicted and measured tree biomass and volumes, suggesting effectiveness of the models in biomass prediction across sites. Subsequently, model development and model validation data were pooled to develop national models. Basal diameter was found to be the best variable in the development of power models for biomass and volume prediction across the country. When logarithmically transformed, biomass and volume per tree had strong significant linear relationship with basal diameter, and are accordingly recommended for quick biomass and volume estimation in the field.

Keywords: Biomass, Bura, Marigat, Nadapal, Turkwel, power models, linear models.

Introduction

Wood biomass is the main source of energy in Kenya, with notable localized deficits (Kirubi et al., 2000; Okello et al., 2001; Ng'etich et al., 2009). Provision of wood fuel was one of the main objectives for *Prosopis* species introduction in the country (Mwangi and Swallow, 2008). This objective is not yet fully realized, despite the successful establishment of the species in the initial trials (Maghembe et al., 1983; Olukoye et al., 2003) and their subsequent spread into other unintended areas, as a result of natural seed dispersal by livestock, wild animals and water (Mwangi and Swallow, 2008; Mworia et al., 2011). Recently, the government gave a policy direction for utilization of *Prosopis* species to control their further spread in areas where they are invasive (GOK, 2007). Exploitation of the species for wood fuel, as initially intended, provides excellent opportunities for invasion control and reducing wood biomass energy deficits. However, management guidelines, particularly for biomass quantification are yet to be developed. The species composition of natural stands is also poorly understood because introduced species such *Prosopis chilensis* Stunz, *Prosopis juliflora* (Sw.) and *Prosopis pallida* Kunth are difficult to differentiate because of similar morphology and formation of hybrids of intermediate phenotypes (Saidman et al., 1996; Pasiecznik et al., 2001; Landeras et al., 2006). These species could be coexisting in any of the natural stands.

Allometric equations are used to predict tree and stand biomass, based on easily measured tree variables such height, diameters and crown. Normally, developed equations are specific to species, sites, tree age and management (Lott et al., 2000; Claesson et al., 2001; Kairo et al., 2009), thus limiting their generalized transferability. Although biomass prediction models were developed in the early stages of *Prosopis* species introduction, the models were for localized use in *Prosopis juliflora* plantation trial (Maghembe et al., 1983) and comparison of species growth within species screening trials (Rosenschein et al., 1999). Therefore, their application in naturally established *Prosopis* species stands is limited by species composition, sites variations and the lack of any prescribed management in the naturally established stands.

Basal or stump diameter, height, crown area and depth are the commonly used biomass predictors in young trees and multistemmed trees and shrubs (Maghembe et al., 1983; Eshete and Stahl, 1998; Kariuki et al., 2007; Kaonga and Bayliss-Smith, 2010; Zeng et al., 2010). For *Prosopis* species, basal diameter

is one of the most commonly used variable for biomass prediction (Maghembe et al., 1983; Elfadl et al., 1989; Duff et al., 1994) and height inclusion found to improve biomass prediction models (Padron and Navarro, 2004). Although basal diameter is not always specified in literature (Maghembe et al., 1983; Duff et al., 1994), diameter measured at 30 cm above the ground (D_{30}) is more frequently used as basal diameter (Eshete and Stahl, 1998, Padron and Navarro, 2004; Kariuki et al., 2007) and was thus adopted for this study. Furthermore, accurate tree height and crown measurement may not be feasible in naturally established dense *Prosopis* stands, because of interlocking tree canopies. The objective of this study was therefore to evaluate the suitability of diameters (D_{30} and DBH) as variables for biomass estimation in naturally established *Prosopis* stands.

Materials and methods

Sites descriptions

Sites for this study were identified at Katilu and Nadapal during a related study on prediction of *Prosopis* species invasion in Kenya (Muturi et al., 2010). The structure of DBH for *Prosopis* stands in the two sites was evaluated using sixteen intensive sample plots (Barnett and Stohlgren, 2003). Subsequently, Nadapal site was selected for allometric models development. Two more sites:- Marigat and Bura were selected for validation of the developed models. All the sites are within arid areas of Kenya that are characterized by low erratic rainfall, high temperatures and high evapotranspiration potentials, leading to high soil moisture deficits (Sombroek et al., 1982). However, Nadapal and Bura are riverine sites where microclimate is modified by forests, periodic flooding and river flow. Rainfall in all the sites is bimodal with peaks around April and November. Mean annual rainfall along the Turkwel riverine forest ranges from 500 mm upstream to less than 200 mm downstream, with high inter-annual variations (Reid and Ellis, 1995; Stave et al., 2005). The mean rainfall at Katilu is higher (≈ 350 mm) than at Nadapal (≈ 200 mm). Temperatures in the vast arid areas adjacent to Turkwel riverine forest ranges from 28-40 ^{o}C. At Marigat, the mean annual rainfall is estimated at ≈500 mm with mean temperatures of 24-34 ^{o}C (Ekaya et al., 2001; Kipkorir et al., 2002). Bura has a mean annual rainfall of 370 mm and mean daily temperature of 28 ^{o}C (Maingi and Marsh, 2006). The geographical locations of the sites are shown in Figure 6.1.

Tree sampling

Thirty trees from the site selected for allometric equations development were randomly sampled and their height, diameters (D_{30} and DBH), fresh weight and volumes measured in the field. The trees were sampled to represent the known range of diameters for the species in the area, at specified intervals of 2 – 3 cm classes. Tree height was measured with a measuring rod, while diameters were measured using a diameter tape. The choice of basal diameter measurement point (30 cm from ground surface) was influenced by the multistemming of stumps, as most *Prosopis* trees were found to branch at beyond 30 cm from the ground. As the number of merchantable stems (DBH ≥2.5 cm) per stump was occasionally greater than 1, the number of stems used in model development was 45. Each measured tree or merchantable stem was felled and branches for volume and biomass measurement cut off at diameters of ≥1.5 cm (the lower limit for woody material considered suitable for use as fuel wood). Several tree discs or segments totaling about 1kg were sampled at 2.5 m intervals from the base of each tree upwards for dry weight determination. For multistemmed trees, only one stem was sampled and uniformity of tree characteristics assumed for the other stems. The actual weight of all the sampled tree components was then determined with a spring balance and sample volumes determined immediately using water displacement method. In this method, a bucket was placed in a large container, water filled to the brim and tree samples submerged in water. Displaced water was collected in the container where the bucket was placed and the volume of water displaced by each sample measured with graduated containers.

For determination of whole tree weight and volume, trees were cut into small sizes immediately after felling, depending on the depth of the bucket used in water displacement. Tree segments of weights that could be easily lifted were fastened together with a sisal twine and weighed with a spring balance until the entire tree materials were exhausted; and their volumes determined using the aforementioned water displacement method. Volumes and weights were then recorded separately for each tree or merchantable stem.

Samples collected for moisture content determination were kept under field conditions while in field, and at room temperature after each day, until the field sampling was complete. Samples were then taken to KEFRI laboratory, weighed and oven dried at 105 ^{o}C for 72 hours and re-weighed daily until constants weight was achieved for each sample as previously described (Maghembe et al.,

1983; Padron and Navarro, 2004). Percentage dry weight of the samples was determined after the drying process and the values obtained for each tree sample used to convert fresh weight into dry weight for the respective tree. The procedure was repeated for trees sampled at Marigat and Bura for model validation. The characteristics of trees in the three sites are summarized in Table 6.1.

Modeling

Square and log transformed (Duff et al., 1994; Padron and Navarro, 2004; Alvarez et al., 2011) and untransformed (Maghembe et al., 1983; Padron and Navarro, 2004) basal diameters have been used for *Prosopis* biomass prediction depending on the species and nature of the stand studied. Therefore, transformed and untransformed data were evaluated for model development in the current study, using linear and power regression between tree height, D_{30} and DBH as the independent variables and tree volume or biomass as the dependent variables. Goodness of fit and model comparisons were evaluated using coefficient of determination (R^2), the standard error (se) and F values (Sokal and Rohlf, 1981). Models with high R^2, low se and high F value were selected and used to predict volume and tree biomass for trees sampled at Marigat and Bura. Subsequently, linear regression was used to test the effectiveness of selected models in predicting tree volume and biomass using measured volumes and weights as the independent variables and those predicted as the dependent variables. The best models based on R^2 and standard error were selected, the data from the three sites pooled and variables in the selected models used to develop overall models for predicting tree biomass and volumes in naturally established stands. The selected models were tested in predicting tree biomass along the Turkwel using data collected from the DBH structure evaluation plots. Statistical variation of selected models was evaluated with paired t-test, using predicted tree weights or volume for diameter models (D_{30} and DBH) and diameters and multiplicative (H*D) models. All statistical analyses were carried out using SPSS.

Results

The DBH distribution structures for stands at Katilu revealed a mixed trend while a near normal distribution trend was found at Nadapal (Figure 6.2). The Nadapal site was therefore considered more suitable for model development. Preliminary evaluation of model development using transformed and untransformed data could not justify data transformation as reliable models were obtained with untransformed data. Untransformed data was therefore used for allometric equations development. Power models ($y = aX^b \pm e$) were stronger than linear models ($y=aX+b\pm e$) in relating tree volumes, fresh weight and dry weights to tree diameters and height (Table 6.2). This fact is exemplified by comparison of height and D_{30} multiplicative power ($Y = aHD_{30}^{b}$) and linear ($Y=aHD_{30} + b$) models for fresh weight, volume and dry weight (Table 6.2). From this comparison, both R^2 and F values were higher in power than in linear models, while a contrary trend was observed for standard error. Compared to diameter models, height models were weak on all comparison attributes (Table 6.2). Statistical comparisons of predicted tree biomass and volumes revealed insignificant differences between diameters models and between comparable diameter and multiplicative models (t-test data not shown).

The diameter and multiplicative models selected for validation at Marigat and Bura were all effective in correlating predicted and measured tree weights and volumes, with DBH model yielding the best results (Table 6.3). Multiplicative models revealed mixed results (Table 6.3). Prediction was slightly better at Bura than Marigat, when models parameters were compared between the two sites (Table 6.3). However, this was statistically insignificant as exemplified by the overlapping linear models fitted between predicted and measured dry weight and volume, using D_{30} models (Figure 6.3).

Results for models developed using pooled data from all sites is shown in Table 6.4. From the table, D_{30} models were superior to DBH models according to model evaluation parameters (R^2, F value and SE), and compared favourably with the corresponding multiplicative models. Linear D_{30} models were therefore developed using log transformations for biomass and volumes estimation in the field (Figure 6.4), while the power dry weight model was used to estimate dry biomass in plots used for DBH structure evaluation. The predicted biomass ranged from 769 to 18,953 Kilograms per hectare, depending on variation of mean plot basal diameter.

Discussion

Prosopis stands in Kenya can be described as very dynamic in terms of diameter distribution structures (Figure 6.2). This observation may be associated with invasion trends, a spontaneous process that can vary with site conditions. For example, Katilu is an irrigated agriculture area, where invasion is primarily driven by continuous farm abandonment unlike Nadapal where abandonment was incidental, according to local informants and a previous study (Muturi et al., 2010). From the current study, it was apparent that basal diameter was consistently the best variable for predicting both tree volume, and tree biomass, a finding that was consistent with previous studies on *Prosopis* allometric models (Maghembe *et al.,* 1983, Elfadl et al., 1989, Duff *et al.,* 1994). Although multiplicative models were slightly better than basal diameter models (Table 6.2), multiplicative models lead to a higher error in models validation (Table 6.3), a factor that can be attributed to the challenges of accurate height measurement in closed canopy *Prosopis* stands. Since DBH models were also highly effective in biomass and volume prediction, the study confirms the suitability of diameters in volume and biomass prediction in naturally established *Prosopis* stands where canopy and height cannot be accurately measured.

Trees sampled from Nadapal were representative of trees found in the other two *Prosopis* stands in Kenya, as evident from good model biomass and volumes prediction at Marigat and Bura (Table 6.3), despite the distance between the three sites (Figure 6.1). The slight difference in model validation outputs could be attributed to site variation, since models are sensitive to site conditions (Kairo et al*.,* 2009), among other factors. Compared to Marigat, Bura is a riverine site and sites conditions at Bura may compare favourably with those of Nadapal than site conditions between Marigat and Nadapal. However, the sensitivity of developed models to sites appeared negligible because of overlaps on fitted linear prediction models for both sites (Figure 6.3). Also site effects were mitigated by pooling all the data in development of final models (Table 6.4) and (Figure 6.3).

Biomass and volumes of sampled trees were lower than what was recorded for trees of comparable basal diameters under plantation conditions at the early stages of *Prosopis* introduction to Kenya (Maghembe et al*.,* 1983), despite the use of a lower utilizable diameter branch limit in the current study. The possible explanation for this deviation could be variations in management, sites conditions, the species studied and lack of clarity in point of basal diameter measurement

in the previous study. While the species studied under plantation condition was positively identified as *P. juliflora* and their initial management well prescribed (Maghembe et al*.,* 1983), the trees that were sampled in the current study could be a mixture of *P. chilensis, P. juliflora* and *P. pallida*, following multiple introductions of *Prosopis* species, subsequent seeds exchange and seed dispersal by livestock and wildlife (Barrow, 1980; Herlocker et al., 1980; Paetkau, 1980; Mworia et al., 2011). The naturally established stands are also not subjected to any management. Compared to three sites where trees were sampled in this study, Mombasa has an annual rainfall ≈1200mm (Maghembe et al., 1983), which is higher than in the sites of the current study. It is likely therefore, that soil moisture in the study sites was more limiting to tree growth than in Mombasa.

Stands densities in plots sampled for DBH structure evaluation was within the range found in areas of *Prosopis* invasions (van Klinken et al., 2006). Although comparative studies of biomass in invaded riverine ecosystems is generally lacking, the potential contribution of *Prosopis* to biomass energy was evident from the observed dry weight range. The predicted biomass provides a basis for planned resource exploitation, by selecting trees and or stands that have best fuel wood based on stem diameters.

Conclusion

The trees selected for model development were representative enough for trees found in other *Prosopis* stands in Kenya, as evident from the capacity of developed models to predict tree weights and volume at Bura and Marigat, the distance between sites notwithstanding. By pooling the data for model development and validation, the potential for site sensitivity was mitigated. Therefore, the developed models have a wide application in predicting *Prosopis* biomass and volume in natural stands, particularly in Kenya. Since diameter models were better than height models and height inclusion in multiplicative models did not result to significant model improvement, the use of diameter for biomass and volume prediction is recommended. A choice can be made between use of D_{30} and DBH in biomass and volume estimation, depending on stand characteristics, because the difference between models prediction outputs were insignificant between the two diameters. However, use of D_{30} is highly recommended based on model evaluation parameters. The logarithmic linear D_{30} models recommended for biomass and volume estimation in the field are:

(a) Ln(Fresh weight (Kg)) = $0.292D_{30} + 0.59$ ($R^2 = 0.94$),

(b) Ln(Dry weight (Kg)) = $0.2933D_{30} - 0.03$ ($R^2 = 0.92$) and

(c) Ln(Volume (m^3)*1000) = $0.3025D_{30} + 0.32$ ($R^2 = 0.92$).

Table 6.1: Range of basal diameter (D_{30}), diameter at breast height (DBH) and dry weight of *Prosopis* trees sampled at Nadapal, Marigat and Bura. At Nadapal, 30 trees were sampled but individual stems were 45 because some trees multistemmed.

