Impacts of *Prosopis juliflora* Linnaeus emend. Burkart on aspects of biodiversity and selected habitat conditions in Baringo Kenya

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DECLARATION

This thesis is my original work and has not been presented for the award of a degree in any other University.

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To my wife Caroline Wambura, who offered me unconditional love and support throughout the study period.

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ANOVA	Analysis of Variance
AMOVA	Analysis of Molecular Variance
df	Degrees of freedom
EC	Enzyme Commission number
MWP	Modified Whittaker Plot
TFPGA	Tools for Population Genetic Analyses

ABSTRACT

Invasive alien species are a leading cause of biodiversity loss in the world today. In Kenya, *Prosopis juliflora* Linnaeus emend. Burkart is one of the most problematic invasive plant species. The origins and pattern of introduction of *Prosopis juliflora* into East Africa are not well known but large-scale introductions occurred in the 1980s. Little information is available on how its innate characteristics interact with the local habitat characteristics. Four hypotheses were tested to explain the effects of the invasion of *P. juliflora* on soil nutrient status, diversity of indigenous plant species, diversity of floral insect visitors of native *Acacia* spp., and how the invasive tree's genetic diversity would relate to the rate of invasion. Plant and soil sampling was carried using modified Whittaker plots. *P. juliflora* density had significant influence on total organic carbon, and pH. The invasive species also had a negative effect on overall native plant species richness and density of *Acacia* species. This was a clear indication that *P. juliflora* is having an effect on the species richness of local species and that either *P. juliflora* is slowly replacing the indigenous *Acacia* species, or that the established stands of *Acacia* in non-disturbed conditions are a good deterrent to the encroaching *P. juliflora.* The results showed that *P. juliflora* is a preferred source of floral resources for *A. mellifera* during the dry season. Allozyme analysis revealed minimal genetic distance between populations. This study shows that the invasive species has negative consequences to the local ecosystem at high densities.

Key words: *Prosopis juliflora*, *Acacia* species, species richness, soil properties, pollinators, genetic diversity

CHAPTER ONE

1.0 INTRODUCTION

Invasive species are the second leading cause of biodiversity loss worldwide, mainly due to their ability to outcompete and replace native species (Gaertner *et al.*, 2009; Wilcove *et al.*, 1998). As many as 80% of the endangered species are threatened by the invasion by alien species around the world (Pimentel *et al.*, 2005).

Invasive alien species have the ability to alter ecosystem processes (Ehrenfeld, 2010), decrease native species abundance and richness via competition, predation, hybridization and indirect effects (Blackburn *et al.*, 2004; Gaertner, et al., 2009), change community structure (Hejda *et al.*, 2009) and alter genetic diversity (Ellstrand & Schierenbeck, 2000). The actual numbers of individuals and species being transported across biogeographical barriers every day is presumably enormous but only a small fraction of those transported species become established, and of these generally only about 1% become pests (Mooney & Cleland, 2001). Introduction of invasive species has been facilitated by humans for millennia for agricultural production, erosion control, and ornamental purposes (Reichard, 1997).

Invasion can be divided into four stages: introduction, establishment, lag period, and expansion (Holzmueller & Jose, 2009). The ability of an invasive plant species to become established and develop a self-sustaining population, is dependent on its ability to overcome environmental conditions that may limit reproduction. These include low initial genetic diversity and the time that it takes for the species to evolve with a new set of environmental constraints (Mack *et al.*, 2000; Sakai *et al.*, 2001).

Characteristics of successful invaders often include: broad ecological requirements and tolerances, sometimes reflected in large geographical ranges (Sax & Brown, 2000) and r-selected life histories (Holzmueller & Jose, 2009). Characteristics of invaded environments often include: geographical and historical isolation, low diversity of native species (Levine & D'Antonio, 1999), high levels of natural disturbance or human activities, and absence of co-adapted enemies, including competitors, predators, herbivores, parasites, and diseases (Davis *et al.*, 2000). Invasive species cause serious environmental damage and in some cases, displace or extirpate native organisms (Gurevitch & Padilla, 2004). Preventing the importation of non-indigenous species in the first place is an important tool for invasive species management. However, a strategy for effectively containing harmful non-indigenous species once they have become firmly established is also needed (Schlaepfer *et al.*, 2005). Intensive management aimed at eradicating invaders is likely to fail unless it precludes re-invasions by addressing the ecological conditions or vectors that made the invasion of the non-indigenous species possible in the first place (Byers, 2002).

In any one ecosystem, there is likely to be more than one mechanism to explain invasion success of a species and in fact, a single hypothesis may not explain invasion in totality. Hence any effort to understand the invasive success of a species should consider an integrative approach, which must be combined with rigorous field observations and experiments in order to evaluate these hypotheses (Blumenthal, 2005).

1.1 Background to the problem

The impact of invasive species on indigenous species, communities, and ecosystems has been widely recognized and studied for decades (Elton, 1958; Lodge, 1993; Mack, et al., 2000). Invasive species are viewed as a significant component of global climatic change (Vitousek *et al.*, 1997). The severe economic impact of these species is evident and the costs of eradication of invasive species are estimated to range from millions to billions of dollars (Pimentel, et al., 2005). In addition to economic impacts, invasive species have negative impacts on biodiversity (Cronk & Fuller, 1998; Foxcroft *et al.*, 2010; Wilcove, et al., 1998; Williamson, 1996). The adverse impacts of invasive species are expected to extend to all ecosystems, as increasing numbers of invasive species become established in new locations (Pejchar & Mooney, 2009).

The effects of biotic and abiotic factors have been investigated separately in studies of invasions, but few studies have directly compared their effects or examined their potential interactions (Davis, et al., 2000). Several studies have addressed the relative roles of belowground and aboveground resource enrichment in promoting invasions (Davis & Pelsor, 2001; Gross *et al.*, 2005; Hobbs & Atkins, 1988; Leishman & Thomson, 2005; Lenz & Facelli, 2005; Prober & Lunt, 2009).

The genus *Prosopis* Linnaeus emend. Burkart, belongs to the family Leguminosae (Fabaceae), subfamily Mimosoideae, tribe Mimoseae. The genus is native to the Americas, and comprises 44 species (Burkart, 1976). Prosopis species are adapted to arid and semi-arid zones, display tree or shrub phenotypes, and are predominantly out-crossing (Solbrig & Cantino, 1975), with insect-mediated pollination (Simpson, 1977).

The origins and pattern of introduction of *Prosopis* species into East Africa are not well known as it clearly existed before the large-scale introductions that occurred in the 1980s (Tessema, 2012). The first documented introduction of the tree in Kenya was in 1973, when seeds were imported for the rehabilitation of quarries in the saline soils at Baobab Farm near Mombasa (Jama & Zeila, 2005).

P. juliflora was first planted in Kenya at the beginning of the 1970s (Maghembe *et al.*, 1983). In the early 1980s, *P. juliflora* was introduced in places such as lower Baringo County through the Fuelwood Afforestation Extension Project (FAEP). Initially, *P. juliflora* was seen as a suitable medium to provide shade, prevent soil erosion and sandstorms (Kariuki, 1993). Unfortunately, after about ten years, the spread of *P. juliflora* could no longer be kept under control. However, its role in the alteration of vegetation structure, ecology and specific losses of endemic species of other plant species in Kenya has not been documented (Pasiecznik *et al.*, 2004).

1.2 Statement of the Problem

This investigation considers the role that population biology can play in understanding invasive species through knowledge of the ecology and evolution of both invasive and native species in a community context. Exotic plant invasions displace native species, disrupt ecosystem processes, and consequently inflict substantial environmental costs to ecosystems worldwide (Mack, et al., 2000; Pimentel, et al., 2005; Vitousek, et al., 1997). In light of such consequences, it is important to understand the factors that deter or promote plant invasions. Evaluating the causes of plant invasions can also provide insight into fundamental processes of community assembly and structure (Fargione & Tilman, 2005). Many of the species introduced with agriculture and forestry are beneficial and desirable, and hence identifying beforehand those that should not be introduced or should be controlled is much harder (Williamson, 1999).

In the early 1980s *P. juliflora* was introduced in the Lake Baringo area through the Fuelwood Afforestation Extension Project (Kariuki 1993). Initially *P. juliflora* was seen as a suitable medium to provide shade, prevent soil erosion and sandstorms. Its pods were also used as a source of food for livestock. However after about ten years the spread of *P. juliflora* could no longer be kept under control. ICRAF, (2000), reported that *P. juliflora* has enhanced the loss of biodiversity especially in the areas over which it thrives. It was introduced to rehabilitate and transform degraded landscapes, but it got established began suffocating native species as it spreads into their habitats (Huston, 1993). The extent of this devastation is yet to be well documented in Kenya. Its role in the alteration of vegetation structure the ecology and specific losses of endemic species of other plant species of the dry lands of Kenya has not been documented. Predicting invasions based on studies carried out elsewhere has not been successful and hence there is still a need for better and wider quantification and measurement of how invasive species interact with particular environments (Williamson, 1999) and in this case, Baringo. Furthermore, patterns of invasion observed in the field at one site may be difficult to extrapolate to other sites because those observations are specific to a time, place and spatial scale (Theoharides & Dukes, 2007).