Site	No. of trees	D_{30} (cm)	DBH (cm)	Height (m)	Dry weight (kg/tree)
Nadapal	30 (45)	2.8 - 18.5	2.5 - 18.0	3.6 - 10.4	0.50 - 180.1
Marigat	11	3.6 - 18.0	2.5 - 17.5	3.9 – 12.0	1.10 – 148.8
Bura	10	2.6 - 18.0	2.5 - 16.8	6.3 - 11.5	0.76 - 134.0

Table 6.2: Models for tree volumes and weight prediction for tree samples collected at Nadapal. Power models were better than linear models based coefficient of determination (R^2), standard error (se) and F value (F), as exemplified by HD_{30} models (in bold) for fresh weight, volume and dry weight prediction.

Fresh weight Equations	**R^2**	**SE**	**F**	**P Value**
$Fw= 0.0004H^{5.9471}$	0.76	0.64	138.6	<0.01
$Fw= 0.1283D_{30}^{2.5194}$	0.97	0.21	1641.3	<0.01
$Fw= 0.2772DBH^{2.3624}$	0.94	0.33	646.1	<0.01
$Fw= 0.0134H*D_{30}^{1.9096}$	**0.98**	**0.17**	**2589.5**	**<0.01**
$Fw=0.0276H*DBH^{1.812}$	0.95	0.29	847.3	<0.01
$Fw= 1.3554H*D_{30}$ -37.071	**0.92**	**16.3**	**494.0**	**<0.01**

Volume Equations	**R^2**	**SE**	**F**	**P Value**
$V=0.0002H^{6.3337}$	0.74	0.72	122.7	<0.01
$V= 0.0664D_{30}^{2.7308}$	0.98	0.20	2047.0	<0.01
$V= 0.1578DBH^{2.5446}$	0.93	0.37	576.8	<0.01
$V= 0.0059H*D_{30}^{2.0608}$	**0.98**	**0.20**	**2116.4**	**<0.01**
$V= 0.0134H*DBH^{1.9464}$	0.93	0.35	666.9	<0.01
$V= 1.1298 H*D_{30}$-29.898	**0.94**	**11.7**	**666.4**	**<0.01**

Dry weight Equations	**R^2**	**SE**	**F**	**P Value**
equations	R^2	se	F	P Value
$Dw=0.0001H^{6.3237}$	0.75	0.70	131.3	<0.01
$Dw= 0.0483D_{30}^{2.6906}$	0.97	0.24	1398.7	<0.01
$Dw= 0.1114DBH^{2.5164}$	0.93	0.38	559.6	<0.01
$Dw= 0.0044H*D_{30}^{2.0372}$	**0.98**	**0.21**	**1844.2**	**<0.01**
$Dw= 0.0096H*DBH^{1.9293}$	0.94	0.34	695.9	<0.01
$Dw=0.7833H*D_{30}$ – 21.619	**0.89**	**10.7**	**381.9**	**<0.01**

Table 6.3: Coefficient of determination (R^2), standard error (SE) and F values (F) for linear regression between predicted and measured tree volumes and weights for samples collected at Marigat and Bura. The measured and predicted weight or volume were based on either D_{30}, $H*D_{30}$, DBH or H*DBH as the model variable. For all cases $P < 0.01$.

Parameter/s used	Marigat			Bura		
	R^2	SE	F	R^2	SE	F
Fresh weight (Kg)						
D_{30}	0.92	17.9	95.4	0.98	9.7	381.7
$H*D_{30}$	0.93	30.9	106.6	0.97	19.2	299.1
DBH	0.97	13.7	273.5	0.99	7.1	1010.0
H*DBH	0.92	36.3	105.6	0.98	17.0	463.3
Volume (m^3)						
D_{30}	0.93	16.1	109.0	0.97	10.4	304.9
$H*D_{30}$	0.89	38.6	65.3	0.96	24.6	172.7
DBH	0.98	10.9	403.6	0.99	8.1	707.9
H*DBH	0.89	44.7	67.5	0.97	23.0	240.1
Dry weight (Kg)						
D_{30}	0.94	10.1	116.2	0.98	5.9	402.8
$H*D_{30}$	0.94	18.4	130.2	0.99	8.8	602.9
DBH	0.98	8.0	318.8	0.99	5.3	700.9
H*DBH	0.94	22.4	120.5	0.99	7.2	1062.8

Table 6.4: Power models for biomass and volume prediction developed with pooled data from Nadapal, Marigat and Bura. Coefficient of determination (R^2), standard error (SE) and F value (F) of allometric equations developed from pooled data that was collected at Nadapal, Marigat and Bura. The equations were derived with basal diameter (D_{30}), diameter at breast height (DBH) and both Height (H) and D_{30} ($H*D_{30}$).

Predicted parameter	Allometric equation	R^2	SE	F	P Value
D_{30} (cm)					
Fresh weight (Kg)	$Y=0.132X^{2.5301}$	0.98	0.21	2457.6	<0.01
Volume (m^3)	$Y=0.00008X^{2.7058}$	0.98	0.23	2506.1	<0.01
Dry weight (Kg)	$Y=0.0507X^{2.6759}$	0.97	0.23	2418	<0.01
DBH (cm)					
Fresh weight (Kg)	$Y=0.2539X^{2.3909}$	0.96	0.28	1385.0	<0.01
Volume (m^3)	$Y=0.002X^{2.5497}$	0.95	0.32	1236.3	<0.01
Dry weight (Kg)	$Y=0.1067X^{2.5142}$	0.95	0.33	1087.7	<0.01
$H*D_{30}$					
Fresh weight (Kg)	$Y=0.01395X^{1.8855}$	0.98	0.19	2948.9	<0.01
Volume (m^3)	$Y= 0.000007X^{2.0147}$	0.98	0.21	2785.0	<0.01
Dry weight (Kg)	$Y= 0.005X^{1.9797}$	0.96	0.27	1714.5	<0.01

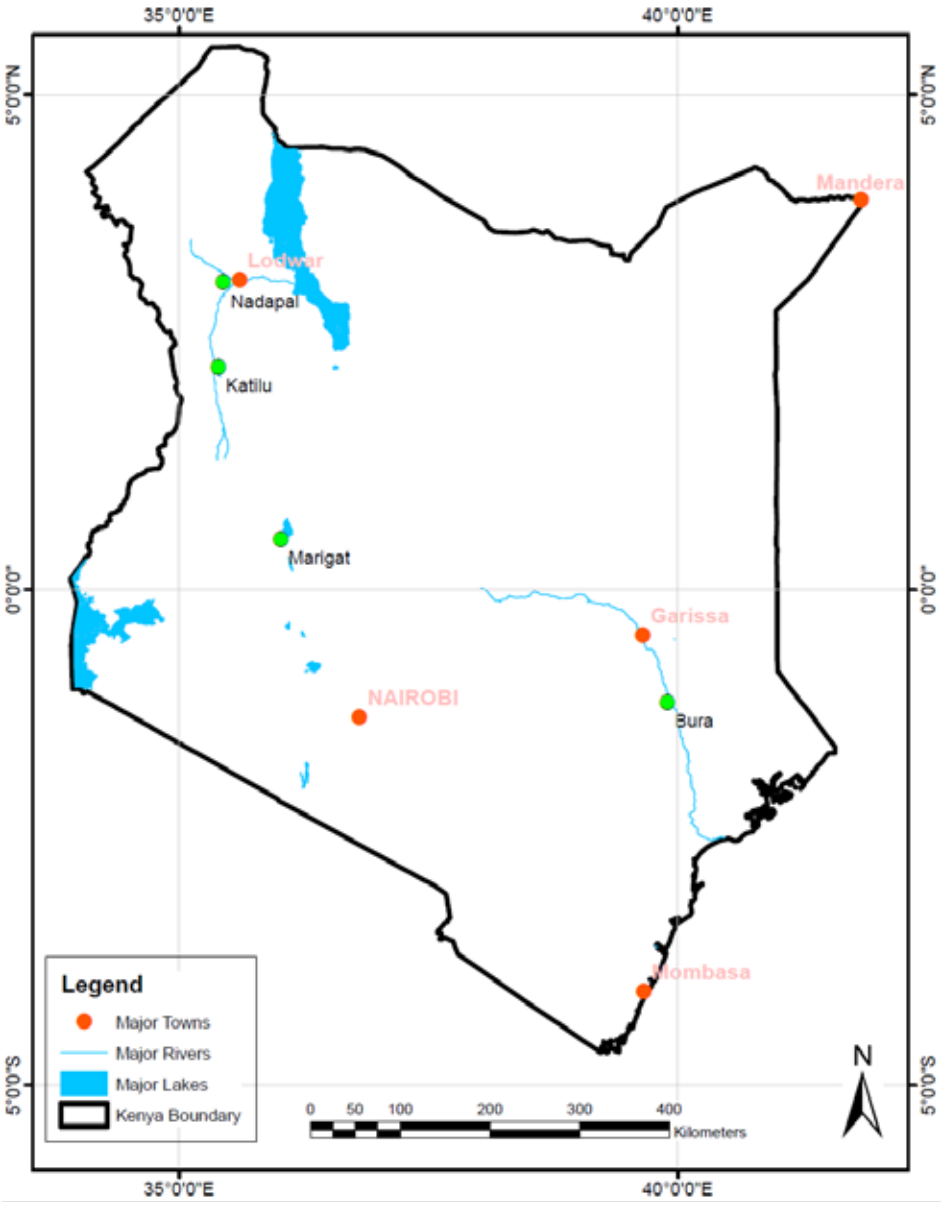


Figure 6.1: Approximate geographical locations of data collection sites (circular symbols) in Kenya. Nadapal, Katilu and Bura are riverine sites, whereas Marigat is a flat low lying site that receives seasonal runoff.

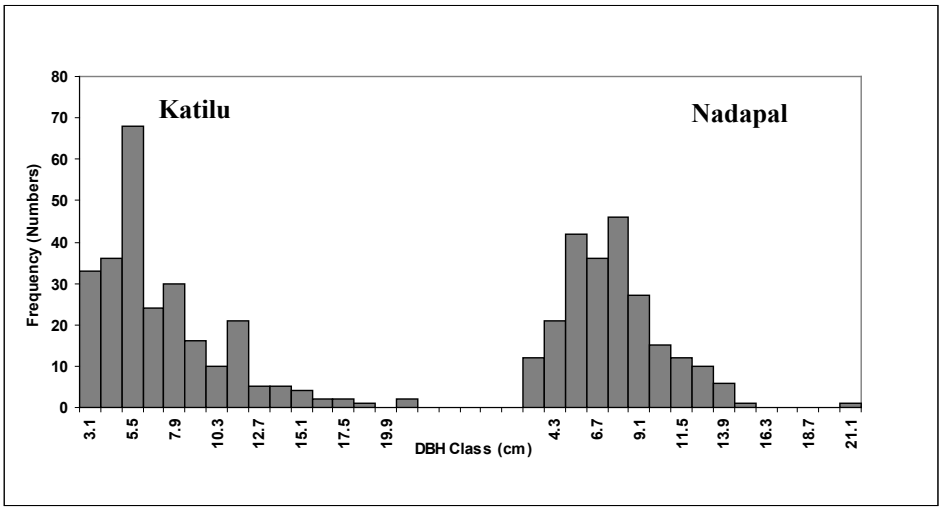


Figure 6.2: Structure of *Prosopis* diameter at breast height (DBH) at Katilu and Nadapal. The DBH structure at Nadapal was a near normal distribution compared to the DBH at Katilu, hence a stand at Nadapal was selected for biomass and volume prediction models development.

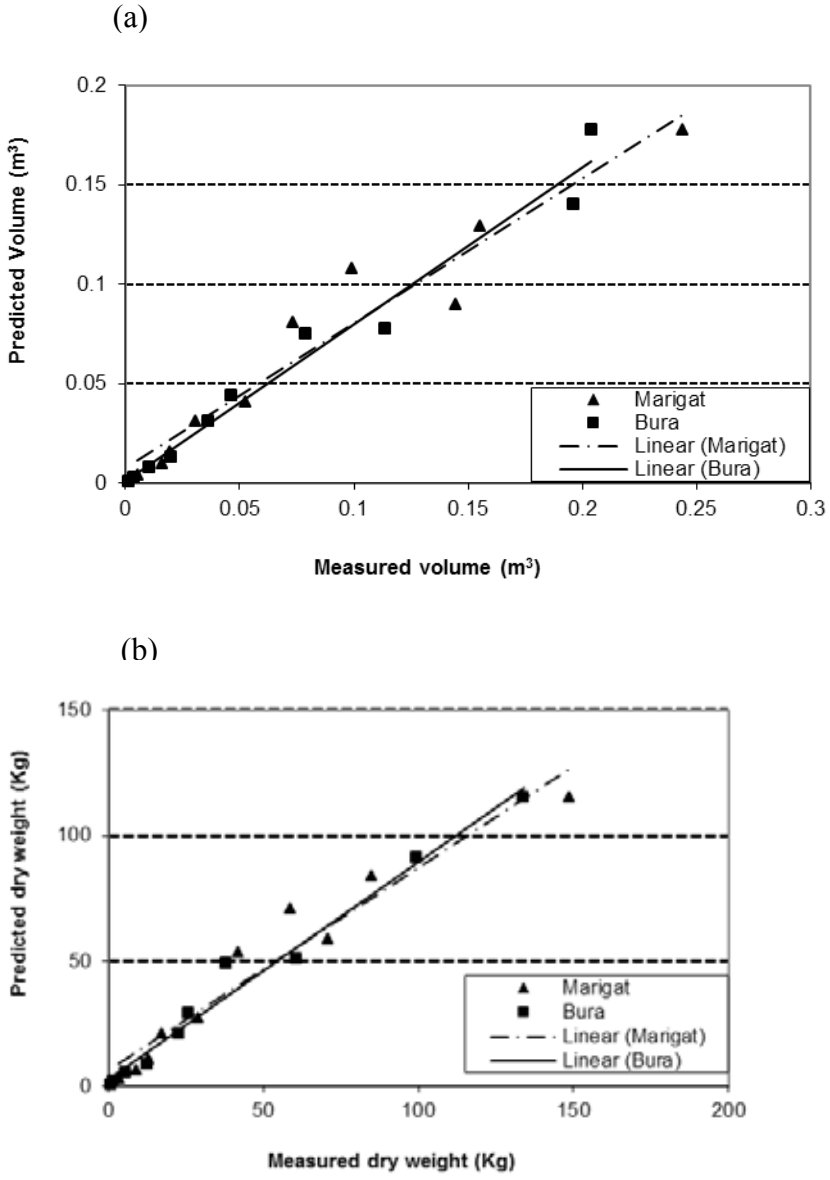


Figure 6.3: Scatterplots between measured and predicted tree volumes (a) and dry weight (b) for Marigat and Bura. Prediction was based on basal diameter (D_{30}) models. The fitted linear regression lines overlapped in both cases.

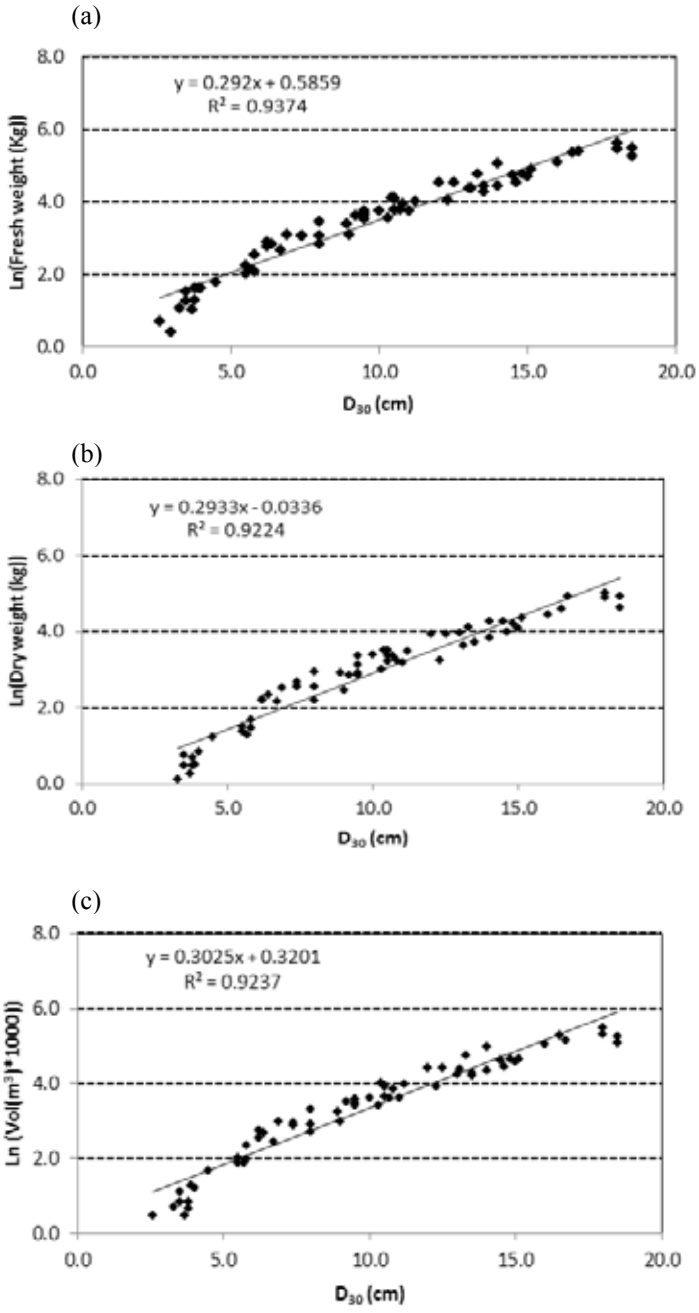


Figure 6.4: Relationship between basal diameter (D_{30}) and logarithmically transformed (Ln) fresh weight (a), dry weight (b) and volume (c), and basal diameter in *Prosopis* trees For each case, a linear model (y=ax ±b) and coefficient of determination (R^2), and linear regression model lines are included in the scatterplot.

Chapter 7

Synthesis

Introduction

A species is labeled invasive if it causes negative ecological and socio economic impacts outside its natural range (Pimentel 2001, Shackleton et al. 2007, Mwangi and Swallow 2008, Aguilera et al., 2010). Negative ecological impacts of invasive trees include biodiversity loss, reduction of ecosystem productivity and nutrient cycling. On the other hand, negative socio economic impacts may comprise the direct costs of managing invasive trees or loss of environmental services provided by the habitat before invasion. Often, invasion is associated with exotic species when they cause natural disequilibrium amongst species previously found in the invaded environment (Lockwood et al., 2007). Allelopathy, evolution of competitive ability, enemy escape and hybridization are amongst the widely acknowledged invasion hypotheses (Callaway and Ridenour, 2004, Schierenbeck and Ellstrand, 2009, van Kleunen et. al., 2010). Comparative studies between species' invasion traits in their native range and in introduced environments have revealed evolution of superior invasive traits by varieties found in the introduced environments than those in the native range (e.g., Callaway et al., 2008, Inderjit et al., 2011). To a great extent, development of superior invasive traits is attributed to progressive natural selection of most adapted genotypes or genetic evolution of hybrids of formerly separated genotypes (Schierenbeck and Ellstrand, 2009) and polyploidy (te Beest et al., 2012).

Besides species invasiveness, biological invasions may be invoked by habitat susceptibility. Habitat disturbance, empty niche, resource fluctuations and low biodiversity are among the factors that may render habitats susceptible to invasion (Lockwood et al., 2007). In riverine forests, both natural and anthropogenic factors have contributed to habitat degradation and resource fluctuation (Maingi and Marsh 2006, Richardson 2007). In some cases riverine biodiversity is also naturally low (Wyant and Ellis 1990, Stave et al 2003). Therefore riverine forests are highly susceptible to invasions due resource fluctuations, disturbance and low biodiversity.

The main factors that cause biological invasions relate to: 1) species invasiveness, and 2) habitat invasibility). In this thesis, we investigated invasibility of riverine ecosystems by *Prosopis* species, followed by *Prosopis* species invasiveness through a combination of retrospective assessments of vegetation change, empirical field studies, and controlled greenhouse experiments. To address these issues, the following research questions were addressed:

What abiotic factors make riverine forests vulnerable to *Prosopis* invasion?

Analysis of Landsat satellite images (Chapter 2) revealed: 1) an increase in ground vegetation cover or improvement of existing vegetation condition, 2) a decrease of ground vegetation cover or deterioration of existing vegetation condition, or 3) stable conditions either in pre-existing vegetation cover or other ground condition. Along the entire riverine forest 120 vegetation plots were randomly established in areas where: ground vegetation cover had increased or vgetation condition had improved (n = 41), ground vegetation cover had decreased or condition of existing vegetation deteriorated (n = 38) and ground vegetation cover or exiting ground condition had not changed (n = 41). The plots were further grouped into land cover or land use after field sampling. Of all the 120 plots, 76 plots (63%) occurred in forest and 44 (37%) plots occurred outside the forest. Ecologically, the forests represents more stable conditions than those of other areas; and such forests are naturally less susceptible to invasion than the other areas (Richardson et al., 2007, Mworia et al., 2011).The forest are dominated by wood trees that yield stable results from remote sensing data (Huttich et al., 2011).

Prior to *Prosopis* introduction in this region, the Turkwel riverine forest was dominated by *Acacia tortilis* followed by *Hyphaene compressa* (Adams 1989, Wyant and Ellis 1990). However, *Prosopis* species encroachment has occurred since 1998 (Stave et al., 2003, Ngunjiri and Choge 2004). In Chapter 2, we presented a detailed distribution of *Prosopis* species according to land cover or land use and the periodic vegetation status. Two approaches were used to clarify whether invasibility is a key determinant to *Prosopis* species invasion in the Turkwel riverine forest or not. First it was evaluated whether distribution of *A. tortilis, H. compressa* and the encroaching *Prosopis* species differed among the vegetation change status derived in Chapter 2. Secondly, land cover and land use were categorized into either forest or other areas, based on field observations and historical information collected from local informants. Other areas included forests gaps, farms and bare land (Chapter 2).

A forward logistic regression analysis was the undertaken to determine whether distribution of *A. tortilis*, *H. compressa* and *Prosopis* species differed among vegetation status (Figs. 2.3a and 2.3b) and between forest and other areas. We tested two hypotheses that: 1) *Prosopis* occurrence would be higher in areas

where ground vegetation cover had increased or vegetation condition had improved than in areas where vegetation cover had decresed or was stable, 2) *Prosopis* occurrence would be higher in other areas than in forest. We found no significant differences in distribution of *A. tortilis*, *H. compressa* and *Prosopis* among the three vegetation status (Table 7.1, Figure 7.1a). Similarly the distribution of *H. compressa* and *Prosopis* species between forest and other areas was insignificant, but distribution of *A. tortilis* was lower in other areas than in the forest (Table 7.1, Figure 7.1b). The findings contradicted our expectations, and other studies that attribute riverine forest invasion to habitat disturbances (Richardson et al., 2007, Mworia et al., 2011). Under the current scenario and the results elaborated in Chapter 2, it appears that *Prosopis* invasion was spontaneous and independent of habitat disturbance as forest and other areas were equally invasible. Accordingly, further studies on invasion impacts and underlying invasion mechanisms were undertaken in subsequent chapters.

What are the ecological implications of *Prosopis* invasion in riverine forests

In Chapter 2, we demonstrated a contrasting increase of *Prosopis* and decrease of *A. tortilis* in the Turkwel riverine forest. Besides proving fodder, *A. tortilis* stimulates the growth of herbaceous fodder species (Belsky et al., 1993). In Chapter 3, we compared the effects of *A. tortilis* and *Prosopis* canopies on herbaceous species ground cover, herbaceous species diversity and regeneration of indigenous trees. This is important, because both exotic and indigenous trees may have negative effects on the herbaceous layer (Schade et al., 2003, Kahii et al, 2009). Three discrete canopies: 1) *Acacia tortilis* canopy, 2) *Prosopis* species canopy, and 3) a mixture of *A. tortilis* and *Prosopis* species canopies were used in this study. Single species canopies facilitates direct comparison of effects of *Acacia* canopy and *Prosopis* canopy on herbaceous layer, while a mixture species canopy facilitates detection of change in herbaceous layer as *Prosopis* species encroach *A. tortilis* stands and becomes part of the canopy trees. In the study, we tested hypotheses that: 1) canopy closure was higher in high tree density *Prosopis* stands than in low density *A. tortilis* stands and intermediate in mixed species stands 2) dense *Prosopis* stands inhibited regeneration of pioneer *A. tortilis* and other indigenous species, 3) Herbaceous ground vegetation cover and herbaceous

species diversity were high under relatively open *A. tortilis* canopy and low in closed Prosopis canopy.

We measured stand canopy closure, determined tree density, sampled and analyzed the soils to determine variation of site conditions among the three canopy types. For herbaceous layer, all emerging tree seedlings were identified and enumerated according to species, herbaceous ground cover estimated; and herbaceous plants identified and enumerated, using $1m^2$ sub-plots. We found similar mean canopy closure among the three canopy types and similar soils characteristics under *Prosopis* and mixed species that contrasted with soil characteristics under A. tortilis canopy. Tree density was high in *Prosopis* stands, intermediate in mixed species stands and low in *A. tortilis* stand. *Ficus sycomorus* and *Prosopis* species regenerated well under all the three canopy types but *A. tortilis* did not regenerate in *Prosopis* and mixed species canopies. Herbaceous species ground cover was higher under *A. tortilis* and mixed species canopy than under *Prosopis* canopy. Herbaceous species diversity was high under *A. tortilis*, intermediate under mixed species and low under *Prosopis* canopies.

Our results show clearly that *Prosopis* species inhibit regeneration of *A. tortilis* and reduce herbaceous ground vegetation cover and herbaceous species diversity. We have clarified that reduction of herbaceous ground vegetation cover and herbaceous species diversity partly arose from tree effect as implied by the significant negative regression coefficients between: 1) herbaceous species ground cover and *Prosopis* species tree dummy, and 2) herbaceous species diversity and *Prosopis* tree dummy. Our findings are consistent with other studies that have demonstrated negative impact of *Prosopis* on herbaceous species (van Klinken et al., 2006, El-Keblawy and Al-Rawai 2007, Teague et al, 2008, Kahii et al., 2009, Mworia et al., 2011) and have established a direct negative correlation between tree density and herbaceous species ground vegetation cover and herbaceous species diversity. Negative effect of trees on herbaceous species arises from competition between tree and herbaceous species (Schade et al., 2003) or from the negative physical and chemical effects of litter on herbaceous species (Hata et al., 2010; Ruprecht et al., 2010).

What mechanisms underlie inhibition of *A. tortilis* regeneration by *Prosopis* species?

In Chapter 4, we conducted three greenhouse studies to determine whether *Prosopis* litter could inhibit *A. tortilis* regeneration. We evaluated the effect of *Prosopis* and *A. tortilis* litter on germination and seedling growth of *A. tortilis* and *Prosopis*. The effect of irradiance treatment on growth of *A. tortilis* and *Prosopis* seedlings was also tested. We found that increasing concentration of fresh *Prosopis* litter in the soil inhibited germination of both species much more strongly than increasing concentration of fresh *A. tortilis* litter in the soil. When the soil-litter mixtures were watered for one month, both *Prosopis* and *A. tortilis* litter had no effect on seed germination and were beneficial to seedling growth. Seedlings dry weight decreased significantly with decrease in irradiance. However, seedling dry weights for both species were similar within each irradiance or litter treatment levels. *Prosopis* litter was more inhibitive to seedling nodulation than *A. tortilis* litter.

The study revealed higher initial concentration of soluble phenols in *A. tortilis* litter than *Prosopis* litter, but soluble *A. tortilis* phenols were readily leached by water, and after two weeks the phenolic concentrations were lower than in *Prosopis* litter. Hence, soluble phenols in *Prosopis* litter are more resistant to water leaching than those of *A. tortilis*, and *Prosopis* litter may therefore have a longer-lasting allelopathic effect. Results on litter leaching were consistent with water solubility of phytotoxins of *Acacia confusa* (Chou et al., 1998), *Acacia melanoxylon* (Hussain et al., 2011) and low decomposition rate of *Prosopis juliflora* litter (Goel et al., 1989). It therefore seems that trees from *Acacia* and *Prosopis* genus may differ in their ecological impacts based their variation in phenols solubility and litter decomposition. In the field, allelopathic effects of *Prosopis* litter are aggravated by accumulation of high litter quantities below *Prosopis* canopies (Garg 1992, van Klinken 2006). Unlike *Prosopis* species, *A. tortilis* trees cannot accumulate large quantities of litter because of low tree density (Legesse and Eddy 1990, Oba 1998) and consumption of *A. tortilis* litter by livestock (Wyant and Ellis 1990, Reid and Ellis 1995).

We confirmed that canopy closure did not inhibit *A. tortilis* regeneration under *Prosopis* canopy because of three factors; 1) in the field, the mean canopy closure was similar among the three canopy types but *A. tortilis* did not regenerate

under *Prosopis* canopy, 2) in the greenhouse, seeds germination and seedlings survival were high under all irradiance treatments, and 3) seedling biomass did not differ between *A. tortilis* and *Prosopis* under similar irradiance treatment levels. Therefore the results suggest that allelopathy of *Prosopis* litter contributes to inhibition of *A. tortilis* regeneration in the field, and may also be partially responsible for a reduction of herbaceous ground vegetation cover and herbaceous species diversity. Besides the direct allelopathic effects, reduction of seedling nodulation at high *Prosopis* litter concentration demonstrated the possibility of poor symbiotic interactions between soil microbes and plants in *Prosopis* invaded areas, thus interfering with plant nutrition and growth (Cardos and Kuyper 2006, Kaschuk et al., 2009).

Which *Prosopis* species occur in *Prosopis* invaded areas of Kenya?

Focused invasion management requires proper identity of the invading species, for comparative analysis and for identification of management interventions such as biological control which may be species-specific. In addition, invasion management through utilization may require proper labeling of *Prosopis* products. Unfortunately, *Prosopis* species introduction in Kenya was haphazard (Ngunjiri and Choge 2004), sometimes with unknown parent material, and as a consequence there may be discrepancies in populations description, depending on sites of introduction (Stave et al, 2003, Mwangi and Swallow 2008, Trenchard et al., 2008). In Chapter 5, we investigated whether invasion within sites is caused by a single species, by mixtures of species or by mixtures of species and their hybrids, since several species were introduced in some sites. In earlier publications (Maghembe et al., 1983, Rosenschein et al., 1999, Oba et al., 2001) *P. chilensis, P. juliflora* and *P. pallida* were recorded as the most commonly introduced species. Therefore, reference provenances of these species were obtained from University of Copenhagen, Denmark (*P. chilensis* and *P. pallida*) and Kew Botanical Gradens, UK (3 *P. juliflora* provenances). For all the three species, there was a reference from the natural range; *P. chilensis* from Chile, *P. juliflora* from Peru and *P. pallida* from Venezuela, as confirmed by the seeds supplier.