1.3 Justification

In Kenya, there is minimal empirical data available on how this species interacts with the local habitat. The decision on whether *P. juliflora* will continue to be viewed as a noxious plant or managed as a resource will be made on both economic realities and environmental consciousness, which will only be arrived at after a detailed study of its ecology. Management strategies based on sound empirical information are therefore necessary. With such information, some benefit may accrue from the exploitation of this species. Such benefits may probably include enhanced soil fertility, shade for livestock, wildlife habitat, protection for some plant species, modified microclimate for cool-season plant species, and the potential for wood products. However, this observation can specifically be applied to the Kenyan situation only if the specific species-habitat interactions are well understood. Few studies have been done in Kenya on the ecology of *P. juliflora* and they have mainly only attempted to record the rate of spread and the social impacts it has had on the local pastoral communities (Kariuki, 1993; Muturi *et al.*, 2010; Mwangi & Swallow, 2005). Studies designed to evaluate the interactive effects of resource enrichment and resident diversity on community invasibility in Kenya are lacking, and such studies are needed to identify the relative importance of key factors in promoting invasions.

This study is offering a contribution to the sustainability of the environment and to improving the livelihoods by striving to understand and provide solutions to a problem of land degradation that is applicable at the grassroot-level systems used by the pastoralists and farmers. This study has offered empirical insights of the effects of *P. juliflora* and has also offered recommendations on how this invasion may be best addressed by conservation managers and policymakers.

1.4 Main Objective

To determine the impacts of *Prosopis juliflora* on aspects of biodiversity and selected habitat conditions in Baringo, Kenya

1.5 Specific Objectives

1. To investigate the impact of *Prosopis juliflora* on the edaphic properties of the Lake Baringo Ecosystem.
2. To establish the effects of *Prosopis juliflora* on the diversity of indigenous plant species in the study area.
3. To establish the effects of *Prosopis juliflora* on floral visitors diversity of local *Acacia* species
4. To estimate genetic relatedness of different populations of *P. juliflora in* Kenya, and establish the role of multiple introductions

1.6 Hypotheses

1. *P. juriflora* density has no significant influence on soil properties
2. *P. juriflora* density has no significant influence on indigenous plant species richness.
3. *P. juriflora* has no significant influence on diversity of floral visitors of Acacia
4. There is no significant genetic difference among different populations of *P. juriflora*

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Theories of Plant Invasions

Invasive species provide an exceptional opportunity for basic research in the population biology and short-term evolution of species (Allendorf & Lundquist, 2003). Several non-mutually exclusive hypotheses have been proposed to account for the proliferation and habitat expansion of species in invaded environments compared to their native range. These hypotheses include enemy release hypothesis (ERH), (Crawley, 1987), increased competitive ability (Blossey & Notzold, 1995; Keane & Crawley, 2002), increased resource availability (Denslow, 2003), appearance of more vigorous genotypes in the areas of introduction. and novel phytochemistry (Blossey & Kamil, 1996; Blossey & Notzold, 1995) These hypotheses all propose a limitation to abundance or habitat distribution in the area of origin and then a change, shift, or release in the area of introduction (DeWalt, 2003). The three hypotheses suggest that the changes involve a plastic response to differences in environmental conditions, and that genotypes in the native and introduced ranges are different (DeWalt, 2003).

2.1.1 Enemy Release Hypothesis (ERH)

The ERH states that plant species, when introduced to an exotic region, they should experience a decrease in herbivory and other natural enemies, resulting in an increase in distribution and abundance. The hypothesis is based on the observation that natural enemies are important regulators of plant populations, and that plants are able to capitalize on a reduction in enemy regulation, resulting in increased population growth (Keane & Crawley, 2002). This potential for enemy release varies across species. Enemy release may play a role in some exotic invasions, whereas different mechanisms, such as community disturbance, are important in others (Shea & Chesson, 2002).

2.1.1.1 Role of plant defences

Most plant species have evolved defenses to minimize the impact of natural enemies either by producing chemicals or structures to deter enemy attack or by developing ways to tolerate the loss of biomass to enemies. For these species, enemies have little impact on individuals in ecological time, but enemies have obviously been important in evolutionary time, selecting for better-defended genotypes. This leads to a fitness cost to investing in resistance and tolerance, meaning that defended genotypes would be outcompeted by undefended genotypes in an enemy-free environment (Agrawal *et al.*, 1999; Redman *et al.*, 2001). Some species may be well defended against some enemies but poorly defended against others. Enemies can therefore have important impacts at the scale of plant populations. However, enemies might impact individuals with little resultant effect on populations. This is because recruitment by new individuals might be limited by other factors, such as microsite availability (Edwards & Crawley, 1999). Enemies might remove a large proportion of the annual seed production of a population, but owing to the low number of microsites available for seedling establishment, the enemies have no impact on population recruitment (Agrawal *et al.*, 2005). Hence, over evolutionary time, enemies select for better-defended individuals; but in ecological time, the enemies are not regulating the population (Agrawal & Kotanen, 2003).

2.1.1.2 Role of Specialist versus Generalists

The Enemy Release Hypothesis predicts that specialist enemies of an exotic species will be absent in areas where it has been introduced. By definition, specialist enemies that attack a single species (i.e. single-species specialists) do not occur outside the native range of their host (Keane & Crawley, 2002). However, there are two main mechanisms through which specialist enemies can be found in the exotic region: host switching and co-introduction of enemies. If a plant species is introduced to a region that contains closely related native congeners, the specialist enemies of those congeners might switch to attack the exotic species (Maron & Vilà, 2001). Several studies have shown that specialist insect herbivores can switch to exotic congeners (Bowers *et al.*, 1992; Ros *et al.*, 1993; Sheldon & Creed Jr, 1995). Sometimes, plant species will not escape their enemies when introduced to a new region because their enemies might also be introduced to the same area (Orians & Ward, 2010). It is possible for a plant and its enemy to be introduced to the same region, although most cases involve generalist insect herbivores, such as widespread exotic pests and it may be difficult for an exotic plant to escape from enemies that can survive on the propagules of the plant such as seed-borne pathogens (Ros, et al., 1993). Another prediction of Enemy Release Hypothesis is that generalist enemies will have a greater impact on native host competitors than on the invasive exotic host species. This shift in generalist enemy impact towards the natives should result in less interspecific competition for the exotic in its new region, resulting in invasive behaviour (Keane & Crawley, 2002). However, the studies of local adaptation of enemies to their native hosts provide limited evidence that generalist enemies might be better adapted to attacking native species than to attacking exotics (Gandon & Van Zandt, 1998).

Native plants might however have evolved better defenses against the native generalists than have exotic plants. A few studies have shown that generalist enemies (grasshoppers and mammals) might prefer natives as food plants (Joern, 1989; Olckers & Hulley, 1991; Schierenbeck *et al.*, 1994) and some exotic species seem more tolerant to generalist enemy attack than are their native competitors (Schierenbeck, et al., 1994). A common occurrence is the invasion of well-defended exotics into communities that are grazed by domestic livestock, such as sheep and cattle (Caldwell *et al.*, 1981).

If an exotic species is impacted by enemies in its native region and there is a reduction in this impact in its exotic region, the logical conclusion is that the species should be able to capitalize on this with a greater abundance in the exotic region (Orians & Ward, 2010). However, there are several reasons why an exotic might fail to become invasive. A primary reason for failure might be the unsuitability of the climate of the exotic region, such that an introduced plant species cannot establish in sufficient numbers to capitalize on enemy release. An exotic might fail to capitalize on enemy release if it is less competitive than the native species, even when there is a greater enemy impact on the natives (Liu & Stiling, 2006).

2.1.1.3 Role of native species adaptability

Invasive exotics are often hypothesized to have a greater inherent competitive ability compared with the natives. Through evolution, natives should be better adapted to local conditions than are introduced species. Unless the native community has been perturbed by humans, native species should outcompete introduced exotics (Blumenthal, 2006). If the level of enemy release is not enough to compensate for this greater local adaptation by the natives, an exotic species is unlikely to successfully compete and become invasive. Species might also fail to capitalize if the first assumption of the ERH is not fulfilled (i.e. natural enemies are regulating the native population). Poorly defended species presumably persist under high enemy impact through high fecundity, and these species would be expected to capitalize on a reduction in enemy regulation. However, a species might be sufficiently well defended such that removal of enemies in the native region does not allow it to increase in abundance (Hierro *et al.*, 2004). Such a species might fail to become invasive in the exotic region, even with the decreased impact of enemies. However, if generalist enemies are more important than are specialists in structuring the plant community in the exotic region, we would still expect increased abundance of well-defended exotics through competitive release. If specialists are more important, well-defended exotics might not benefit from the relative lack of specialist enemies (Alba *et al.*, 2012).

Various studies have tested the hypothesis on the presence or effects of parasites, pathogens or predators on native and introduced populations. Memmott and Waser, (2002) examined diversity and biomass of enemies without measuring their impact while Wolfe (2002), examined both incidence of enemies and their effects. Each of these studies found support for the enemy release hypothesis. *Prosopis juliflora* is preferred for foliage by several bird species. However, no data for natural enemies is available in its introduced ranges (Beltrán & Wunderle, 2013)

2.1.2 Evolution of Increased Competitive Ability (EICA)

The EICA hypothesis predicts improved competitive ability through a shift in allocation from defence to growth (Blossey & Kamil, 1996). The hypothesis predicts that, under identical growing conditions, individuals of a species growing in an introduced area will produce more biomass than individuals growing in the species native site (Blossey & Notzold, 1995). It predicts that in the absence of herbivores, costly chemical defences should be reduced in invasive plants. In addition, this loss should increase host plant quality to herbivores. Studies comparing herbivores or pathogens on exotic plants in their native and introduced ranges have generally supported this hypothesis (Wolfe, 2002). Higher performance has been observed in several invasive species. For example, in *L. salicaria* biomass of plants in the non-native habitat was greater than biomass in the native habitat(Blossey & Notzold, 1995). However, this prediction should only apply to specialist herbivores, as generalist herbivores are likely to be encountered in the introduced range (Joshi & Vrieling, 2005; Müller-Schärer *et al.*, 2004). It is also possible that introduced plants could retain their ability to induce defences against herbivores, as induced defences should be less costly than constitutive defences. The *Prosopis* canopy may exert a profound influence on neighbouring vegetation, soils and subcanopy microclimate. High densities of *Prosopis* spp (>25% canopy cover) have been observed to suppress grass growth and may reduce understory species diversity (Ansley *et al.*, 1997).