Six Kenyan *Prosopis* populations were sampled and compared for relatedness and genetic diversity with reference species, using Random Amplified

Polymorphic DNA. The Kenyan populations were obtained from Bamburi, Bura, Isiolo Marigat, Taveta and Turkwel (Fig. 1.2). Bura, Marigat and Turkwel sites are within more invaded areas than Bamburi, Isiolo and Taveta (Ngunjiri and Choge 2004, Mwangi and Swallow 2008). In Chapter 5, we have demonstrated that, besides *P. juliflora, P. chilensis, P. pallida* and probably *P. chilensis – P. juliflora* hybrids are all present in Kenya. However, our hypothesis that populations in areas of mixed species introduction consisted of a mixture of species was not sustained by the results. Instead, only one of the introduced species or a hybrid had established within a site. This suggests that other introduced species are not adapted.

The populations at Bura, Marigat and Isiolo clustered with *P. juliflora*, Taveta clustered with *P. chilensis*, Bamburi clustered with *P. pallida*, whereas Turkwel lay between *P. chilensis* and *P. juliflora*. As the identity of references was undisputed, we concluded that populations at Bura, Marigat and Isiolo were *P. juliflora*, Taveta was *P. chilenis*, Bamburi was *P. pallida* and Turkwel was most likely a *P. chilensis – P. juliflora* hybrid. *Prosopis juliflora* and its hybrid were found within areas classified as most invaded in Kenya (Ngunjiri and Choge 2004, Mwangi and Swallow 2008), thus *P. juliflora* and the hybrid are confirmed as the most aggressive invaders. The results were consistent with global invasion database that identifies *P. juliflora* as one of the most invasive species in the tropics (http://www.issg.org/database/welcome/) and hybridization as invasion stimuli (Schierenbeck and Ellstrand, 2009).

The clear differentiation of *Prosopis* populations between sites, evident from private markers found in four (Bamburi, Isiolo, Taveta and Turkwel) out of the six populations was unexpected; as genetic homogenization of Kenyan materials was anticipated from seeds exchange between sites (Kaarakka et al., 1990, Otsamo et al., 1993) or natural seed dispersal by livestock and wildlife (Mwangi and Swallow 2008, Mworia et al 2011). Based on the results, it was concluded that natural seed dispersal is localized within sites and that the sampled populations are indeed geographically isolated. Two factors may have contributed to uniqueness of Kenyan *Prosopis* germplasm in relation to site. First, at introduction some sites may have received unique germplasm, as sourcing of introduction materials was fairly random. Second, some introduced genotypes were not adapted and may have been selectively eliminated within each site, leaving only those that were adapted. As environmental factors vary naturally

among sites, adaptability of introduced germplasm may also vary with sites. This is supported by higher molecular variance amongst, as compared to within, *Prosopis* populations found in this study. As a result of the observed genetic diversity among Kenyan populations, some management intervenetions may not be generalized across sites but may require initial piloting in certain areas.

Ecological implications of study findings

According to Chapter 2, *Prosopis* species are more opportunistic colonizer of any available gap than *A. tortilis*, yet *A. tortilis* was the main pioneer species in Turkwel riverine forest and adjacent *Acacia* woodlands (Adams 1989, Wyant and Ellis 1990). Ecologically, the gradual replacement of *A. tortilis* by *Prosopis* species in riverine forests seems perpetual, and is indeed a serious threat to sustenance of *A. tortilis* in indigenous riverine vegetation. This may be related to three factors. First, *Prosopis* species are phenotypically plastic (Hunziker et al., 1986, Guevara et al., 2010). Second, invasive species such *P. juliflora* outcompete other species by extravagant water use, as demonstrated in physiological study (Elfadl and Luukkanen 2006). Third, seed studies have revealed prolific seeding of *Prosopis* species (Zimmerman 1991, Shiferaw et al. 2004), more Bruchids infestation of *A. tortilis* seeds in the native range (Abdullah and Abulfatih 1995, Miller 1996), high germination of *Prosopis* seeds at high temperature (El-Keblawy and Al-Rawai 2005), larger recoverable quantity of *Prosopis* species as compared to *A. tortilis* seeds per unit area of soil seed bank (Witkowski and Garner 2000, Shiferaw et al 2004) and long-term viability retention by *Prosopis* seeds in the soil seed bank (Shiferaw et al 2004).

We found consistently high germination of *Prosopis* seeds irrespective of the seed lot, and inconsistency in germination of *A. tortilis* seeds depending on seed lot used in our experiments. Moreover, *A. tortilis* seeds required more elaborate pretreatment than *Prosopis* seeds. Accordingly, *Prosopis* seeds germinate more readily than *A. tortilis* seeds in the field, whereas abundance of *Prosopis* seeds increases their germination probability. Taken together, all these factors infer increased competitive ability in *Prosopis* species compared to *A.tortilis.*

Management recommendation

To a great extent, Kenya's woodlands are still subjected to traditional management, where resource exploitation is entrusted to elders (Barrow 1990, Castro 1991), and ecological resilience achieved by seasonal movements between pastures (Macpherson 1995, Sitters et al., 2009) and shifting cultivation (Oba et al., 2001). However, conflicts have arisen between traditional management practices and emerging government policies or lifestyles, thus complicating woodland management (Stave et al., 2001). Despite the complexity of management, woodlands have enormous economic potential, mainly as wood fuel source (Kituyi 2004, Bailis 2009). *Acacia tortilis* is a preferred charcoal species and its pods are harvested as fodder (Barrow 1990, UNEP 2000, Okoti et al., 2004). *Prosopis* species have high fuelwood quality and their pods are a valuable fodder resource (Pasiecznik et al., 2001, Gallaher and Merlin 2010). With the calorifc values 17.8 for A. tortilis, 19.4 for Prosopis cineraria and 16.8 for *Prospis juliflora* (Puri et al., 1994, Bhoi et al., 2006), it appears that fuelwood quality of *A. tortilis* and *Prosopis* species are almost similar. Therefore, utilization of *Prosopis* species is interchanged with that of *A. tortilis,* particularly for wood fuel. However*, Prosopis* species have not been extensively used probably because of the traditional preference of *A. tortilis* and lack of management and exploitation guidelines for *Prosopis* species. Because of utilization contrast between *A. tortilis* and *Prosopis* species, extensive intact monoculture stands of *Prosopis* species and invasion of mature *A. tortilis* stands by *Prosopis* species were encountered while conducting studies in Chapter 2 and 3. Thus the contrasting increase of *Prosopis* and decrease of *A. tortilis* observed in Chapter 2 can partially be attributed to the prevailing lack of *Prosopis* utilization and overutilization of *A. tortilis*; and the trend can be reversed by *Prosopis* exploitation.

In Chapter 6, we developed a biomass prediction model that can be used to quantify available *Prosopis* biomass in any site, once the diameter density distribution of a stand is known. We recommended the use of these models in systematic exploitation of *Prosopis* wood resource. However, exploitation requires stump management, such as uprooting to prevent further establishment of impenetrable thickets through coppicing (Shiferaw et al 2004).

Prosopis invasion is associated with pasture loss (Mwangi and Swallow 2008), yet the pods are valuable fodder resource. Therefore pasture loss can be partially compensated through utilization of pods as livestock feeds supplement. Milling of *Prosopis* species pods would be effective in seeds destruction, thus reducing their abundance in the soil seed bank. However, such intervention should be preceded by resource quantification and production trends. By targeting *Prosopis* for wood fuel and livestock feeds supplement, tree density can be partially controlled. Subsequently, litter accumulation and the resultant litter allelopathy would be reduced and negative invasion impacts mitigated. However, farm abandonment should also be minimized to prevent further establishment of expansive *Prosopis* stands.

Research recommendation

This study disclosed several issues that may warrant further investigations, but two were most outstanding. First, growth is normally one criterion used in species introduction, yet our study revelaed similar biomass production in *A. tortilis* and *Prosopis* seedlings at nursery stage. As this was a single case comparison, a more comprehensive nursery and field growth comparison with several *A. tortilis* provenances and *Prosopis* populations is recommended. The studies would clarify whether any of existing *Prosopis* germplasm has superior growth than the most fast growing *A. tortilis* provenance. However, response to environmental stresses should be included in such studies, as field conditions are environmentally stressful. Second, genetic differentiation of *Prosopis* populations depending on site was unexpected. From resource utilization viewpoint, such diversity may imply variation of targeted products, which should be tested. Ecologically, the variation dictates the need for comparing whether allelopathy effects of *Prosopis* species on indigenous vegetation vary among the genetically differentiated populations.

Outstanding conclusions

This study shows that *Prosopis* invasion in riverine forests is spontaneous. *Prosopis juliflora* is the most widespread species, but *P. chilensis, P. pallida* and a likely *P. chilensis – P. juliflora* hybrid is also present in Kenya. At the site level, all species and the hybrid have monoculture tendencies, indicating that only one species or a hybrid is best adapted to a site following the introduction of several species in some sites. Based on the current national invasion patterns, the study confirmed that *P. juliflora* and its hybrids are the most aggressive invaders. The salient invasiveness traits found in this study are: 1) Allelopathy of *Prosopis* litter which reduce herbaceous species ground vegetation cover and herbaceous species diversity; and inhibits regeneration of *A. tortilis*. The net effect of allelopathic impacts results in loss of herbaceous fodder and decimation of *A. tortilis* in riverine forest, if unchecked; 2) Specialized site adaptation of introduced germplasm evident from the genetic differentiation of introduced germplasm depending on site. Genetic differentiation may pose challenges in biological control, as certain genotypes may resist introduced biological pests, and 3) hybridization that is evident from occurrence of a *P. chilensis –P. juliflora* hybrid in Turkwel. Invasion by the hybrid in the Turkwel is rated higher than invasion by *P. chilensis* at Taveta.

Although the study revealed three invasion mechanisms, allelopathy appears to be most outstanding. This is because, hybridization is often associated with fast growth, yet our nursery experiments found no significant difference between biomass production in *A. tortilis* and *P. chilensis-P.juliflora* hybrid seedlings. Allelopathy of *Prosopis* litter is aggravated by prolific seeding of *Prosopis* species and high germinability of *Prosopis* seeds, in contrast to that of *A. tortilis*. Therefore invasion management should focus more on reduction of surface *Prosopis* litter and seed accumulation and reduction of *A. tortilis* pods and wood overutilization.

Table 7.1: Logistic regression coefficients (β), Wald values (Wald) and significance level (P) distribution of *Acacia tortilis*, *Hyphaene compressa* and *Prosopis* species among areas with positive vegetation change, negative vegetation change and stable vegetation (vegetation status) and between forests and other areas (Land cover). Stable vegetation was used as the reference (constant) for comparison of species distribution within vegetation status and forest used as the reference for comparison of species distribution between forest and other areas.

Factor	β	Wald	P
Vegetation status			
Acacia tortilis	-	-	0.954
Hyphaene compressa	-	-	0.188
Prosopis species	-	-	0.269
Constant (stable vegetation)			
Land cover (forest or others)			
Acacia tortilis	-1.44	11.28	0.001
Hyphaene compressa	-	-	-
Prosopis species	-	-	-
Constant (Forest)	0.21	0.84	0.36

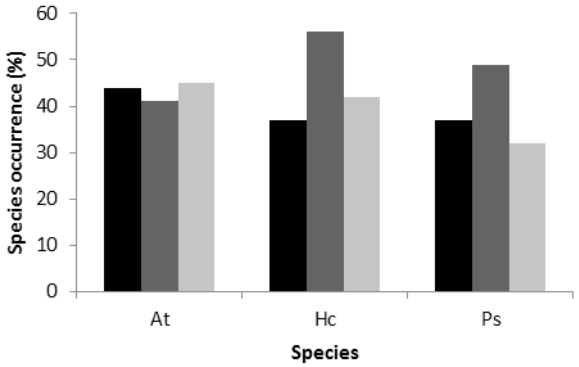


Figure 7.1a: Distribution Acacia tortilis (At), *Hyphaene compressa* (Hc) and *Prosopis* species (Ps) in areas without change (black shade), areas with positive (gray shade) and areas with negative change (light gray shade).

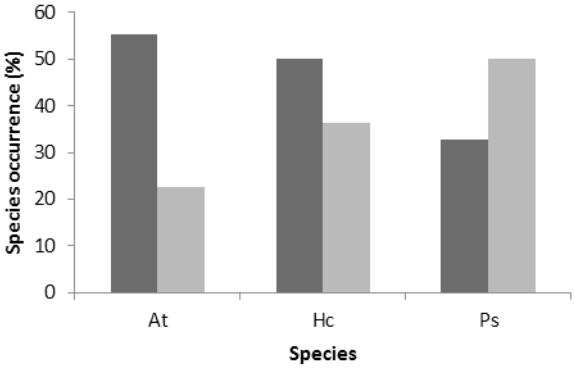


Figure 7.1b: Distribution of *Acacia tortilis* (At), *Hyphaene compressa* (Hc) and *Prosopis* species (Ps) between forests (black shade) and other areas (gray shade).

References

Abdullah, M.A.R., Abulfatih, H.A. 1995. Predation of Acacia seeds by Bruchi beetles and its relation to altitudinal gradient in South Western Saudi Arabia. Journal of Arid Environments 29: 99-105.

Adams, W.M., 1989. Dam construction and the degradation of floodplain forest on the Turkwel River, Kenya. Land Degradation and Development 1:189-198.

Alvarez, J.A., Villagra, P.E., Villalba, R., Cony, M.A., Alberto, M. 2011. Wood productivity of Prosopis flexuosa DC woodlands in the central Monte: Influence of population structure and tree-growth habit. Journal of Arid Environments 75: 7-13.

Anderson, S. 2005. Spread of the introduced tree species Prosopis juliflora (Sw.) DC, in the lake Baringo area, Kenya. Institutionen for Skoglig vegetationsekologi. ISSN 1652-4918.

Anderson, D. 1984. Depression, dust bowl, demography and drought – the colonial state and soil conservation in East Africa during the 1930's. African Affairs 83: 321-343.

Bailis, R. 2009. Modeling climate change mitigation from alternative methods of charcoal production in Kenya. Biomass & Bioenergy 33: 1491-1502.

Barnett, D.T., Stohlgren, T.J. 2003. A nested-intensity design for surveying plant diversity. Biodiversity and Conservation 12: 255-278.

Barrow, E.G.C. 1990. Usufruct Rights to Trees - the Role of Ekwar in Dryland Central Turkana, Kenya. Human Ecology 18:163-176.

Barrow, E. G. C., 1980. Multipurpose trees, current experience and future possibilities. Pp. 499-505 in Buck, L. (editor) Proceedings on Kenya National Seminar on Agroforestry. 12-22 October 1980, Nairobi.

Beentje 1994. Kenya trees, shrubs and lianas. National Museums of Kenya, Nairobi, Kenya.

Belsky, A.J. et al. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26: 1005-1024.

Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M., Ali, A.R. 1993. Comparative effects of isolated trees on their undercanopy environments in high-rainfall and low-rainfall savanna. Journal of Applied Ecology 30: 143-155.

Besnard, G., Henry, P., Wille, L., Cooke, D., Chapuis, E. 2007. On the origin of the invasive olives (Olea europaea L., Oleaceae). Heredity 99: 608-619.

Bhoi, P.R., Singh, R.N., Sharma, A.M., Patel, S.R. 2006. Performance evaluation of open core gasifier on multi-fuels. Biomass & Bioenergy 30:575-579.

Blackburn, T.M. et al. 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26: 333-339.

Blossey, B., Notzold, R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. Journal of Ecology 83: 887-889.

Bryant, J.P., Heitkonig, I., Kuropat, P., Owensmith, N. 1991. Effects of severe defoliation on the long-term resistance to insect attack and on leaf chemistry in 6 woody species of Southern African Savanna. American Naturalist 137: 50-63.

Browne, S., de Gans, G. 1981.Crop production in the context of Turkana rehabilitation project. 19Pp.

Burkart, A. 1976. Monograph of the genus Prosopis (Leguminosae-subfam-Mimosoideae). Journal of the Arnold Arboretum 57: 219-249, 450-525.

Bush, J.K., Vanauken, O.W. 1987. Light requirements for growth of Prosopis glandulosa seedlings. Southwestern Naturalist 32: 469-473.

Callaway, R.M. et al. 2008. Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89: 1043-1055.

Callaway, R.M., Ridenour, W.M. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2: 436-443.

Cardoso, I.M., Kuyper, T.W. 2006. Mycorrhizas and tropical soil fertility. Agriculture Ecosystems & Environment 116:72-84.

Castro, A.P. 1991. Indigenous Kikuyu Agroforestry - a Case-Study of Kirinyaga, Kenya. Human Ecology 19:1-18.

Chou, C.H., Fu, C.Y., Li, S.Y., Wang, Y.F. 1998. Allelopathic potential of Acacia confusa and related species in Taiwan. Journal of Chemical Ecology 24: 2131-2150.

Claesson, S., Sahlen, K., Lundmark, T. 2001. Functions for biomass estimation of young Pinus sylvestris, Picea abies and Betula spp. from stands in northern Sweden with high stand densities. Scandinavian Journal of Forest Research 16: 138-146.

Coetzer, W., Hoffmann, J.H. 1997. Establishment of Neltumius arizonensis (Coleoptera: Bruchidae) on mesquite (Prosopis species: Mimosaceae) in South Africa. Biological Control 10: 187-192.

Coughenour, M.B., Ellis, J.E., 1993. Landscape and climatic control of woody vegetation in a dry tropical ecosystem – Turkana District, Kenya. Journal of Biogeography 20, 383-398.

Darkoh, M.B.K. 1998. The nature, causes and consequences of desertification in the drylands of Africa. Land Degradation & Development 9: 1-20.

Dawson, W., Fischer, M., van Kleunen, M. 2011. The maximum relative growth rate of common UK plant species is positively associated with their global invasiveness. Global Ecology and Biogeography 20:299-306.

Dharani, N., 2006. A field guide to common trees and shrubs in East Africa. Struik publishers, South Africade Knegt, H.J., van Langevelde, F., Coughenour, M.B., Skidmore, A.K., de Boer, W.F., Heitkonig, I.M.A., Knox, N.M., Slotow, R., van der Waal, C., Prins H.H.T. 2010. Spatial autocorrelation and the scaling of species-environment relationships. Ecology 91:2455-2465.

Diallo, M.D. et al. 2006. Biological effects of native and exotic plant residues on plant growth, microbial biomass and N availability under controlled conditions. European Journal of Soil Biology 42: 238-246.

Donath, T.W., Eckstein, R.L. 2010. Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. Plant Ecology 207: 257-268.

Dregne, H.E. 2002. Land degradation in the drylands. Arid Land Research and Management 16: 99-132.

Duff, A.B., Meyer, J.M., Pollock, C., Felker, P. 1994. Biomass production and diameter growth of 9 half-sib families of mesquite (Prosopis glandulosa var galndulosa) and a fast growing Prosopis alba half sib family grown in Texas. Forest Ecology and Management 67: 257-266.

Dussart, E., Lerner, P., Peinetti, R. 1998. Long term dynamics of 2 populations of Prosopis caldenia Burkart. Journal of Range Management 51: 685-691.

Edwards, K., Johnstone, C., Thompson, C. 1991. A simplified rapid method for preparation of plant genomic DNA for PCR analysis. Nucleic Acids Research 19: 1349-1349.

Ekaya, W.N., Kinyamario, J.I., Karue, C.N. 2001. Abiotic and herbaceous vegetation characteristics of an arid rangeland in Kenya. *Afr. J. Range Fora Sci* 18, 125-129.

Elfadl, M.A. et al. 1989. Regression equations to predict fresh weight and 3 grades of lumber from large mesquite (Prosopis glandulosa var glandulosa) in Texas. Forest Ecology and Management 26: 275-284.

El-Keblawy, A., Al-Rawai, A. 2005. Effects of salinity, temperature and light on germination of invasive Prosopis juliflora (Sw.) DC. Journal of Arid Environments 61: 555-565.

El-Keblawy, A., Al-Rawai, A. 2007. Impacts of the invasive exotic Prosopis juliflora (Sw.) DC on the native flora and soils of the UAE. Plant Ecology 190: 23-35.

Ellstrand, N.C. 2009. Evolution of invasiveness in plants following hybridization. Biological Invasions 11: 1089-1091.

Ellstrand, N.C., Schierenbeck, K.A. 2006. Hybridization as a stimulus for the evolution of invasiveness in plants? Euphytica 148: 35-46.

Erfmeier, A., Bruelheide, H. 2010. Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive Rhododendron ponticum populations. Biological Invasions 12: 657-676.

Eriksen, S., Lind, J. 2009. Adaptation as a Political Process: Adjusting to Drought and Conflict in Kenya's Drylands. Environmental Management 43: 817-835.

Eshete, G., Stahl, G. 1998. Functions for multi-phase assessment of biomass in acacia woodlands of the Rift Valley of Ethiopia. Forest Ecology and Management 105: 79-90.

Ferreyra, L.I., Vilardi, J.C., Tosto, D.S., Julio, N.B., Saidman, B.O. 2010. Adaptive genetic diversity and population structure of the "algarrobo" Prosopis chilensis (Molina) Stuntz analysed by RAPD and isozyme markers. European Journal of Forest Research 129: 1011-1025.

Franks, S.J., Pratt, P.D., Dray, F.A., Simms, E.L. 2008. Selection on herbivory resistance and growth rate in an invasive plant. American Naturalist 171: 678-691.

Gallagher, R.V. et al. 2011. Invasiveness in introduced Australian acacias: the role of species traits and geneome size. Diversity and Distributions 17: 884-897.

Garg, V.K. 1992. Litter production and its nutrient concentration in some fuelwood trees grown in sodic soil. Biomass & Bioenergy 3: 323-328.

Garg, V.K., Jain, R.K. 1992. Influence of fuelwood trees on sodic soils. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22: 729-735.

Geiger, J.H., Pratt, P.D., Wheeler, G.S., Williams, D.A. 2011. Hybrid vigor for the invasive exotic Brazilian pepper tree (Schinus terebinthifolius Raddi., Anacardiaceae) in Florida. International Journal of Plant Sciences 172: 655-663.

Gibson, M.R. et al. 2011. Reproductive biology of Australian acacias: important mediator of invasiveness? Diversity and Distributions 17: 911-933.

Gicheru, P., Gachene, C., Mbuvi, J., Mare, E. 2004. Effects of soil management practices and tillage systems on surface soil water conservation and crust formation on a sandy loam in semi-arid Kenya. Soil & Tillage Research 75: 173-184.

Goel, U., Saxena, D.B., Kumar, B. 1989. Comparative allelopathy as exhibited by Prosopis juliflora Swartz and Prosopis cineraria (L) Druce. Journal of Chemical Ecology 15: 591-600.

Gowda, J.H., Palo, R.T. 2003. Age-related changes in defensive traits of Acacia tortilis Hayne. African Journal of Ecology 41: 218-223.

Government of the Republic of Kenya (GoK) 2007. Kenya Vision 2030: A globally competitive and prosperous Kenya.

Guevara, A., Giordano, C.V., Aranibar, J., Quiroga, M., Villagra, P.E. 2010. Phenotypic plasticity of the coarse root system of Prosopis flexuosa, a phreatophyte tree, in the Monte Desert (Argentina). Plant and Soil 330: 447-464.

Harris, P.J.C., Pasiecznik, N.M., Smith, S.J., Billington, J.M., Ramirez, L. 2003. Differentiation of Prosopis juliflora (Sw.) DC. and P-pallida (H. & B. ex. Willd.) HBK using foliar characters and ploidy. Forest Ecology and Management 180: 153-164.

Hata, K., Kato, H., Kachi, N. 2010. Litter of an alien tree, Casuarina equisetifolia, inhibits seed germination and initial growth of a native tree on the Ogasawara Islands (subtropical oceanic islands). Journal of Forest Research 15: 384-390.

Hamza, B.N. 2010. Genetic variation within and among three invasive Prosopis juliflora (Leguminosae) populations in the River Nile State, Sudan. Int. J. Gen. Mol. Biol. 2:92-100.

Hauser, L.A., Crovello, T.J. 1982. Numerical analysis of generic relationships in Thelypodieae (Brassicaceae). Systematic Botany 7: 249-268.

Herlocker, D. J., Barrow, E., Paetkau, P., 1980. A preliminary report on trial plantings of woody species in Arid and Semi-Arid Northern Kenya. Pp 511-578 in Buck, L. (editor) Proceedings on Kenya National Seminar on Agroforestry. 12-22 October 1980, Nairobi.

Hughes, F.M.R. 1990. The influence of flooding regimes on forest distribution and composition in the Tana River Floodplain, Kenya. Journal of Applied Ecology 27: 475-491.

Hughes, F.M.R., Rood, S.B. 2003. Allocation of river flows for restoration of floodplain forest ecosystems: A review of approaches and their applicability in Europe. Environmental Management 32: 12-33.

Hunziker, J.H. et al. 1986. Hybridization and genetic variation of Argentine species of Prosopis. Forest Ecology and Management 16: 301-315.

Huttich, C., Herold, M., Strohbach, B., Dech, S. 2011. Integrating in-situ, Landsat, and MODIS data for mapping in Southern African savannas: experiences of LCCS-based land-cover mapping in the Kalahari in Namibia. Environmental Monitoring and Assessment 176:531-547.

Ihwagi, F.W., Vollrath, F., Chira, R.M., Douglas-Hamilton, I., Kironchi, G. 2010. The impact of elephants, Loxodonta africana, on woody vegetation through selective debarking in Samburu and Buffalo Springs National Reserves, Kenya. African Journal of Ecology 48: 87-95.

Im, J., Jensen, J.R. 2005. A change detection model based on neighborhood correlation image analysis and decision tree classification. Remote Sensing of Environment 99: 326-340.

Inderjit et al. 2011. Volatile chemicals from leaf litter are associated with invasiveness of a Neotropical weed in Asia. Ecology 92: 316-324.

Indieka, S.A., Odee, D.W. 2005. Nodulation and growth response of Sesbania sesban (L.) Merr. to increasing nitrogen (ammonium) supply under glasshouse conditions. African Journal of Biotechnology 4: 57-60.

Iponga, D.M., Milton, S.J., Richardson, D.M. 2008. Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree Schinus molle (Anacardiaceae) in South African savanna. Journal of Arid Environments 72: 612-623.

Jennings, S.B., Brown, N.D., Sheil, D. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72: 59-73.

Jensen, J.R., Narumalani, S., Weatherbee, O., Mackey, H.E. 1993. Measurement of seasonal and yearly Cattail and Waterlily chnages using multidate Spot Panchromatic data. Photogrammetric Engineering and Remote Sensing 59: 519-525.

Juarez-Munoz, J., Carrillo-Castaneda, G., Arreguin, R., Rubluo, A. 2002. Inter- and intra-genetic variation of four wild populations of Prosopis using rapd-pcr fingerprints. Biodiversity and Conservation 11: 921-930.

Kaarakka, V., Johansson, S., Luukkanen, O., Maingi, J., 1990. Forestry in Irrigation schemes II. Research activities at Bura, Kenya 1988-1989. Tropical Forestry Report No. 5 of the University of Helsinki.

Kahii, C.H., Ngugi R.K., Mureithi, S.M., Ng'ethe, J.C., 2009. The canopy effects of *Prosopis juliflora* (DC.) and *Acacia tortilis* (Hayne) trees on herbaceous plants species and soil physico-chemical properties in Jemps Flats, Kenya. Tropical & Subtropical Agroecosystems 10, 441-449.

Kairo, J.G., Bosire, J., Langat, J., Kirui, B., Koedam, N. 2009. Allometry and biomass distribution in replanted mangrove plantations at Gazi Bay, Kenya. Aquatic Conservation-Marine and Freshwater Ecosystems 19: S63-S69.

Kaonga, M.L., Bayliss-Smith, T.P. 2010. Allometric models for estimation of aboveground carbon stocks in improved fallows in eastern Zambia. Agroforestry Systems 78: 217-232.

Kariuki, J. G., Machua, J., Luvnda, A. M., Kigomo, J. N., Muindi, F. K., Macharia E. W., 2007. Baseline survey of woodland utilization and degradation around Kakuma Refugee Camp. KEFRI/JOFCA Report.

Kaschuk, G., Kuyper, T.W., Leffelaar, P.A., Hungria, M., Giller, K.E. 2009. Are the rates of photosynthesis stimulated by the carbon sink strength of rhizobial and arbuscular mycorrhizal symbioses? Soil Biology & Biochemistry 41:1233-1244.

Kassas, M. 1995. Desertification – A general review. Journal of Arid Environments 30: 115-128.

Kenya Forestry Seed Centre (KFSC), undated. Unpublished seed distribution database.

Kipkorir, E.C., Raes, D., Massawe, B. 2002. Seasonal water production functions and yield response factors for maize and onion in Perkerra, Kenya. Agricultural Water Management 56: 229-240.

Kirubi, C., Wamicha, W.N., Laichena, J.K. 2000. The effects of woodfuel consumption in the ASAL areas of Kenya: the case of Marsabit forest. African Journal of Ecology 38: 47-52.

Kituyi, E. 2004. Towards sustainable production and use of charcoal in Kenya: exploring the potential in life cycle management approach. Journal of Cleaner Production 12: 1047-1057.

Krebs, J.C., 1999. Ecological methodological (second edition). Addison Wesley publishers.

Landeras, G., Alfonso, M., Pasiecznik, N.M., Harris, P.J.C., Ramirez, L. 2006. Identification of Prosopis juliflora and Prosopis pallida accessions using molecular markers. Biodiversity and Conservation 15: 1829-1844.

Laxen, J. 2007. Is prosopis a curse or a blessing? An ecological-economic analysis of an invasive alien tree species in Sudan. Ph.D. thesis published in the Tropical Forestry Reports 32 of the University of Helsinki.

Legesse, K., Eddy, M. 1990. Population ecology of Acacia tortilis in the semi-arid region of the Sudan. Journal of Vegetation Science 1:419-424.

Lockwood, J.L., Hoopes, M.F., Marchetti, M.P. 2007. Invasion ecology. Blackwell Publishing, Oxford.

Lockwood, J.L., Cassey, P., Blackburn, T.M. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions 15: 904-910.

Loth, P.E., de Boer, W.F., Heitkonig, I.M.A., Prins, H.H.T. 2005. Germination strategy of the East African savanna tree Acacia tortilis. Journal of Tropical Ecology 21: 509-517.