2.1.3 Novel Phytochemistry

Introduced species may sometimes become invasive because they possess novel biochemical weapons that function as unusually powerful allelopathic agents, or as mediators of new plant–soil microbial interactions (Callaway & Ridenour, 2004). The possession of novel weapons by some plant invaders provides them with an advantage that arises from regional differences in coevolutionary trajectories (Thompson, 1999). The reason why there are different regional evolutionary pathways may be the huge number of different biochemicals produced by plants (Callaway & Ridenour, 2004). So far, a diverse array of over 100 000 low-molecular mass natural products have been identified, many of which appear to be species-specific (Bais *et al.*, 2003). If an exotic species possesses novel weapons, it may lead to a greater acquisition of resources and therefore faster growth in the non-indigenous range than in the native range (Orians & Ward, 2010). For example Bais *et al.*,(2003) found evidence that *Centaurea maculosa* (spotted knapweed), an invasive species in the western United States, displaces native plant species by exuding the phytotoxin catechin from its roots. Higher concentrations of allelochemicals has been found in *P. juliflora* compared to other *Prosopis* species (Kaur *et al.*, 2012).

2.1.4 Appearance of More Vigorous Genotypes

There are two primary stages in the process of a species invasion. The first stage is the introduction, colonization, and establishment. The introduced species must arrive, survive, and establish itself (Kolar & Lodge, 2001). The second stage is the spread and replacement of native species by the introduced species. The genetic principles that may help us predict whether or not a nonindigenous species will pass through these two stages to become invasive are the same principles that apply to the conservation of species threatened with extinction: (1) genetic drift and the effects of small populations, (2) gene flow and hybridization, and (3) natural selection and adaptation (Kolar & Lodge, 2001). Propagule pressure has emerged as the most important factor for predicting whether or not a nonindigenous species will become established. Propagule pressure includes both the number of individuals introduced and the number of release events (Drake & Lodge, 2006). Increasing propagule size enhances establishment probability primarily by lessening effects of demographic stochasticity, whereas propagule number acts primarily by diminishing impacts of environmental stochasticity. Hence, a continuing rain of propagules, particularly from a variety of sources, may erase or vitiate the expected genetic bottleneck for invasions initiated by few individuals, thereby enhancing likelihood of survival. Indeed, recent molecular evidence suggests ongoing propagule pressure aids an invasion to spread by introducing genetic variation adaptive for new areas and habitats (Simberloff, 2009). Propagule pressure may be the most important factor in establishment success of exotic species of various taxa in a variety of ecosystems worldwide (Holle & Simberloff, 2005). If propagules are coming from different native source areas and that these native populations show spatial genetic structure, genetic diversity can be increased over that observed within any of the native populations. For example the non-native populations of the *Anolis sagrei*, this increase resulted from the inter-mingling of distinct native haplotypes within the non-native populations in Florida. *Prosopis* species and provenances have been introduced in various parts of the world sometimes in a single event, but often by multiple introductions which may have implications for rate of spread (Muturi *et al.*, 2012)

2.1.5 Increased Resource Availability

The increased resource hypothesis suggests that plant invasion is caused by availability of resources such as light, water, and soil nutrients (Davis, et al., 2000). Resources may become available when resource supply increases, as with atmospheric nitrogen deposition, or when resource capture by other plants decreases, as with disturbances such as fire or ploughing (Blumenthal, 2005). High resource availability benefits fast-growing native or exotic species. Fast growing, high-resource species also tend to be highly susceptible to enemies. When introduced to a new range, these species are likely to benefit from both high resource availability and enemy release. Where resources necessary for plant growth are scarce, growth is slow and the metabolic cost of producing new plant tissue is high; therefore, plants from such habitats have evolved defenses to protect that tissue (Coley *et al.*, 1985). Conversely, plants from high resource habitats grow quickly, produce tissue at low metabolic cost, and invest little in defense (Coley, et al., 1985; Grime *et al.*, 1997). Such high-resource species are also nutritious, with little structural material and high tissue nutrient concentrations (Grime, et al., 1997; Mattson, 1980). Poorly defended, nutritious, high resource species tend to be preferred by herbivores (Coley, et al., 1985), tend to lose more tissue to herbivory (Cebrian & Duarte, 1994), and to be more strongly regulated by herbivory (Fine *et al.*, 2004; Fraser & Grime, 1999), than low-resource species. They may also be particularly susceptible to pathogens (Hoffland *et al.*, 1996). If, as the evidence indicates, high-resource plant species are more strongly affected by enemies than are low-resource species, they should also gain more from leaving those enemies behind. The effect of enemy release in a new environment should therefore increase with the resource availability to which a species is adapted. This concept, referred to here as the resource–enemy release hypothesis, predicts that enemy release and increased resource availability may act in concert to promote invasion (Blumenthal, 2005). For example, in California's nutrient-poor serpentine grassland, macronutrient additions were found to increase the overall productivity of the community, decreased species richness, and increased non-indigenous species biomass with or without soil disturbance. These results indicate that some the non-indigenous species respond more strongly to increased resource availability than native species (Theoharides & Dukes, 2007). *P. juliflora* has broad ecological amplitude and is adapted to a very wide range of soils and site types from sand dunes to cracking clays. It is generally found in areas where water and poor soil fertility are the principal agents limiting plant growth, and its able to survive and even thrive on some of the poorest land, unsuitable for any other tree species. The plant dominates in dry, or seasonally dry water courses or depressions, and the presence and depth of the water table is an important decisive factor in the distribution, size and growth of *Prosopis* species (Simpson, 1977).

2.1.6 The Role of Disturbance

Disturbance is commonly implicated in exotic plant invasions (Burke & Grime, 1996; Levine & D'Antonio, 1999; Lodge, 1993). Although the mechanism by which disturbance facilitates invasion is rarely investigated, it may be due to reduced competition, higher resource availability, and/or increased propagule pressure (Davis, et al., 2000; Hobbs & Huenneke, 1992). Furthermore, changes in the severity, frequency, and type of disturbance could alter community susceptibility to invasion (Hobbs & Huenneke, 1992)

Many invasion biologists have targeted disturbance as a crucial component that makes habitats vulnerable to invasion, since disturbance disrupts strong species interactions (Burke & Grime, 1996; Crawley, 1987; Didham *et al.*, 2005; Hobbs & Huenneke, 1992; Lake & Leishman, 2004; Vitousek, et al., 1997). Disturbance may create an empty niche that the invader can occupy (Ward, 2009). Alternatively, by increasing colonization opportunities, disturbance may simply provide an opportunity from which an invasion can proceed (Mack & D'Antonio, 1998; Parker *et al.*, 1993).

Disturbance as it relates to invasion may be defined as a discrete event in time which, by increasing resource i.e. substrate availability, may disrupt the ecosystem, community or population structure (Hobbs & Huenneke, 1992). However, although disturbances such as flash floods are an integral part of some ecosystems (Avni & Gichua, 2001), natural disturbances have been shown to sometimes prevent or slow invasions (Mack, 1989; Mooney & Drake, 1989). When an exotic species gets into and occupies an empty niche free of competition within a non-indigenous range, it may have an advantage in resource acquisition and therefore faster growth than in its native range (Orians & Ward, 2010). Eschtruth and Battles, (2009)quantified the relative importance of canopy disturbance, in determining exotic plant invasion in 10 eastern hemlock forests in Pennsylvania and New Jersey (USA). They found out that canopy disturbance and propagule pressure appear was the most important predictors of invasion over and above native species diversity and herbivory. In view of this then, how an invasive species responds to disturbance may determine its success or failure in a new ecosystem. Maximum *Prosopis* seedling establishment appears to be episodic and are related to periods of drought or overgrazing when competing plant cover and vigour are reduced and germination is enhanced when seed are scarified by passage through animal digestive tracts (Archer, 1989). *Prosopis* species are known to regrow aggressively immediately after disturbance events or overgrazing (Brooks & Pyke, 2000)

2.1.7 Consequences of Plant Invasions

Evidence strongly suggests that when the species composition of a community changes due to the invasion and spread of an exotic, there are likely to be consequent changes in nutrient cycling processes that arise due to changes in flora (Ehrenfeld, 2003). Nutrient dynamics may also become altered as a result of changes in the physical properties of the soil caused by the introduction of new species (Boettcher & Kalisz, 1990; Ehrenfeld, 2003; Finzi *et al.*, 1998). Changes may also result from alterations in the patterns of species dominance within the plant community, since the effects of a given species on ecosystem processes are modulated by its relative abundance within the community (Grime, 1998). Changes in plant functional types—herbaceous versus woody plants, N-fixing versus non-fixing species, C3 versus C4 species, and so on—are also associated with changes in the distribution and dynamics of soil nutrients (Gill & Burke, 1999).

Plants can affect nutrient and carbon dynamics through a variety of mechanisms. These mechanisms reflect the ways in which plants interact with both the physical medium and the biota of the soil (Ehrenfeld, 2003). Some traits are described as “qualitative,” because they are either present or absent within a given species; these include the ability to fix atmospheric N, the presence of perennial tissues, and the photosynthetic pathway (Chapin III *et al.*, 1996; Mack *et al.*, 2001). When a new species is introduced, its effects on nutrient cycling will depend on how different it is from the constellation of traits present within the existing plant community, and studies have found that soil properties change in response to the introduction of new traits and new functional groups (Aguiar *et al.*, 1996; Gill & Burke, 1999).

Invasive plants may also affect pollination networks. Given the fact that alien plants are well integrated into local plant–pollinator webs (Aizen *et al.*, 2008; Memmott & Waser, 2002; Nielsen *et al.*, 2008), they can alter the pollination of other plants through their shared pollinators (Bjerknes *et al.*, 2007; Traveset & Richardson, 2006). Sympatric co-flowering plant species experience interspecific interactions due to pollinator sharing (Armbruster & Herzig, 1984; Campbell & Motten, 1985). Such pollinator-mediated interactions may have negative (competitive), neutral or positive (facilitative) impacts on pollination and, in turn, in the reproductive success of one or both of the interacting species (Rathcke, 1983), assuming that changes in pollinator visitation and pollination translate into changes in plant reproduction.

Competition for pollination occurs when a plant species suffers pollen limitation (i.e. produces fewer fruits ⁄ or seeds than it would with adequate pollen receipt as a result of pollinator sharing (Knight *et al.*, 2005). Such competition may result from competition for pollinator visits which occurs when the pollinator visitation to one plant species is sufficiently reduced in the presence of other preferred species so that conspecific pollen deposition is diminished (Campbell & Motten, 1985) or through interspecific pollinator transfer which occurs when pollinators switch between flowers of different species in floral mixtures, in the process increasing heterospecific pollen deposition and ⁄ or decreasing conspecific pollen deposition (Morales & Traveset, 2008). Much of the research on the impacts of invasive alien plants on plant-pollinator interactions has focussed on the indirect impacts of alien plants on native plant pollination (Bjerknes, et al., 2007). Impacts can be positive (alien plants facilitate pollination of native species by acting as "magnets" and drawing pollinators into a plant community), negative (alien plants compete with native plants and reduce visitation and hence their pollination success) or non-existent (alien plants have no impacts on native ones) (Stout & Morales, 2009). Studies so far have found a range of results (Aigner, 2004; Bartomeus *et al.*, 2008; Moragues & Traveset, 2005). In addition, interactions between the same alien and native plant species at different locations have found contradictory results (Stout & Morales, 2009). Few studies have investigated the impacts of invasion by alien plants on the structure of pollinator diversity (Aizen, et al., 2008).

Many studies have shown that grass production increases following control of *Prosopis* (Bedunah & Sosebee, 1984; Dahl *et al.*, 1978). However, response is highly variable and dependent on many factors such as density of *Prosopis* prior to treatment, effectiveness of treatment, soil type, and precipitation. In south Texas, *Prosopis* colonizes grasslands, and then serves as a nurse plant for other shrub species that establish in its understory (Archer, 1989).

Prosopis is a nitrogen fixer and may modify soil fertility. Soil nitrogen can be 3 to 7 times greater beneath *Prosopis* canopies than in interspaces between *Prosopis* (Nilsen *et al.*, 1983; Shearer *et al.*, 1983; Tiedemann & Klemmedson, 1986). In south Texas, Boutton *et. al.,* (1996) found that soil organic carbon (C) and total nitrogen (N) in the 0 to 0.2 m soil layer was 44% (2600 vs. 1800 g C/ m^2) and 35% (260 vs. 170 g N/ m^2) greater, respectively, in *Prosopis* groves than in open grasslands. Soil carbon and nitrogen were 3.5 and 3.1 times greater, respectively, in drainage woodlands than in grasslands.

The capacity of *Prosopis* or related woody legumes to fix nitrogen and enrich soil fertility beneath their canopies may significantly alter responses of individual and/or assemblages of herbaceous species beneath canopies. Jacoby *et al.* (1982) found that understory vegetation is distributed into zones with taller grass species beneath *Prosopis* canopies and shortgrass in interspaces. Control of *Prosopis* provides regions of enhanced soil N and C which are temporarily exploited by associated grasses. Therefore, in the long-term, *Prosopis* at low densities may enhance recruitment of grasses into the landscape at a greater rate than *Prosopis*-free areas (Brown *et al.*, 2008).

While adult *Prosopis* plants are not palatable and are not browsed by mammals (with the possible exception of new regrowth sprouts), they provide cover for many wildlife species. In addition, many species of insects including bruchid beetles depend on *Prosopis* (Ansley *et al.*, 1990)

2.2 The Biology of Prosopis juliflora

Prosopis juliflora (Swartz.) DC. has a large crown, an open canopy and can grow to a height of 14 m (Andersson, 2005) and the root system has a deep taproot that allows the tree to reach deep into the water table. The leaves have a high tannin content (Matthews & Brand, 2004; Pasiecznik, et al., 2004). The pods contain a high level of sugar and are palatable to livestock when ripe (Batista *et al.*, 2002; Talpada & Shukla, 1988). A mature *P. juliflora* tree can produce 40 kg of pods per year, from which 60 000 seeds can be obtained (Alban *et al.*, 2002). Total per plant leaf area of 1.5 to 5 m tall adult tree ranges from 50 to 150 m^2 (one leaf surface) Leaf area index (LAI; canopy cover/total leaf area) is usually between 1.0 to 1.5 (Ansley *et al.*, 1992).

2.2.1 Seed ecology and dispersal

Most pods of *Prosopis juliflora* that fall to the ground are destroyed by insects or fungi or are consumed by animals. A study conducted in Arizona showed that seeds deposited in the soil may remain viable for up to 10 years, especially when seed were within the pod (El-Keblawy & Al-Rawai, 2005).

Germination of *Prosopis* seeds may occur throughout the year especially when soil moisture is favourable. Maximum emergence of *Prosopis* occurs when seeds are planted at 0.6 cm depth and soil temperature is near 25°C (Scifres & Brock, 1971). A substantial proportion of the carbohydrate in the embryo is devoted to root system development and many young *Prosopis* plants which appear to be seedlings may actually be 3-4 years old (Brown & Archer, 1989). Brown and Archer (1989) have found that *Prosopis* is capable of establishing from seed in thick swards of grass. Faecal-deposited seed have an immediate source of nutrients in the dung which may enhance seedling survival. However, large-sized faecal deposits, especially those from cattle may dry more rapidly than the surrounding soil and actually inhibit seedling survival (Archer, 1989). Kramp *et al*. (1998) found that 40% of faecal sites of both cattle and deer that were initially observed to have emerging seedlings eventually produced at least one established seedling.

Emerging seedlings are killed if clipped (or grazed) below the cotyledons (Scifres & Brock, 1971). Wright *et al*. (1976) observed that *Prosopis* seedlings less than 2-3 years old were killed by fire, apparently because the bud-zone meristem was still exposed. Older seedlings tolerate fire or other disturbances by resprouting from the bud zone if above ground parts are destroyed or damaged.

2.2.2 Rooting characteristics and water use patterns

Prosopis is deep-rooted, water-using "phreatophyte" which avoids drought (Mooney *et al.*, 1977). This characterization is based primarily on research in the Sonoran desert of California, an area of 70mm annual precipitation, but which has unlimited water occurring at about 5m depth. In a study in north Texas, severing the lateral roots of adult *Prosopis* trees significantly reduced transpiration by as much as 50% when compared to unsevered trees (Ansley, et al., 1992). *Prosopis* that rely mainly on lateral roots grow deeper roots during drought and compete successfully with grasses by using soil moisture in subsoil layers (Ansley *et al.*, 1991). Adult *Prosopis* trees (3-4 m tall) in Texas were found to use up to 75 litres of water per day during ideal mid-summer growing conditions and adequate soil moisture (Ansley, et al., 1991).

2.2.3 Breeding System and Pollination

Floral evolution in legumes is characterised by clear trends towards maximising pollen and nectar economy, leading to the development of increasingly sophisticated pollinators (Arroyo, 1981). In mimosoid legumes, a reduction in flower size was compensated for by compaction and transference of attraction to the entire inflorescence, with sterility and neutering playing an integral part in this process (Arroyo, 1981). Flower biology is similar in all *Prosopis* species and is generally asynchronous. *Prosopis* flowers are produced in masses, mainly on spike-like racemes (Arroyo, 1981).

Although very large numbers of flowers are produced, not all are fertile and high rates of ovary abortion are found. Intra-populational dimorphism in nectar production was observed in *Prosopis* flowers in Mexico (Golubov *et al.*, 1999; López-Portillo *et al.*, 1993). Not all flowers are fertile or receptive and differences in nectar production may be due to resource limitation, with high energy demands made on plants for reproduction, and because few pollinator visits are required to set fruit (López-Portillo, et al., 1993).

Prosopis species are generally self-incompatible (Felker & Clark, 1981; Solbrig & Cantino, 1975). This was confirmed with no successful pollination or fruit set recorded after bagging and selfing flowers in Brazil (Zaitoun *et al.*, 2009) and India (Goel & Behl, 1996). Some limited self-compatibility (4%), however, has been observed in *P. juliflora* in India (Pasiecznik *et al.*, 2001). Self-incompatibility has probably been positively selected for in desert environments, with obligate outcrossing leading to high variability in progeny produced, both within and between natural populations (Pasiecznik, et al., 2001). The maintenance of high genetic variability in *P. juliflora* can be seen as a mechanism for survival in dry zones with a high variability in rainfall, temperature and soil types, and for continued evolutionary adaptations to a changing environment (Pasiecznik, et al., 2001).