Lott, J.E., Howard, S.B., Black, C.R., Ong, C.K. 2000. Allometric estimation of above-ground biomass and leaf area in managed Grevillea robusta agroforestry systems. Agroforestry Systems 49: 1-15.

Lu, D., Mausel, P., Brondizio, E., Moran, E. 2004. Change detection techniques. International Journal of Remote Sensing 25: 2365-2407.

MacDonald, A.A.M., Kotanen, P.M. 2010. The effects of disturbance and enemy exclusion on performance of an invasive species, common ragweed, in its native range. Oecologia 162: 977-986.

Machua, J., Muturi, G., Omondi, S.F., Gicheru, J. 2011. Genetic diversity of Jatropha curcas L. populations in Kenya using RAPD molecular markers: Implication to plantation establishment. African Journal of Biotechnology 10: 3062-3069.

Macpherson, C.N.L. 1995. The effect of transhumance on the epidemiology of animal diseases. Preventive Veterinary Medicine 25: 213-224.

Maghembe J.A., Kariuki E.M., Hallerm, R.D., 1983. Biomass and nutrient accumulation in young Prosopis juliflora at Mombasa, Kenya. Agroforestry Systems 1:313-321.

Maingi, J.K., Marsh, S.E. 2002. Quantifying hydrologic impacts following dam construction along the Tana River, Kenya. Journal of Arid Environments 50: 53-79.

Maingi, J.K., Marsh, S.E. 2006. Composition, structure, and regeneration patterns in a gallery forest along the Tana River near Bura, Kenya. Forest Ecology and Management 236: 211-228.

Martinez-Ghersa, M.A., Ghersa, C.M. 2006. The relationship of propagule pressure to invasion potential in plants. Euphytica 148: 87-96.

Masamba, C. 1994. Presowing seed treatments on 4 African Acacia species – Appropriate technology for use in forestry for rural-development. Forest Ecology and Management 64: 105-109.

McKenney, J.L., Cripps, M.G., Price, W.J., Hinz, H.L., Schwarzlander, M. 2007. No difference in competitive ability between invasive North American and native European Lepidium draba populations. Plant Ecology 193: 293-303.

Mekuria, W. et al. 2007. Effectiveness of exclosures to restore degraded soils as a result of overgrazing in Tigray, Ethiopia. Journal of Arid Environments 69: 270-284.

Miettinen, P., Luukkanen, O., Johansson, S., Eklund, E., Mulatya, J. 1988. Rhizobium nodulation in Prosopis juliflora seedlings at different irrigation levels in Eastern Kenya. Plant and Soil 112: 233-238.

Miller, M.P. 1997. Tools for population genetic anlyses (TFPGA) 1.3 A Windows program for the analysis of allozyme and molecular population genetic data.

Miller, M.F. 1996. Acacia seed predation by bruchids in an African savanna ecosystem. Journal of Applied Ecology 33: 1137-1144.

Morgan, W.T.W. 1981. Ethnobotany of the Turkana – use of plants by a pastoral people and their livestock in Kenya. Economic Botany 35: 96-130.

Murphy, S.R., Lodge, G.M. 2002. Ground cover in temperate native perennial grass pastures. I. A comparison of four estimation methods. Rangeland Journal 24: 288-300.

Murray, S., Burke, L., Tunstall, D. 1999. Drylands population assessment II. Technical report, Wild Resources Institute, Washington D.C. USA.

Muturi, G. M., Poorter, L. Mohren, G.M.J and Kigomo, B.N. (in prep). Ecological impact of Prosopis species invasion in Turkwel Riverine Forest, Kenya.

Muturi, G.M., Mohren, G.M.J., Kimani, J.N. 2010. Prediction of Prosopis species invasion in Kenya using geographical information system techniques. African Journal of Ecology 48: 628-636.

Mwalyosi, R.B.B. 1990. The dynamic ecology of Acacia tortilis woodland in lake Manyara National Park, Tanzania. African Journal of Ecology 28: 189-199.

Mwangi, E., Swallow, B. 2008. Prosopis juliflora invasion and rural livelihoods in Lake Baringo area of Kenya. Conservation and Society 6: 130-140.

Mworia, J.K., Kinyamario, J.I., Omari, J.K., Wambua, J.K. 2011. Patterns of seed dispersal and establishment of the invader Prosopis juliflora in the upper floodplain of Tana River, Kenya. African Journal of Range & Forage Science 28: 35-41.

Nakafeero, A.L., Reed, M.S., Moleele, N.M. 2007. Allelopathic potential of five agroforestry trees, Botswana. African Journal of Ecology 45: 590-593.

Nakano, H. et al. 2002. Isolation and identification of plant growth inhibitors as candidate(s) for allelopathic substance(s), from aqueous leachate from mesquite (Prosopis juliflora (Sw.) DC.) leaves. Plant Growth Regulation 37: 113-117.

Nei, M. 1978. Estimation of average heterozygosity and genetic distsnace form a small number of individuals. Genetics 89: 583-590.

Ngetich, K.A., Birech, R.J., Kyalo, D., Bett, K.E., Freyer, B. 2009. Caught between Energy Demands and Food Needs: Dilemmas of Smallholder Farmers in Njoro, Kenya. Journal of Agriculture and Rural Development in the Tropics and Subtropics 110: 23-28.

Ngunjiri, F. D., Choge, S.K., 2004. Status and impact of Prosopis species in Kenya. In Choge S.K. and Chikamai, B.N. (eds) Proceedings of the workshop on integrated management of Prosopis species in Kenya. KEFRI.

Noor, M., Salam, U., Khan, M.A. 1995. Allelopathic effects of Prosopis juliflora Swartz. Journal of Arid Environments 31: 83-90.

Noumi, Z., Touzard, B., Michalet, R., Chaieb, M. 2010. The effects of browsing on the structure of Acacia tortilis (Forssk.) Hayne ssp raddiana (Savi) Brenan along a gradient of water availability in arid zones of Tunisia. Journal of Arid Environments 74: 625-631.

Oba, G. 1998. Effects of excluding goat herbivory on Acacia tortilis woodland around pastoralist settlements in northwest Kenya. Acta Oecologica-International Journal of Ecology 19: 395-404.

Oba, G. et al. 2001. Growth performance of exotic and indigenous tree species in saline soils in Turkana, Kenya. Journal of Arid Environments 47: 499-511.

Oba, G., Stenseth, N.C., Weladji, R.B. 2002. Impacts of shifting agriculture on a floodplain woodland regeneration in dryland, Kenyxa. Agriculture Ecosystems & Environment 90: 211-216.

Odee, D.W. et al. 2002. Genetic and symbiotic characterization of rhizobia isolated from tree and herbaceous legumes grown in soils from ecologically diverse sites in Kenya. Soil Biology & Biochemistry 34: 801-811.

Okello, B.D., O'Connor, T.G., Young, T.P. 2001. Growth, biomass estimates, and charcoal production of Acacia drepanolobium in Laikipia, Kenya. Forest Ecology and Management 142: 143-153.

Okoti, M., Ng'ethe,J.C., Ekaya, W.N., Mbuvi, D.M., 2004. Land use, ecology, and socio-economic changes in a pastoral production system. Journal of Human Ecology 16: 83-89.

Olukoye, G.A., Wamicha, W.N., Kinyamario, J.I. 2003. Assessment of the performance of exotic and indigenous tree and shrub species for rehabilitating saline soils of Northern Kenya. African Journal of Ecology 41: 164-170.

Orloci, L. 1978. Multivariate analysis in vegetation research The Hague: Dr W. Junk B. V.

Otsamo, A., Laxen, J., Johansson, S., Kaarakka, V., Luukkanen, O., Maua, J.O., 1993. Forest research in Bura, Kenya 1984-1993.

Final report of Research component in the Bura fuelwood project. Tropical Forestry Report No. 8 of the University of Helsinki.

Padron, E., Navarro, R.M. 2004. Estimation of above-ground biomass in naturally occurring populations of Prosopis pallida (H.& B. ex. Willd.) HBK in the north of Peru. Journal of Arid Environments 56: 283-292.

Paetkau, P. 1980. Tree seed distribution report – August 1979 –July 1980. In L. Buck (editor) Proceedings on Kenya National Seminar on Agroforestry. Pp 603-609.

Pairon, M. et al. 2010. Multiple introductions boosted genetic diversity in the invasive range of black cherry (Prunus serotina; Rosaceae). Annals of Botany 105: 881-890.

Paletto, A., Tosi, V. 2009. Forest canopy cover and canopy closure: comparison of assessment techniques. European Journal of Forest Research 128: 265-272.

Palm, C.A., and Rowland, A. P. 1997. Minimum data set for characterization of plant quality for decomposition. In (G. Cadisch and K.E. Giller Eds) Driven by natuer: Plant litter quality and decomposistion. CAB International, Wallingford, UK.

Pasiecznik, N.M., Felker P., Harris, P.J.C., Harsh, L.N., Cruz, G., Tewarri, J.C., Cadoret, K., Maldonado, L.J. 2001. The Prosopis juliflora-Prosopis pallida complex: A monograph. HDRA.

Patten, R.S., Ellis, J.E. 1995. Patterns of species and community distributions related to environmental gradient in an arid tropical ecosystem. Vegetatio 117: 69-79.

Peakall, R., Smouse, P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6: 288-295.

Pimentel, D. et al. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture Ecosystems & Environment 84: 1-20.

Pisani, J.M., Distel, R.A., Didone, N.G. 2001. Goat preference for Prosopis caldenia and Prosopis flexuosa. Journal of Arid Environments 47: 173-179.

Pizzonia, J. 2001. Electrophoresis gel image processing and analysis using the KODAK 1D software. Biotechniques 30: 1316-+.

Puri, S., Singh, S., Bhushan, B. 1994. Evaluation of fuelwood quality of indigenous and exotic Tree Species of India Semiarid Region. Agroforestry Systems 26:123-130.

Rasanen, L.A., Sprent, J.I., Lindstrom, K. 2001. Symbiotic properties of sinorhizobia isolated from Acacia and Prosopis nodules in Sudan and Senegal. Plant and Soil 235: 193-210.

Reid, R.S., Ellis, J.E. 1995. Impacts of pastoralists on woodlands in Southern Turkana, Kenya – Livestock mediated tree recruitment. Ecological Applications 5: 978-992.

Richardson, D.M. et al. 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Diversity and Distributions 13: 126-139.

Richardson, D.M., Rejmanek, M. 2011. Trees and shrubs as invasive alien species - a global review. Diversity and Distributions 17: 788-809.

Rieseberg, L.H. et al. 2007. Hybridization and the colonization of novel habitats by annual sunflowers. Genetica 129: 149-165.

Robinson, T.P., van Klinken, R.D., Metternicht, G. 2008. Spatial and temporal rates and patterns of mesquite (Prosopis species) invasion in Western Australia. Journal of Arid Environments 72: 175-188.

Rosenschein, A., Tietema, T., Hall, D.O. 1999. Biomass measurement and monitoring of trees and shrubs in a semi-arid region of central Kenya. Journal of Arid Environments 42: 97-116.

Ross, C.A., Auge, H. 2008. Invasive Mahonia plants outgrow their native relatives. Plant Ecology 199: 21-31.

Ruprecht, E., Jozsa, J., Olvedi, T.B., Simon, J. 2010. Differential effects of several “litter” types on the germination of dry grassland species. Journal of Vegetation Science 21: 1069-1081.

Saidman, B.O., Vilardi, J.C., Pocovi, M.I., Acreche, N. 1996. Genetic divergence among species of the section Strombocarpa, genus Prosopis (Leguminosae). Journal of Genetics 75: 139-149.

Sakai, T. et al. 1999. Riparian disturbance and community structure of a Quercus-Ulmus forest in central Japan. Plant Ecology 140: 99-109.

Sayed, W.F., El-Sharouny, H.M., Zahran, H.H., Ali, W.M. 2002. Composition of Casuarina leaf litter and its influence on Frankia-Casuarina symbiosis in soil. Folia Microbiologica 47: 429-434.

Schade, J.D., Sponseller, R., Collins, S.L., Stiles, A. 2003. The influence of Prosopis canopies on understorey vegetation: Effects of landscape position. Journal of Vegetation Science 14: 743-750.

Scherr, S.J. 2000. A downward spiral? Research evidence on the relationship between poverty and natural resource degradation. Food Policy 25: 479-498.

Schierenbeck, K.A., Ellstrand, N.C. 2009. Hybridization and the evolution of invasiveness in plants and other organisms. Biological Invasions 11: 1093-1105.

Sharifi, M.R., Nilsen, E.T., Rundel, P.W. 1982. Biomass and net primary production of Prosopis galndulosa (Fabaceae) in the Sonoran Desert of California. American Journal of Botany 69: 760-767.

Sherry, M. et al. 2011. RAPD and microsatellite transferability studies in selected species of Prosopis (section Algarobia) with emphasis on Prosopis juliflora and P. pallida. Journal of Genetics 90: 251-264.

Shiferaw, H., Teketay, D., Nemomissa, S., Assefa, F. 2004. Some biological characteristics that foster the invasion of Prosopis juliflora (Sw.) DC. at Middle Awash Rift Valley Area, north-eastern Ethiopia. Journal of Arid Environments 58: 135-154.

Sietz, D., Ludeke, M.K.B., Walther, C. 2011. Categorisation of typical vulnerability patterns in global drylands. Global Environmental Change-Human and Policy Dimensions 21: 431-440.

Sitters, J., Heitkonig, I.M.A., Holmgren, M., Ojwang, G.S.O. 2009. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. Biological Conservation 142: 738-750.

Smith, T.M., Shackleton, S.E 1988. The effect of shading on establishment and growth of Acacia tortilis seedlings . South African Journal of Botany 54: 375-379.

Sneath, P.H.A., Sokal, R.R. 1973. Numerical taxonomy. Freeman San Fransisco, USA.

Sokal, R. R., F. J. Rohlf, F.J. 1981. Biometry (2nd Ed.). W. H. Freeman and Co., New York.

Solbrig, O.T., Bawa, K.S. 1975. Isoenzyme variation in species of Prosopis (Leguminosae). Journal of the Arnold Arboretum 56: 398-412.

Sombroek, W. G., Braun, H.M.H. Van Der Pouw 1980. Exploratory soil map and agro-climatic map of Kenya. Scale 1:1,000,000. Kenya Soil Survey Nairobi.

Speranza, C.I., Kiteme, B., Wiesmann, U. 2008. Droughts and famines: The underlying factors and the causal links among agro-pastoral households in semi-arid Makueni district, Kenya. Global Environmental Change-Human and Policy Dimensions 18: 220-233.

Stave, J. et al. 2003. Spatial and temporal woodland patterns along the lower Turkwel River, Kenya. African Journal of Ecology 41: 224-236.

Stave, J., Oba, G., Stenseth, N.C., Nordal, I. 2005. Environmental gradients in the Turkwel riverine forest, Kenya: Hypotheses on dam-induced vegetation change. Forest Ecology and Management 212: 184-198.

Stave, J., Oba, G., Nordal, I., Stenseth, N.C. 2006. Seedling establishment of Acacia tortilis and Hyphaene compressa in the Turkwel riverine forest, Kenya. African Journal of Ecology 44: 178-185.

Stave, J., Oba, G., Nordal, I., Stenseth, N.C. 2007. Traditional ecological knowledge of a riverine forest in Turkana, Kenya: implications for research and management. Biodiversity and Conservation 16: 1471-1489.