Insects are instrumental in the pollination of *Prosopis* species and relative attractiveness of *Prosopis* flowers may have a direct impact on both yield and quality. Efficient pollination is crucial for seed production (Keys *et al.*, 1995). Goel and Behl (1996) found *P. juliflora* pollen viability to be 79-96%, but maximum pollen production occurred at midday, and insects are less mobile during the high temperatures found at this time.

2.2.4 Habitat Requirements

Soil is not often a limiting factor to distribution. Nitrogen fixation and soil improvement leads to an increase in soil fertility as *Prosopis* trees mature (Geesing *et al.*, 2000). *Prosopis* trees have been noted to fix nitrogen under conditions of high pH (Singh, Gurbachan, 1996), high salinity (Felker *et al.*, 1981) and high water deficits (Felker & Clark, 1981). Low phosphorus levels can affect nitrogen fixing ability by limiting the activity of *Rhizobium* (Jarrell & Virginia, 1990). *Prosopis* species can survive and grow with salinity levels equal to that of sea water (Felker, et al., 1981) and in soils with a pH of 10.5 (Singh, Gurbachan, 1996).

P. pallida was found to tolerate salinity levels up to 18000 mg NaCl/l with no reduction in growth or survival, and still grew at 36000 mg/l NaCl, equivalent to sea water (Felker, et al., 1981). *P. juliflora* and *P. pallida* are known to tolerate saline sites in their native range such as lowland flats and coastal dunes and in such conditions they can often dominate. *P. juliflora* has been successfully raised using saline irrigation water, with an electrical conductivity of 20 dS/m in India (Singh, Gurbachan, 1996).

P. juliflora can also particularly well able to tolerate alkaline soils, with marginal reduction at pH 9.0, but can survive and grow in soils of pH 11 although it will perform much better following soil amendments (Singh, Gurbachan, 1996). *Prosopis* species, are not be well suited to acidic soils, and the possibility that low pH is a limiting factor to the distribution has been suggested for *P. glandulosa* (Jarrell & Virginia, 1990) but not specifically for *P. juliflora* (Pasiecznik, et al., 2001).

Altitude does is not a factor directly limiting distribution. In the native range, *P. juliflora* is abundant at altitudes of below 200 m, less common between 200 m and 500 m, and frequency increases again above this with some trees found up to 1500 m altitude. Other *Prosopis* species can be found at even higher altitudes, with *P. chilensis* native to areas up to 2900 m and *P. ferox* up to 3700 m altitude. *P. juliflora* is also generally well adapted to different altitudes where introduced (Pasiecznik, et al., 2001).

2.3 Economic importance of Prosopis juliflora

Prosopis juliflora poses major problems due to its aggressive invasion and colonisation of pasturelands, farmlands, swamps and displacement of native species of socio-economic importance. However it may provide for many solutions to the local communities. Fuelwood wood from *Prosopis* species is of high quality makes excellent charcoal (Choge *et al.*, 2009).

The *Prosopis* wood resource on the Niger side of Lake Chad was estimated to be 2.2 million m^3 and the average yearly increment to be around 75,000 m^3 (Geesing *et al.*, 2004). In addition, *Prosopis* timber is hard and resistant to decay, and has been used to make fence posts, small carpentry items, furniture, and railway ties (Simpson, 1977).

The pods of some *Prosopis* species have been used as a staple food, especially in the deserts of Mexico and in the south-western United States (Simpson, 1977). Oduol *et al.*, (1986) has reported that the seeds may contain up to 9 to 17 % protein and 15 to 37 % sugar. In addition, flowers of *Prosopis* species are regarded as a valuable source of bee forage, and honey has become the most widely derived food product from *Prosopis* (Geesing, et al., 2004).

Work on the impacts of *P. juliflora* has been carried out on before in Kenya. Mwangi and Swallow (2005), in ICRAF have carried out an assessment of the livelihood effects, costs of control, and local perceptions of the invasive tree of *P. juliflora,* on rural residents in the Lake Baringo area of Kenya. They reported a strong local preference for eradication and replacement of the tree. Ngujiri and Choge (FAO, 2006) looked at the status and social impacts of *Prosopis* sp. introduction. They report the evident dilemma of eradication considering the positive and negative impacts it may contain. Makhanu and Waswa (2007) did a review of the aftermath of the introduction of *P. juliflora* in Baringo District in Kenya as a case study of uncontrolled alien species introductions. They articulate the difficulties involved in eradicating the tree but suggest that the most viable means of control and management would be to involve, on a common purpose, the local community, the researchers and the government.

CHAPTER THREE

3.0 THE IMPACT OF *Prosopis juliflora* ON SELECTED SOIL PROPERTIES IN BARINGO COUNTY

3.1 Introduction

Climate and edaphic conditions have been regarded as fundamental determinants of potential distribution of introduced plant populations (Mitchell *et al.*, 2006). Physiological properties, reproductive and life-history characteristics are also cited frequently to explain invasiveness of plant species (Dukes & Mooney, 1999; Pyšek, 1998; Reichard & Hamilton, 1997; Rejmanek & Richardson, 1996; Sasek & Strain, 1991; Schweitzer & Larson, 1999; Williamson, 1996). In addition, diversity of native plant species also influences success of an invasive plant (Elton, 1958; Shea & Chesson, 2002; Zedler & Kercher, 2004). Studies have however shown that the influence of these properties is not universal in all invasive species in all ecosystems (Pysek *et al.*, 1995; Williamson, 1993; Williamson & Fitter, 1996). This occurs as a result of the effect of the complex interactions between plants and soil which can change soil properties (Ehrenfeld, 2003), thereby influencing invasiveness.

Numerous mechanisms have been identified by which plants can alter the physical, chemical, and biological properties of soils (Bezemer *et al.*, 2006; Castro-Díez *et al.*, 2011; Ehrenfeld *et al.*, 2001; Gichua *et al.*, 2002; González-Muñoz *et al.*, 2012; Hedlund *et al.*, 2003; Kardol *et al.*, 2007; Kelly *et al.*, 1998; Van Der Putten *et al.*, 2009; Wardle *et al.*, 2004). Many involve changes in the quantity, quality, and/or timing of inputs of plant-derived substrate through such processes as nitrogen cycling and/or litter dynamics; others may result from changes in microclimate associated with changes in the density and height of the vegetation, or changes in water relations consequently leading to differences in soil properties to occur at the scale of shrubs or individual trees (Ehrenfeld, et al., 2001; Ehrenfeld & Toth, 1997; Finzi, et al., 1998), or can be associated with both natural and anthropogenic-driven changes in plant species composition (Binkley & Giardina, 1998; Mitchell *et al.*, 1997).

Shifts in plant community composition resulting from exotic invasions are just as likely to be associated with changes in soil properties as those associated with natural succession processes. Despite the ubiquity of plant-mediated changes in soil properties, there has been little research documenting such effects following exotic invasions. Vitousek *et al.* (1997) pointed out that exotic species could alter soil processes; he identified differences in resource acquisition or utilization by exotic plants as the mechanism driving changes in soil-based processes.

Changes in soil biogeochemistry following a shift in species composition could be another pathway of change (Ehrenfeld, et al., 2001). This alternative mechanism would act indirectly through the effects of the introduced species on the soil biota and/or on soil physical conditions, rather than directly through the traits of the invading species. Either mechanism could allow introduced species to create a feedback system where changes in soil ecology either accelerate its own growth or promote its competitive superiority to native species, and hence promote the spread of the exotic species (Wilson & Agnew, 1992). Wilson and Agnew (1992) argue that the establishment of an initial population of the exotic species would begin a process of changing the structure and function of the soil biota, which would promote the spread of the exotic and/or the competitive reduction in native species' populations.

Either mechanism would enhance the spread of the invader. Thus, changes in soil ecology induced by the interaction of the exotic species and the soil could provide an explanation for the rapid increase in abundance of the invasive species (Ehrenfeld, et al., 2001).

Prosopis juliflora, which in invasive in many arid and semi-arid regions in Kenya provides a good candidate to test this proposition. The role of *Prosopis juliflora* and its interactive effects with soils of the dry lands of Baringo has not been well documented. Different studies elsewhere have found either positive or negative effects of *Prosopis* species on nutrient status of soils (Archer, 1989; El-Keblawy & Al-Rawai, 2007; Herrera-Arreola *et al.*, 2007; Reyes-Reyes *et al.*, 2003). *P. juliflora* has also been found to cause a decrease in soil pH (Garg, 1999)

This study aimed at determining the impact of the invasive *P. juliflora* on the edaphic dynamics of the ecosystem of its introduced range. Soil quality was predicted to be enhanced along the increasing *Prosopis* sp. gradient due to its ability to fix nitrogen and deposit phosphates (Bhatia *et al.*, 1998). *P. juliflora* was also predicted to cause a marked decrease in soil pH as a result of increased carbonic acid from CO_2 released from respiration from roots of *P. juliflora* (El-Keblawy & Al-Rawai, 2005).

3.2 Materials and Methods

3.2.1 Site Description

The study was carried out in Baringo County, which is located in the North Rift region of Kenya (Appendix one). Baringo covers an area of 8,655 km^2 and it encompasses a variety of eco-climatic zones that range from fertile, well-watered highlands to semi-arid rangelands in the lowlands. In the whole county, the forest cover totals 24,346.99 ha, which is heavily threatened by rapid encroachment for agricultural and wood products. The lowlands are predominantly covered by sparse thorny *Acacia* spp. interspersed with grassy environments. The most predominant species include *Acacia tortilis, Acacia elatior, Acacia melifera, Salvadora persica, Commiphora spp., Delonix elata, Moring stenopetala, and Terminalia sp* all of which prevail to varying degrees. However, the different *Acacia* species predominate in the the rest of the county (Nauru, 2004). Altitude in Baringo County varies from 762 m above sea level in the lowlands up to 2600 m in the steep hills that are bounded by escarpments on the eastern and eastern parts. The valley floor consists of dry plains and the land rises once more in the eastern part of the Baringo County towards the Laikipia escarpment (Denich *et al.*, 2003). The soils in the lowland area are mainly moderately to poorly drained, very deep, strongly calcareous, saline and sodic. The texture is fine sandy loam to clay (Andersson, 2005). The lower part of Baringo County has suffered severe environmental degradation in recent years that has resulted in low vegetation cover, caused by deforestation and overgrazing, and is exacerbated by high intensity, sporadic rainfall on steep slopes. In recent years, two thirds of the total catchment (8655 km^2) has been grazing and the rest of the land under agriculture, apart from <1 % forest. All the grazing area and two thirds of the agricultural land is environmentally degraded; almost 90 % of the catchment. The Baringo County’s human population is at least 360 000 and growing (2.65 % p.a.). Associated livestock numbers are correspondingly large approximately 900 000 goats, 200 000 sheep and 300 000 cattle occur there (Hickley *et al.*, 2004). The climate is semi-arid (Owen *et al.*, 2004) and the average minimum and maximum temperatures are 20 °C and 30 °C respectively. The area has highly variable rainfall with a coefficient of variation of 36% (Rowntree, 1989) and a mean annual rainfall of 635 mm (Kassilly, 2002) accompanied by flash floods, erosion and high potential evapotranspiration (Wijdenes & Bryan, 2001). The annual precipitation amount alone, does not determine the conditions in the Baringo region as semi-arid as indeed, most of the precipitation disappears quickly back to the atmosphere again, due to evapotranspiration. In the lowland, including the slopes surrounding the valley floor, the potential evapotranspiration ranges from 1800 to over 2200 mm a year dependent on elevation and temperature and the rainfall/potential evapotranspiration ratio in the lowland is between 25-40 % (Johansson & Svensson, 2002). The rainy season occurs from April to July while the peak dry season commences in November and ends in February of every year (Mala *et al.*, 2011).

Three areas were selected for the sampling. Kampi ya Samaki which is situated near Lake Baringo (00:36:28N, 00:36:01E) because it is next to a freshwater lake, Loboi is situated next to Lake Bogoria (00:26:28N, 36:00:90E), a saltwater lake, while Endau lies between the two sites (00:31:42N, 035:59:28E). These three sites were selected because they are among the locations in Baringo with the highest density of the invasive *P juliflora*, and indeed Kenya. The three sites are separated by a distance of at least 20 km.

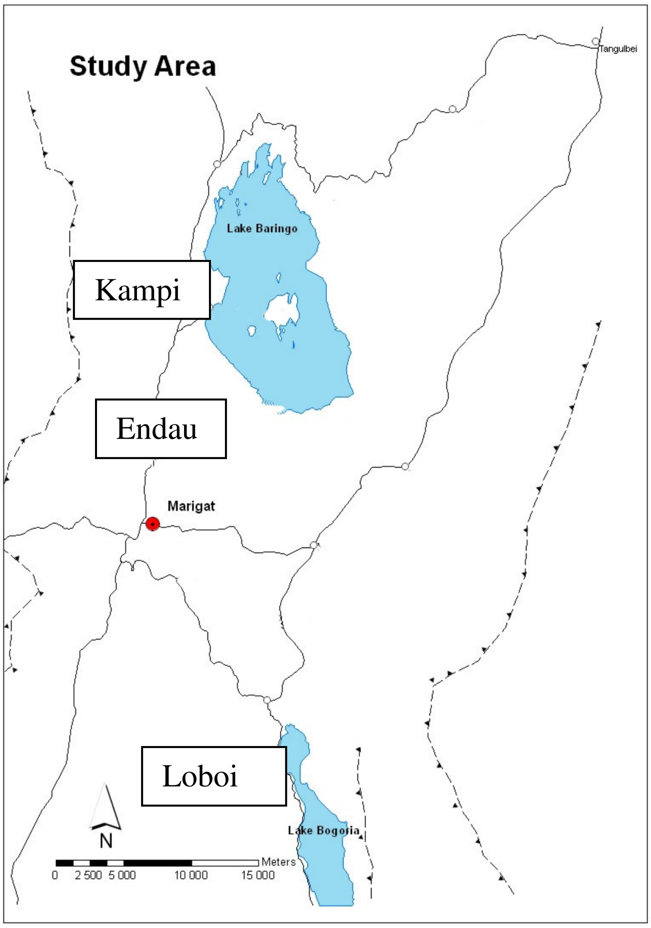

Figure 1: Map of the study area

3.2.2 Soil Sampling

Soil sampling was carried out within a total of 75 modified Whittaker plots each measuring 0.1 ha (Ward *et al.*, 1993). 25 plots were sampled for each of three sampling sites (Kampi ya Samaki, Endau and Loboi) sing a systematic sampling design. This constituted high density, low density and *Prosopis*-free plots. In each site, ten plots were laid out in an area with more than 200 individuals of *P. juliflora* and were considered high-density stands. Another ten plots in a low-density area contained less than 200 individuals of *P. juliflora* species while 5 plots were placed in an area deficient of any *P. juliflora* individuals. Kampi ya Samaki (00:36:28N, 00:36:01E) is situated near Lake Baringo, a fresh water lake, Loboi (00:26:28N, 36:00:90E) is situated next to Lake Bogoria, a salt water lake, while Endau (00:31:42N, 035:59:28E) lies between the two sites, leaving a distance of at least 20 km to either of the other two sites.

Within each site, sampling plots were placed parallel to the slope which was the major environmental gradient to encompass the most heterogeneity. Using core auger size 9.5cm, five soil samples, 30g each (one at the centre and the rest at the four corners) were collected from a depth of 15 cm within each of the Whittaker plots in order to determine soil properties. The number of *Acacia* species in each plot was also counted.

All the soil samples were put in bags and taken to Jomo Kenyatta University of Agriculture and Technology laboratory for analysis. Each of the soil samples were analysed separately and the mean value for a plot was used for analysis.

Nitrogen was analysed using the Kjeldahl method. The samples were first digested in strong sulphuric acid in the presence of a catalyst, which helped in the conversion of the amine nitrogen to ammonium ions. The ammonium ions now converted into ammonia gas, was heated and distilled. The ammonia gas was then led into a trapping solution where it was dissolved and became an ammonium ion once again. Finally, the amount of the ammonia trapped was determined by titration with a standard solution, and calculation on the percentage nitrogen made (Jone, 1991). Phosphorus was determined using Colorimetric determination where soluble reactive phosphorus was measured colorimetrically using an RFA – 500 rapid flow analyzer

(Alpkem Corp). Organic carbon was measured using the Walkley-Black Method where Organic carbon, potassium dichromate ($K_2Cr_2O_2$) and concentrated H_2SO_4 were added to between 0.5g and 1.0g of soil or sediment. The sample and extraction solutions were gently boiled at 150^oC for 30 minutes, allowed to cool, and then water was added to halt the reaction. The solution was swirled and allowed to cool before determination. Soil pH was determined using a pH meter and electrical conductivity as an index of salinity, was measured using a conductivity meter. (Chapman & Pratt, 1961; Jones, 1991; Okalebo *et al.*, 1993). Data were analysed using Nested ANOVA to compare the differences of the variables between plots along the tree density gradient. In order to meet assumptions of normality, nitrogen data was $\log_{10}$ transformed.

3.3 Results

The level of %N within areas of high species density of *Prosopis* was 0.0146% while it was was 0.0259 in areas with low density of *Prosopis*. Within Prosopis-free areas the % N 0.0290%. Therefore, N was much higher in *Prosopis*-free areas (Figure 3.1). There were significant differences between sites ($p<0.001$, $F_{(2,66)=}7.70$)and between factors ($p<0.001$, $F_{(6,66)}=17.37$) in the amounts of N.

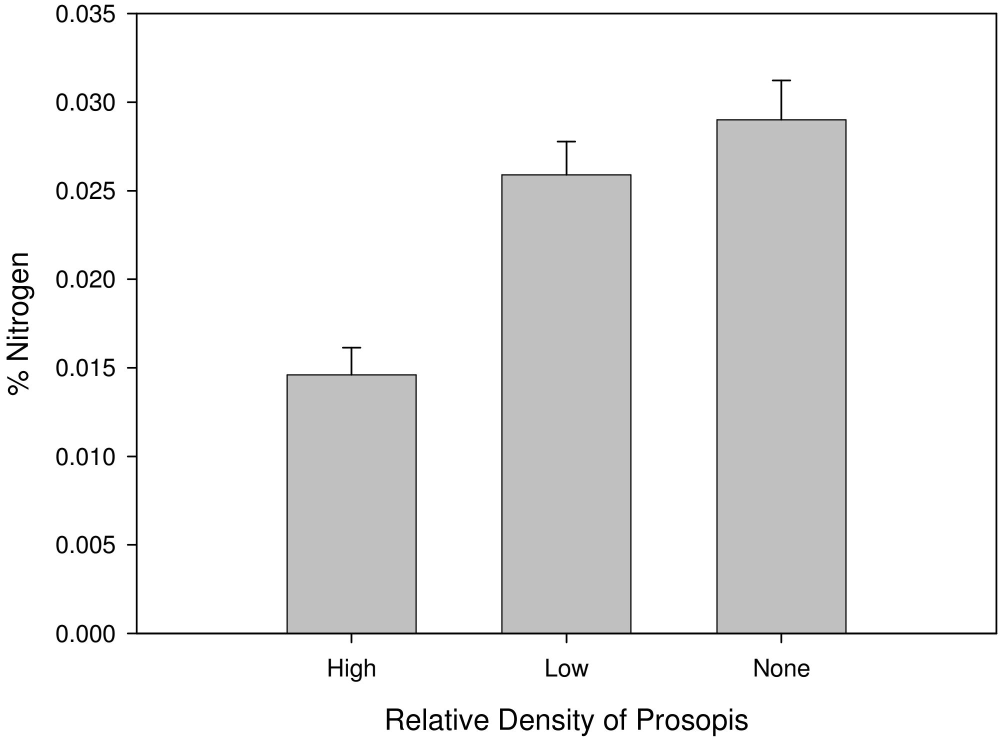

Figure 3.1: Amount of nitrogen along the *Prosopis* density factors applied as high density, low density and *Prosopis*-free habitats

The highest amount of Total Organic Carbon (TOC) was found in areas with the low densities of the invading species where it was 1.699%. It was 0.551% and 0.752% in high density and *Prosopis*-free areas respectively. There were significant differences in the TOC between sites (p= 0.002, $F_{(2,66)}$=7.02) and between factors (p=0.029, $F_{(6,66)}$=10.99) (Figure 3.2).