Teague, W.R. et al. 2010. Soil and herbaceous plant responses to summer patch burns under continuous and rotational grazing. Agriculture Ecosystems & Environment 137: 113-123.

te Beest, M. Le Roux, J.J., Richardson, D.M., Brysting, A.K., Suda, J., Kubesova, M., Pysek, P, 2012. The more the better? The role of polyploidy in facilitating plant invasions. Annals of Botany 109:19-45

Ter Braak, C.J.F. 1997. CANOCO – a FORTRAN for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (Version 4.15). Institute of applied computer science, 95, Wageningen, the Netherlands.

Timberlake, J., 1994. Venacular names and uses of plants in northern Kenya. Journal of East African Natural History 83, 31-69.

Thomas, R.B., Bashkin, M.A., Richter, D.D. 2000. Nitrogen inhibition of nodulation and N-2 fixation of a tropical N-2-fixing tree (Gliricidia sepium) grown in elevated atmospheric CO2. New Phytologist 145: 233-243.

Thoyabet, S.A., Ray, R.H., Sven, V., George, S.E., 2009. Effects of leaf extract of *Zizyphus spina-christi* and *Prosopis juliflora* on each others seedlings roots. Allelopathy Journal 23**,** (abstract).

Tiegs, S.D., O'Leary, J.F., Pohl, M.M., Munill, C.L. 2005. Flood disturbance and riparian species diversity on the Colorado River Delta. Biodiversity and Conservation 14: 1175-1194.

Trenchard, L.J., Harris, P.J.C., Smith, S.J., Pasiecznik, N.M. 2008. A review of ploidy in the genus Prosopis (Leguminosae). Botanical Journal of the Linnean Society 156: 425-438.

UNEP 2000. Devastating droughts in Kenya: Environmental impacts and responses, Nairobi, Kenya.

van Bremen, H., Kinyanjui, H.C.K., 1992. Soils of Lodwar area: an inventory, an evaluation of present land use and recommendations for future land use. Reconnaissance Soil Survey Report No. R17. Soil Survey Nairobi, Kenya.

van Kleunen M., Dawson, W., Schlaepfer, D., Jeschke, J.M., Fischer, M. 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecology Letters 13:947-958.

van Klinken, R.D. 1999. Developmental host-specificity of Mozena obtusa (Heteroptera : Coreidae), a potential biocontrol agent for Prosopis species (Mesquite) in Australia. Biological Control 16: 283-290.

van Klinken, R.D., Graham, J., Flack, L.K. 2006. Population ecology of hybrid mesquite (Prosopis species) in Western Australia: how does it differ from native range invasions and what are the implications for impacts and management? Biological Invasions 8: 727-741.

Vega, M.V., Hernandez, P. 2005. Molecular evidence for natural interspecific hybridization in Prosopis. Agroforestry Systems 64: 197-202.

Verstraete, M.M., Scholes, R.J., Smith, M.S. 2009. Climate and desertification: looking at an old problem through new lenses. Frontiers in Ecology and the Environment 7: 421-428.

Vila, M., Maron, J.L., Marco, L. 2005. Evidence for the enemy release hypothesis in Hypericum perforatum. Oecologia 142: 474-479.

Vilela, A.E., Ravetta, D.A. 2000. The effect of radiation on seedling growth and physiology in four species of Prosopis L. (Mimosaceae). Journal of Arid Environments 44: 415-423.

Walter, K. 2011. Prosopis, an Alien among the Sacred Trees of South India. Ph.D. thesis published in the Tropical Forestry Reports 38 of the University of Helsinki.

Warrag, M.O.A. 1995. Autotoxic potential of foliage on seed germination and early growth of mesquite (Prosopis juliflora). Journal of Arid Environments 31: 415-421.

Warren, J., Topping, C.J., James, P. 2011. An evolutionary modelling approach to understanding the factors behind plant invasiveness and community susceptibility to invasion. Journal of Evolutionary Biology 24: 2099-2109.

Waterman, P. G., Mole, S. 1994. Analysis of polyphenolic plant metabolites. Methods in Ecology. Blackwell Scientific Publications, London, UK.

White, P. R., Nackoney, J., 2003. Drylands, people and ecosystem goods and services: a web-based geospatial analysis. Technical report, Wild Resources Institute, Washington D.C. USA.

Wilson, T.B., Witkowski, E.T.F. 1998. Water requirements for germination and early seedling establishment in four African savanna woody plant species. Journal of Arid Environments 38: 541-550.

Wyant, J.G., Ellis, J.E., 1990. Compositional Patterns of Riparian Woodlands in the Rift-Valley of Northern Kenya. Vegetatio 89:23-37.

Yeh, F.C., Yang, R., Boyle, T. 1987. Popgene Version 1.32. Ag/For Molecular biology and biotechnology centre, University of Alberta and Center for International Forestry Research.

Zeng, H.Q., Liu, Q.J., Feng, Z.W., Ma, Z.Q. 2010. Biomass equations for four shrub species in subtropical China. Journal of Forest Research 15: 83-90.

Zimmermann, H.G. 1991. Biological control of mesquite, Prosopis Spp (Fabaceae) in South Africa. Agriculture Ecosystems & Environment 37: 175-186.

Zou, J.W., Rogers, W.E., Siemann, E. 2008. Increased competitive ability and herbivory tolerance in the invasive plant Sapium sebiferum. Biological Invasions 10: 291-302.

Summary

Drylands occupy over 41% of the global land surface, with Africa and Asia accounting for 32% of the global total each. Because of poor resource management, resource overexploitation and periodic droughts, drylands have experienced severe land degradation. Land degradation is manifested in vegetation loss or deterioration, soil erosion and salinization of soil and water. In Kenya, drylands occupy over 87% of the land surface, and support about 30% of the national population, over 70% of national livestock and the bulk of wildlife that support the tourist sector. Following the prolonged sahelian droughts of the 1970's Kenya's drylands were seriously degraded through extensive loss of ground vegetation cover; thus threatening the survival of local populations, livestock production and sustenance of tourism sector. Subsequently, exotic trees and shrubs were introduced for land rehabilitation and fodder supply. Trees from from *Prosopis* genus emerged as the most adapted and were widely planted.

Since introduction, *Prosopis* species have spread from target rehabilitation sites and invaded riverine and wetlands ecosystems but invasion mechanisms and impacts are not yet well understood. In this study we combined geographical information systems techniques; field, greenhouse and laboratory studies, to evaluate riverine habitat invasibility, invasion impacts, invasiveness of *Prosopis* species and the composition of invasive *Prosopis* species in Kenya. The following questions were addressed: 1) What abiotic factors make riverine forests vulnerable to Prosopis invasion?, 2) What are the ecological implications of *Prosopis* invasion in riverine forests?, 3) What mechanisms underlie inhibition of *A. tortilis* regeneration by *Prosopis* species invasion?, 4) What are the species composition in *Prosopis* invaded areas of Kenya, and 5) What are the implications of our results?

The present study revealed indiscriminate *Prosopis* invasion in all land cover and land use types identified through satellite image analysis, field surveys and historical site information provided by local informants. As a result of this trend, we found a contrasting occurrence increase of *Prosopis* species and decrease of *Acacia tortilis* between 1998 and 2007. Accordingly, the study has demonstrated that *Prosopis* species invasion in the Turkwel Riverine forest is invoked more by species invasiveness rather than habitat susceptibility.

Consequently, we investigated the invasiveness of *Prosopis* species by studying invasion impacts and the underpinning mechanisms.

Our study has shown reduction of herbaceous species ground vegetation cover and herbaceous species diversity, and termination of *A. tortilis* regeneration by *Prosopis* invasion. The negative regression coefficients found between herbaceous species ground cover or between herbaceous species diversity and *Prosopis* canopy dummy, clarifies the partial direct negative effect of *Prosopis* on herbaceous species. We corroborate this finding by greenhouse studies that show stronger inhibition *A. tortilis* and *Prosopis* seed germination by increasing the concentration of fresh *Prosopis* litter than by increasing the concentration *A. tortilis* litter in the soil. Indeed, our study demonstrates potential of seed germination termination at 50% fresh *Prosopis* litter concentration in the soil. After one month of watering of soil-litter mixture, we found no litter effect on seed germination. Since water leaching decreased the concentration of soluble phenols and leached litter had no effect on seed germination, our study has clarified that the inhibition of *A. tortilis* regeneration by *Prosopis* canopy was partially the result of allelopathic effect of *Prosopis* litter on *A. tortilis* seed germination.

There has been great confusion on *Prosopis* species identity in *Prosopis* invaded areas of Kenya, because of similar morphology and introduction of several species within sites. Species misidentification may hamper invasion management. In this study we used Random Amplified DNA markers to differentiate species according to sites. Our study shows that only one species or a hybrid is adapted to any one site, despite the number of species that were introduced to any site. We have further clarified that *P. juliflora* and its hybrid are the most invasive germplasm in Kenya. However, *P. juliflora* and the hybrid trees tended to have similar tree characteristics in riverine forests and wetlands as we could predict tree volumes in wetlands from equations developed from a distant riverine site.

Our study demonstrates potential for perpetual replacement of *A. tortilis* by *Prosopis* species in riverine ecosystems. A notable consequence is reduction of both herbaceous species productivity and diversity. Since both *A. tortilis* and herbaceous species are used for fodder; invasion may have severe consequences on the pastoral economy but this can be reversed by intensified utilization of *Prosopis* biomass for fuelwood and pods for fodder.

Samenvatting

Droge gebieden beslaan 41% van het globale landoppervlak en van dit totaal bevindt zich 32% in Afrika en 32% in Azië. Door slecht beheer, overexploitatie en perioden van droogte is een groot deel van deze droge gebieden gedegradeerd. Deze degradatie manifesteert zich in het verlies of verschraling van de vegetatie, erosie en verzilting van de bodem en het grondwater. Droge gebieden beslaan 87% van het landoppervlak in Kenia. In deze gebieden leeft dertig procent van de bevolking, meer dan 70% van het vee en het gros van de wildpopulaties die belangrijk zijn voor toerisme. Als gevolg van de langdurige droogte in de zeventiger jaren zijn deze gebieden zwaar gedegradeerd, en het verlies van vegetatiebedekking vormt een bedreiging voor de lokale bevolking, de veehouderij en het toerisme. Uitheemse bomen en struiken zijn in het verleden geïntroduceerd voor bodemherstel en de productie van veevoer. Boomsoorten van het geslacht *Prosopis* bleken het best aangepast aan de droge omstandigheden in Kenia, en zijn daarom in het verleden op grote schaal aangeplant.

Sinds hun introductie hebben deze *Prosopis* soorten zich verspreid vanuit de beoogde herstelgebieden naar riviergebieden en wetlands. De onderliggende mechanismen en de gevolgen hiervan zijn echter nog grotendeels onbekend. Het huidige onderzoek gebruikt een combinatie van geografische informatie systemen, veldstudies, kas- en laboratoriumexperimenten om te evalueren hoe kwetsbaar de riviergebieden zijn voor voor *Prosopis* invasie, de gevolgen *Prosopis* invasie, wat het invasieve karakter van *Prosopis* bepaald, en waar verschillende *Prosopis* soorten voorkomen in Kenia. De volgende vragen staan in dit onderzoek centraal: 1) Welke abiotische factoren maken rivierbossen kwetsbaar voor invasie door *Prosopis*? 2) Wat zijn de ecologische gevolgen van *Prosopis* invasie in rivierbossen? 3) Welke mechanismen liggen ten grondslag aan de verminderde regeneratie van *Acacia tortilis* na invasie door *Prosopis*? 4) Wat is de soortsamenstelling van gebieden in Kenia die door *Prosopis* zijn gekoloniseerd? 5) Wat zijn de implicaties van de onderzoeksresultaten voor het beheer van *Prosopis* in Kenia?

Satellietfoto's, veldstudies, en informatie over de historie van het gebied laten zien dat invasie door *Prosopis* soorten plaats vindt in alle typen van landbedekking en landgebruik. Tussen 1998 en 2007 is er sprake van een duidelijke toename van de aanwezigheid van *Prosopis* en een afname van *Acacia*

tortilis. De invasie door *Prosopis* in het Turkwell rivierbos wordt met name veroorzaakt door het invasieve karakter van *Prosopis* soorten, en in mindere mate door van de kwetsbaarheid van het rivierbos voor invasie. In deze studie is daarom het invasieve karakter van *Prosopis* soorten onderzocht, door de gevolgen van invasie en de onderliggende mechanismen te bestuderen.

Deze studie laat zien dat de invasie door *Prosopis* soorten leidt tot een verminderde bodembedekking van kruidachtige planten, verminderde diversiteit in de kruidlaag en tot het uitblijven van verjonging van *Acacia tortilis*. Een multipele regressie analyse geeft aan dat het voorkomen van *Prosopis* soorten een direct negatief effect heeft op de bedekking- en diversiteit van de kruidlaag. Kasexperimenten laten zien dat een toename in de concentratie van vers *Prosopis* strooisel in de bodem het ontkiemen van *A. tortilis* en *Prosopis* soorten belemmert, en dat dit inhiberende effect sterker is dan dat van *A. tortilis* strooisel. Deze resultaten suggereren dat 50% vers *Prosopis* strooisel in de bodem leidt tot volledige remming van de zaadkieming. Dit kiemingsinhiberende effect verdwijnt na een maand bewateren van het grond-strooisel mengsel. Omdat er na uitspoeling een verminderde concentratie aan oplosbare fenolen is, en omdat uitgeloogd strooisel de zaadkieming niet inhibeert, laat deze studie zien dat afwezigheid van *A. tortilis* verjonging onder *Prosopis* bomen deels verklaard kan worden door de allelopatische effecten van *Prosopis* strooisel op de kieming van *A. tortilis*.

Er is onduidelijkheid in Kenia over de identiteit van *Prosopis* soorten in de door *Prosopis* gekoloniseerde gebieden omdat verschillende soorten in hetzelfde gebied geïntroduceerd zijn, en omdat zij een vergelijkbare morfologie hebben. Het verkeerd determineren van soorten kan het beheer van invasieve soorten belemmeren. In deze studie gebruiken we Random Amplified DNA markers om soorten te onderscheiden naar gelang hun voorkomen. De studie wijst uit dat er plaatselijk slechts één enkele soort of hybride voorkom, ondanks het feit dat plaatselijk verschillende soorten zijn geïntroduceerd. Dit suggereert dat er een sterke selectie is voor die soort die het beste is aangepast. Verder bleek dat *P. juliflora* en diens hybride in Kenia de meest invasieve variëteiten zijn. *P. juliflora* en diens hybride hebben een vergelijkbare morfologie in rivierbossen en wetlands, en het was daarom mogelijk om biomassa en stamvolume van bomen in wetlands te schatten op basis van vergelijkingen ontwikkeld in een verder gelegen rivierbos.

De resultaten laten zien dat in de rivierbossen in Kenia *A. tortilis* geleidelijk wordt vervangen door *Prosopis* soorten, met als belangrijke consequentie een vermindering van de productiviteit en diversiteit van de kruidlaag. Omdat zowel *A. tortilis* als kruidachtige planten worden gebruikt als veevoer, kan kolonisatie door *Prosopis* ernstige gevolgen hebben voor de rurale economie. Dit kan mogelijk worden tegengegaan door een intensiever gebruik van *Prosopis* biomassa voor brandstof, en een intensiever gebruik van *Prosopis* peulen voor veevoer.