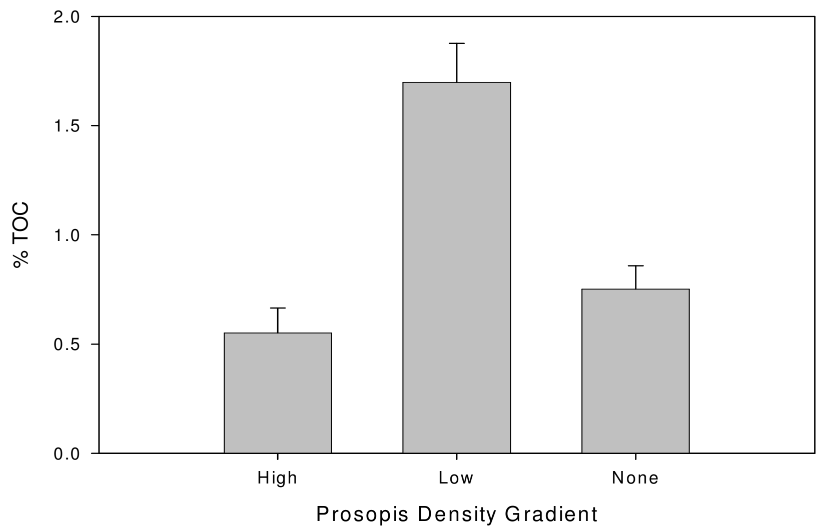

Figure 3.2: Total Organic Carbon along the *Prosopis* density factors applied as high density, low density and *Prosopis*-free habitats

Phosphorus was highest in *Prosopis*-free areas where it was 0.19%. Within high density areas, it was 0.0474% while it was 0.115% in areas with low density (Fig 3.3). There were significant differences both between sites ($p < 0.001$, $F_{(2,66)}=54.80$) and between factors ($p<0.001$, $F_{(6,66)}=7.03$) in the amounts of P.

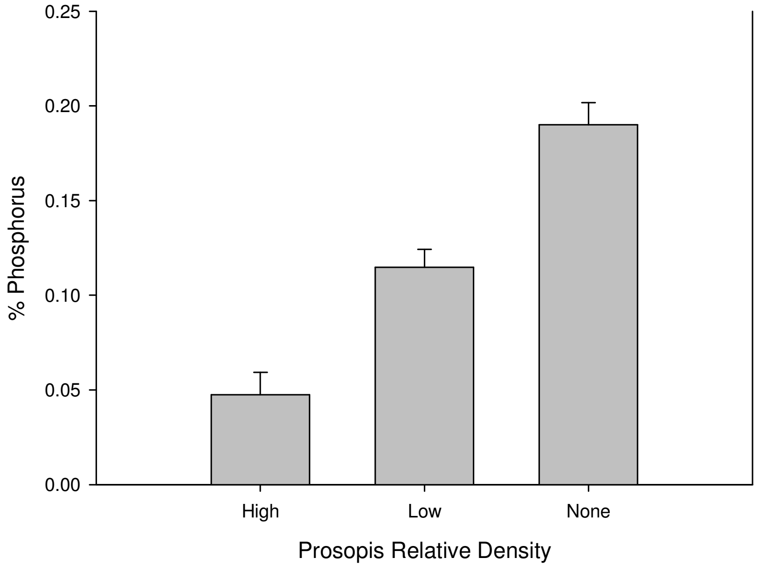

Figure 1.3: Amount of phosphorus along the *Prosopis* density factors applied as high density, low density and *Prosopis*-free habitats

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pH was highest also in areas with no *Prosopis* with a value of 8.68. Areas with high density of *Prosopis* had a value of 8.14 while the areas with low density of *Prosopis* had a value of 7.78 (Fig 3.4). There were also significant differences in pH between sites ($p<0.001$, $F_{(2,66)}=37.82$) and between factors ($p<0.001$, $F_{(6,66)}=8.70$).

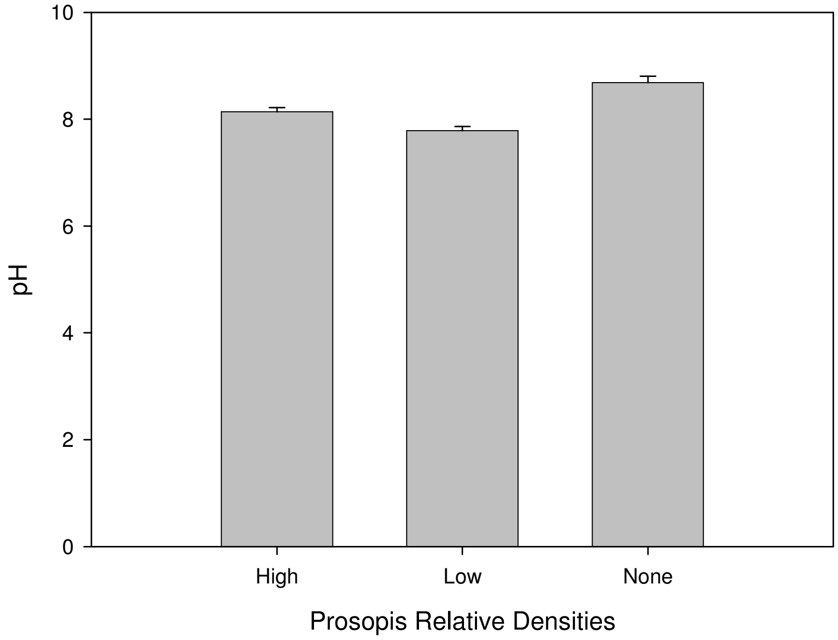

Figure 3.4: The levels of pH along the *Prosopis* density factors applied as high density, low density and *Prosopis*-free habitats

The levels of EC between sites with different densities of *Prosopis* were as follows: High density of *Prosopis* with a value of 0.208 dS/m, low density of *Prosopis* with a value of 0.291dS/m and *Prosopis*-free areas with a value of 0.302. There were significant differences in electrical conductivity (EC) between sites ($p=0.002$, $F_{(2,66)}=6.61$) but not between factors ($p=0.029$, $F_{(6,66)}=2.53$) (Fig 3.5).

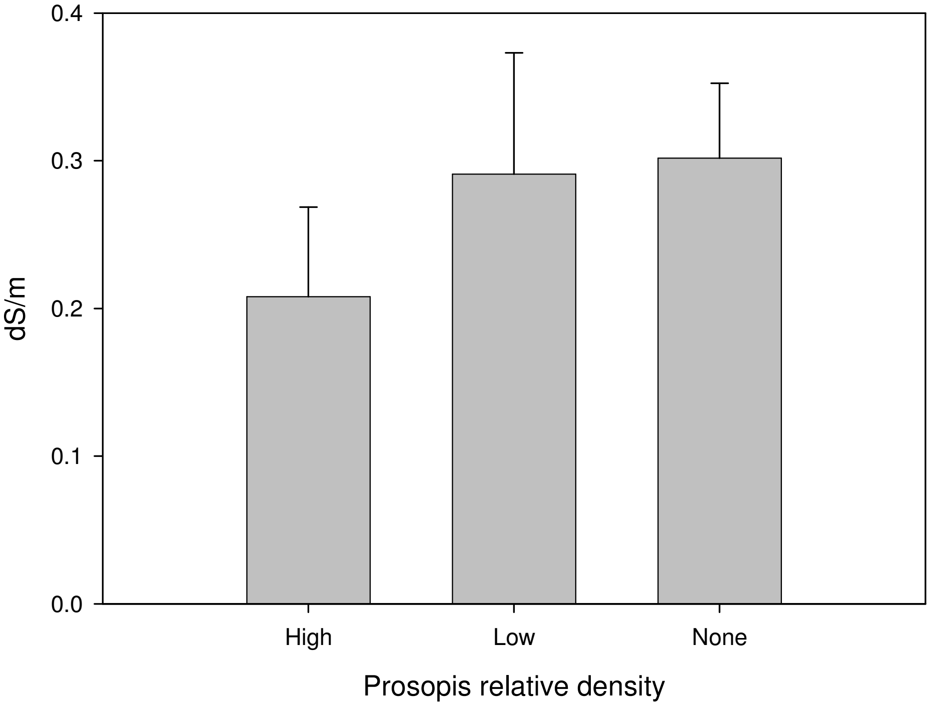

Figure 3.5: Electrical conductivity (dS/m) in high density, low density and *Prosopis*-free habitats in Baringo

Acacia species density was highest in areas with low density of *P. juliflora* and the least in plots with the highest density of *P. juliflora* (Fig 4.3). A correlation between densities of *P. juliflora* and *Acacia* spp. revealed a negative correlation (r^2 =-0.41. There was also a weak correlation between the levels of N and TOC with a correlation coefficient of 0.255.