Acknowledgements

This study came to be as a result of the financial support that I got from NUFFIC and KEFRI. I'm grateful to NUFFIC and KEFRI managements for their financial support.

In the course of the study, I received support from many people to whom I'm very grateful. My first acknowledgment goes to my promoter Prof. Dr. Ir., Godefridus M.J. Mohren (Frits), co-promoter, Dr. Ir. Lourens Poorter and local supervisor Dr. Bernard N. Kigomo. Frits supported my NUFFIC fellowship application and provided the necessary academic guidance required of this study thereafter. Lourens provided personalized attention to ensure that I acquired the right skills for writing journal manuscripts that is evident from the way the thesis is structured. I have no words for expressing my appreciation on this support. Bernard understood the study environment and gave valuable inputs at various stages of study development and implementation. Besides academics, Frits, Lourens and Bernard provided other timely support, advice and encouragement that enabled me to cope with periodic challenges. I'm grateful for your support and advice.

I wish to acknowledge the assistance of Nick Pasiecznik for introducing me to Lars Schmidt of Danish Centre for Forest, Landscape and Planning who supplied the *Prosopis chilensis* and *Prosopis pallida* reference seeds. Additional reference seed for *Prosopis juliflora* were obtained from Royal Botanical Gardens, of UK, courtesy of Timothy Pearce and Janet Terry to whom I'm very grateful.

During proposal development and study implementation, I received support and advice from staffs, friends and colleagues at the Forest Ecology and Forest Management group. I'm indebted to all the staffs: Frits Mohren, Lourens Poorter, Jan den Ouden, Frans Bongers, Frank Sterck, Marielos Pena Claros, Ute Sass-Klaassen, Ellen Wilderink, Neeltje van Hulten, Hans Jansen, Joke Jansen, Patrick Jansen, Leo Goudzwaard, Pieter Zuidema and Hans Polman and colleague students: Abeje Eshete, Ana Jakovac, Arnold van Gelder, Cesar Perez-Cruzado, Canisius Mugunga, Corneille Ewango, Esron Munyanziza, Edward Mufandaedza, Edwin Lebrija, Estela Vallejo, Geovana Carreno, Gijn Ceca, Gustavo Schwartz, Honore Biaou, loan Stetca, Jean Ndyambaje, Tefera Mengistu, Kwame Oduro, Lars Markesteijn, Lennart Suselbeek, Lucy Amissah, Madelon Lohbeck, Marisol Toledo, Mart Vlam, Meenakshi Kaul, Michiel van Breugel, Motuma Tolera,

Noelia Gonzalez-Munoz, Paul Copini, Peter Groenendijk, Peter van der Sleen, Pilar Castro, Robbert Blanken, Walter Loesberg, Yanda Acacio and Yosias Gandhi Zhiquan Cai for their technical inputs. Joke Jansen, the administrator at the Forest Ecology and Forest Management was very effective in logistic supports, which I highly acknowledge.

Kenyan student fraternity at Wageningen provided a replica of a Kenya society away from home. The Kenyan social gatherings provided excellent breaks from the academic routines and a re-energizing homely environment. I appreciate all the Kenyan students that I interacted with while at Wagenigen for their support and encouragements. Specifically, I would like to recognize the assistance of Alice Waringo, Evelyn Kiptot and Stephen Ongaro for facilitating my quick settling upon my first arrival to Wageningen. The effective leadership of Moses Sila, Winnie Wairimu, Fred Onyango, Leah Slones, Jamlick Mwangi and Lina Muhonja facilitated the Kenya gatherings effectively, from where I made more friends.

I would like to appreciate the hospitality accorded by community members in Baringo, Isiolo, Tana River, Taita Taveta and Turkana dsitricts where field research was conducted. In Turkana District, I particularly recognize the contribution of Daniel Ngasike, David Lorot, Eipa Epero, Ekeno Lodelio, Ekaali, John Namojong, Joseph Lokemer, Joseph Tati, Lotiraman Tioko and Wilbert Ekai in fieldwork assistance. At Katilu, the catholic priests (Fathers: Samuel Ndung'u, Crispine Onudu, Dismas Masinde and Peter Kariuki) opened their residence to my field team and I unreservedly. This provided an enabling research environment in an area where accommodation is a real challenge. We are grateful for your assistance.

This study received overwhelming support from my KEFRI colleagues. My first appreciation goes former KEFRI Director, Dr. Paul Konuche and the current Director Dr. Ben Chikamai for extending financial and logistical support to this study. My colleagues: Bernard Kamondo, Jason Kariuki, Joseph Machua, James Kimondo, Mbae Muchiri, John Ngugi, Stephen Ndung'u, Eliud Waweru, Simon Waweru, Cheptumo Relimoi, Kimondo Migunda, Margaret Kuria, Mary Gathara, Lorna Maina, John Gicheru, John Ochieng, George Omollo, Lawrence Kamiri, Peter Mwai, Stephen Kariuki, Zablon Musumba, Michael Obongo, Joyce Muthoni, Hanah Wanjiru, Pauline Bala, Bernard Kigwa, Frouza Maingi, George Orwa and Vincent Maingi were very supportive at the various stages when their

contributions were required. At the Kenya Agricultural Research Institute, I would like to recognize the assistance of Nicholas Kungu and Peter Wakaba in plant and soil analysis. All the technical and logistic support provided by this team is highly appreciated.

Preparation of manuscripts included in this thesis were reviewed by many reviewers most of whom opted to remain anonymous. I'm very grateful for all their contributions. Sadie Ryan and Patrick Kariuki made significant contributions to chapter 3 and wish to acknowledge their inputs in shaping it to published material.

My family members deserve mention for their understanding and encouragements during this study. My wife's ability to cope with all family responsibilities in my absence and my children's understanding during my absence is highly appreciated. My Parents, brothers and sisters were very understanding and encouraging throughout the study and they are highly appreciated.

Lastly but not the least, I'm indebted to individuals and institutions that may have escaped mentioning, but had an input to this study.

Short biography

Gabriel Muturi was born on 31st December 1961 in Murang'a District Kenya. He attended Nguthuru Primary School, Nyeri High School and Njiri's High School between 1969 and 1981 for his pre-university education. He taught in secondary schools from January 1982 to September 1983 before joining University of Nairobi for BSc. Forestry course. In September 1984, the forestry course was transferred to Moi University in Eldoret, Kenya from where he graduated with BSc. Forestry Second Class honors in June 1986. In July 1986, he was employed as an Assistant Research Officer at Kenya Forestry Research Institute (KEFRI). In 1988, he attended a six months training on fodder production with saline water at Institutes of Applied Research of Ben Gurion University of Negev, Israel. In September 1990, he was awarded CIDA Scholarship to study MSc. Forest at the University of Toronto, Canada. He graduated in 1994, specializing in plant physiology. Between 1986 and 2004, Gabriel worked in several capacities in KEFRI and rose from an Assistant Research Officer to Principal Research Officer. During the period he implemented bilateral projects between the Governments of Kenya and Norway, Governments of Kenya and Japan, Government of Kenya projects and collaborative projects between KEFRI and other local and international institutions. He is the founding scientist of Turkana Forestry Research Centre and has contributed enormously to development of drylands forestry technologies development in Kenya. He also worked as a Forestry Restoration Research Officer with Kenya Wildlife Service while implementing a GEF/World Bank Project for Conservation of the Tana River National Primate Reserve in 2001 and 2002. From 2003 to 2007, he was the Assistant National Coordinator for GEF/UNEP funded Desert Margins Program (DMP) in Kenya and was instrumental to upscaling of proven forestry technologies in the drylands. *Melia volkensii* and mango plantations in Eastern Kenya are specifically the results of his contribution. In January 2007, he was awarded NUFFIC fellowship to study PhD at Wageningen University, the Netherlands. In August 2007, he was appointed as Assistant Director and National Program Coordinator for Drylands Forestry Research at KEFRI. His research interests include ecophysiology, invasion ecology, drylands afforestation and rehabilitation. He is a registered lead consultant in Environmental Impact Assessment and Audit; and a life member of Forest Society of Kenya. Gabriel has served the public in several capacities,

including as a board member and Chairman of School Boards of Management, Chairman of KEFRI Scientists Welfare Association and both as a trustee and a Chairman of KEFRI Staff Retirement Benefits Scheme Board of Trustees. Gabriel Muturi is married to Beatrice Waithira and has five children Winfred, Yvonne, John, Leah and Abigail. Gabriel's research and development vision is to develop technologies for the management of invasive species, plantations establishment in Kenya's semi-arid areas, conservation and restoration of degraded arid lands.

(1) **Muturi, G.M.,** Kariuki J.G., Poorter, L. and Mohren G.M.J. (2012). Allometric equations for estimating biomass in naturally established Prosopis stands in Kenya. Journal of Horticulture and Forestry Vol 4(2): 69-77.

(2) Esilaba A.O., M. Okoti, G.A. Keya, J.M. Miriti, J.N. Kigomo, D. Nyariki, G. Olukoye, L. Wekesa, E.W. Ego, **G.M. Muturi** and Cheruiyot H.K. 2011. The Desert Margins Programme approaches in upscaling best-bet technologies in arid and semi-arid lands in Kenya. In: Bationo, A., Waswa, B., Okeyo, J.M., Maina, F. and Kihara, J. (Eds.) Innovations as Key to the Green Revolution in Africa: Exploring scientific facts. Springer, pp. 1177-1191.

(3) Hanaoka, S. **Muturi, G.M.** and Watanabe, A. (2011). Isolation and characterization of microsatellite markers in Melia volkensii Gurke. Conservation Genetic Resources. DOI 10.1007/s12686-011-9558-5.

(4) **Muturi G.,** Kariuki, J., Ndung'u, S.M., Waweru, S.G. and Changkwony M. 2011. Guidellines for the conservation and rehabilitation of degraded woodlands surrounding refugee camps. KEFRI/JOFCA publication.

(5) Machua J., **Muturi G**., Omondi S.F. and Gicheru J (2011). Genetic diversity of Jatropha curcas L. populations in Kenya using RAPD molecular markers: Implication to plantation establishment. African Journal of Biotechnology Vol. 10(16), pp. 3062-3069.

(6) Wekesa, L., Ng'ethe R., Wamahiu, P., Esilaba, A**.,** and **Muturi, G**. (2010). Analysis of the economic potential of *Jatropha* in Kenya. E. Afr. Agric. For. J. 76 (1):43-52.

(7) **Muturi, G.M.**, Mohren, G.M.J. and Kimani, J.N. (2010). Prediction of Prosopis species invasion in Kenya using geographical information system techniques. Afri. J. Ecol. 48, 628–636.

(8) Machua J., **Muturi G.,** and Gicheru J. (2007). Genetic diversity within *Brachylaena huillensis* (O. Hoffin.) populations in Kenya. Implications for conservation for a wood carving tree. Discovery and Innovations. 19:32-36.

(9) Kamondo, B. M., Kimondo, J. M., Mulatya, J.M. and **Muturi G.M**. (eds) (2006) Recent Mukau (*Melia volkensii* Gürke) Research and Development. Proceedings of first National Workshop held at KEFRI Kitui Regional Research center 16th-19th November 2004 51pp.

(10) **Muturi, G.M**., Mulatya, J., Ego, W., Maina, I., Nyariki, D., Muthoka, P., Kariuki, J., Esilaba, A. O. and Cheruiyot, H. K. (2004). Benchmark characterization. Kenya Country Report. Desert Margins Programme, Kenya Agricultural Research Institute, Nairobi, Kenya.

(11) Kariuki, A., Otunga, B., **Muturi, G.**, Perrio, J., Njuguna, P. and Omullo, L. 2001: Tana River National Primate Reserve Management Plan 2001-2006. KWS.

(12) **Muturi, G.M**., Lugadiru, J. K. and Muchoki, C.M. 2000. Performance of Australian, Central American and Kenya tree species in Arid sites of Embu, Meru and Isiolo Districts KEFRI's Technical Note No 20 (Belgian Administration for Development Cooperation Consultancy Report).

(13) Nguvulu, C.Z., Harkonen, S., Chendauka, B., Kigomo, B., Musokonyi, C., **Muturi, G**., Phiri, M., and Pukkala, T. 2000. An expert system for tree species selection for Eastern and southern African Region In Pukkala, T. (Ed.) Selection of tree species for plantations in Eastern and Southern Africa University of Joesuu Research Note No 113. Pp63-80 ISBN 951-708-935-X.

(14) **Muturi G. M. 2000**. The current state of nurseries in Kenya. In Pukkala, T. and Eerikainen, K. (Eds) Establishment and management of tree plantations in Southern and Eastern Africa Region. University of Joensuu Research Note No 120.Pp 9-16 ISBN 951-708-967-8.

Education Certificate

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Riverine forest degradation and degradation assessment methods, plant invasions, ecophysiology of invasive species and ecophysiological research methods

Writing of project proposal (4.5 ECTS)

- Ecophysiological basis for *Prosopis juliflora* invasion in the *Acacia tortilis* dominated Turkwel Riverine Forest, Kenya

Post-graduate courses (7.5 ECTS)

- Multivariate analysis; PE&RC (2007)
- Analysing farming systems and rural livelihoods in changing world: vulnerability and adaption; PE&RC

Laboratory training and working visits (4 ECTS)

- Molecular analysis techniques: KEFRI (2008)
- GIS Techniques; DRSRS, Kenya (2007/08)

Invited review of (unpublished) journal manuscript (1ECTS)

- Land degradation and development: use of landsat ETM +data for detection *Prosopis juliflora* in irrigated zones

Deficiency, refresh, brush-up courses (6 ECTS)

- Ecological methods I (2007)
- Agroforestry; attendance of lectures on selected topics (2007)

Competence strengthening / skills courses (9.6 ECTS)

- PhD Competence assessment; PE&RC (2007)
- Information literacy, including introduction to Endnote; WUR-Library (2007)
- Environmental impact assessment and audit; KIA/Kenyatta University (2007)
- Performance management; Public Sector Reforms Secretariat in the Office of the Prime Minister, Kenya (2009)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.8 ECTS)

- PE&RC Weekend (2007)
- PE&RC Day (2007)
- PE&RC Day: innovation and sustainability: what are neighbours doing? (2011)

Discussion groups / local seminars / other scientific meetings (15 ECTS)

- Forest ecology and forest management chair group scientific presentations (2007/11)
- Forest and conservation ecology PhD group (2007)
- 4th KEFRI scientific conference; oral presentation; Muguga, Kenya (2007)
- KEFRI's Centre Research Advisory Committees (CRACs), scientific meetings and colloquia attendance and contribution (2007/2012)
- Financial management for non-finance managers (2009)

International symposia, workshops and conferences (8 ECTS)

- Status and future of tropical biodiversity; oral presentation; Frankfurt, Germany (2011)
- First IUFRO – FORNESSA regional congress; oral presentation; Nairobi, Kenya (2012)
- 4th International Ecosummit: Ecological sustainability – Restoring the planet's ecosystem services; oral presentation; Columbus, Ohio, USA (2012)

Lecturing / supervision of practical's / tutorials (1.8 ECTS)

- Introduction to multipurpose trees and shrubs: lecture to MSc students at the National University of Rwanda (2007)
- Trees on cropland: lecture to MSc students at National University of Rwanda (2007)

The research described in this thesis was financially supported by NUFFIC PhD grant No CF3671/2007 and by the Government of Kenya through KEFRI research grant.