3.4 Discussion

Various studies have established that soil nitrogen could be the most important factor that determines ecosystem stability (Burke *et al.*, 1998; Carrera *et al.*, 2003; Chen & Stark, 2000). Introduction of a plant species can also have large effects on rates of nitrogen transformation by changing litter quality and quantity (Evans *et al.*, 2001; Hook *et al.*, 2004; Rimer & Evans, 2006; Tamm, 1991). Invasive leguminous plants are commonly considered to increase levels of soil N, perhaps because many successful invaders take advantage of mutualisms with native nitrogen-fixing bacteria (Ehrenfeld, 2003). Because *P. juliflora* is a nitrogen fixer, and has been observed to reduce soil pH (El-Keblawy & Al-Rawai, 2007), it was predicted that soil nutrient concentrations of N, P and Total Organic Carbon would increase where the density of *P. juliflora* was high. Indeed this kind of trend has been observed in several studies. For instance, Reyes-Reyes *et al.* (2003) reported a 3-fold increase in organic carbon for soil sampled under *P. juliflora* species in the central highlands of Mexico compared to soil sampled outside the canopy. In south Texas, Boutton *et al.*, (1996) found that soil organic carbon and total nitrogen in the 0 - 20 cm soil layer was 44% (2600 vs. 1800 grams C per m^2) and 35% (260 vs. 170 grams N per m^2) greater, respectively, in *P. juliflora* species groves than in open grasslands. Soil nitrogen was also 3 - 7 times greater beneath canopies of legumes than in interspaces between them (Munzbergova & Ward, 2002; Wiegand *et al.*, 2005). Although there were significant differences both between sites and between factors in amounts of soil N in this study, soil N was highest in the *Prosopis*-free areas. This was contrary to our prediction. However, the native *Acacia* spp. are also nitrogen fixers and hence nitrogen may cease to be the most important factor in determining invasion in the ecosystem after the introduction of another species with nitrogen fixing ability. *Acacia* spp., which are part of this ecosystem, have been shown to have significant nitrogen-fixing ability in African savannas (Cramer *et al.*, 2007; Hagos & Smit, 2005; Ludwig *et al.*, 2001; Marchante *et al.*, 2008; Wilgen *et al.*, 1986). The invasion of the *P. juliflora* trees in areas that have very low levels of N and P is most likely brought about by disturbance. Disturbance, either natural or human through vegetation clearance and erosion creates an empty niche that the invader can occupy and by increasing colonization opportunities, disturbance may simply provide an opportunity from which an invasion can proceed (Mack & D'Antonio, 1998; Parker, et al., 1993). However, there was no evidence of the effect of N to any other soil element studied. Since *P. juliflora* is salt tolerant,

Vitousek and Walker (1989) studied invader impacts in sites lacking native N fixers and with low natural inputs of N, sparse native vegetation and young volcanic soils with high phosphorus contents that bind large amounts of organic material. They found that the invader species altered ecosystem-level properties significantly, especially in areas with low natural inputs of N. Based on the ecological context and the reported mechanisms, nitrogen-rich and densely vegetated systems would not be expected to show the same impacts. Indeed, studies have failed to find consistent effects of nitrogen-fixing invaders (Haubensak, 2001; Levine *et al.*, 2003; Reynolds & Haubensak, 2009; Ricciardi & Cohen, 2007), or found differing effects across sites varying in parent material (Stock *et al.*, 1995). In addition to this, eroded areas are more easily invaded (by native or exotic species) than non-eroded areas (Hobbs &

Huenneke, 1992; Pauchard & Shea, 2006; Simberloff & Von Holle, 1999) especially under more productive conditions (Huston, 2004; Huston & DeAngelis, 1994; Kondoh, 2001). In many cases of high-impact invasions, there is evidence that the 'natural' environmental conditions had been altered prior to the successful invasion. In general, such changes operate to reduce the stresses and low resource levels to which the native species have become adapted, and thus provide a competitive advantage over other species which do not have the restrictive adaptations (e.g. drought tolerance, slow growth) needed to survive the missing natural stresses (Huston, 2004).

The significant differences between factors in the amount of TOC in the soil, the highest amount being in areas with lower densities of the invading species, indicates that *P. juliflora* has had an effect on the organic carbon in the soil. The accumulation of organic carbon at low densities of the invasive species may be due to litter fall and reduced leaching under the tree canopy. The slow rate of decomposition under the canopy may play a role because of the likelihood that there may be a lower amount of soil moisture under the low density canopy. The resident herbivores could also be responsible for the higher organic carbon observed under the low densities of *Prosopis*. However, at very high densities, the dense growth of the invader may hinder the free movement of resident herbivores that includes cattle, sheep and goats. Also organic matter from other species may be unavailable as a result of stiff competition from the invading species. Higher concentration of carbon in the soils within the canopy than in soils in the adjacent open areas has been reported in other studies (Belsky *et al.*, 1989; Dregne, 1992; Kinyua, 1996; Vetaas, 1992). These studies attributed this enrichment of C and N under the canopy to organic matter accumulation and reduced leaching under the tree canopies.

The results indicate that soil P can also be affected in the same way as the organic carbon. In uncultivated soils the phosphates accumulate near the soil surface because of its cycling through vegetation and deposition in litter. Hence, the circulation that leads to increased soil organic matter content also generally leads to increase in soil organic phosphorus content. It is generally assumed that the soil organic P is derived, directly or after biochemical transformation, from leaf litter that contains P as organic compounds (Russell, 1988).

The significant differences in pH both between sites and between factors indicates that despite the underlying differences in pH, the introduced *P. juliflora* may also be having an effect that is causing a decline in pH. The observed decline in soil pH can be attributed to increased carbonic acid from CO_2 released from respiration from roots of *P. juliflora* (El-Keblawy & Al-Rawai, 2007; Garg, 1999; Singh, G., 1996). Decline in soil pH often reduces nutrient availability and lead to decreased native plant growth, particularly on nutrient-poor sites (Callaway & Aschehoug, 2000; James & Drenovsky, 2007). This may explain why *P. juliflora* is successful in replacing native vegetation in many habitats (Ansley, et al., 1997). The significant differences in electrical conductivity (EC) between sites but not between factors revealed that despite the underlying differences in EC between sites, *P. juliflora* did not have any additional effects on the soil at each site. The site effect may be as a result of the underlying differences between sites because one of the lakes (Bogoria) is saline. Salt stress affects many aspects of plant metabolism and, as a result, growth is reduced. The exposure of nodulated roots of legumes to NaCl results in a rapid decrease in plant growth associated with a short-term inhibition of both nodule growth and nitrogenase activity (Parida & Das, 2005). Mineral uptake by roots is also affected as a result of imbalance in the availability of different ions leading to plants being stressed in two ways under high salt environmental conditions: by the increase in osmotic potential of the rooting medium as a result of high solute content, and by the toxic effect of high concentration of ions (Manchanda & Garg, 2008).

3.5 Conclusion

According to our predictions, there were significant differences in soil nutrient levels between factors along the *P. juliflora* density gradient. However, the differences are not as a result of the effect of the invading species. The presence of the native *Acacia* spp. which are also nitrogen fixers play a significant role in determining the level of such important soil elements as N and P. The potential of a strong symbiotic relationship of *Acacia* spp. with the native soil microbes may act as a good deterrent to potential invaders.

CHAPTER FOUR

4.0 EFFECT OF THE INVASIVE *Prosopis juliflora* ON LOCAL PLANT SPECIES

4.1 Introduction

The majority of studies addressing plant invasions have focused on the characteristics of invasive species (Noble, 1989; Parker, 2000; Reichard & Hamilton, 1997; Vilà *et al.*, 2003), the process of invasion (D'Antonio *et al.*, 2001; Rejmanek & Richardson, 1996), the influence of disturbance on invasion success (Hickley, et al., 2004; Hobbs & Huenneke, 1992; Huston, 2004), and the attributes of invaded systems (Levine & D'Antonio, 1999; Stohlgren *et al.*, 2001). Few studies have examined the effects of invasive species across multiple habitat types or geographical regions (Alvarez & Cushman, 2002). The general pattern observed for most of these studies is that invaded communities to have reduced plant species richness compared to uninvaded communities. Thus, it is important to have comparative studies to help develop a comprehensive understanding of how invading species affects community composition in different habitat types (Alvarez & Cushman, 2002).

The *Prosopis* canopy may exert a profound influence on neighbouring vegetation, soils and subcanopy microclimate and indeed high densities of *Prosopis* spp. (>25% canopy cover) have been observed to suppress grass growth and may reduce understory species diversity (Ansley, et al., 1997).

This study aimed at determining the effects of the introduced *P. juliflora* on the species richness of native plant species between the different factors described as high, low and *Prosopis*-free areas. Different studies have found either positive or negative effects of invasive woody *Prosopis* species on associated vegetation (Archer, 1989; El-Keblawy & Al-Rawai, 2007; Herrera-Arreola, et al., 2007; Reyes-Reyes, et al., 2003). Woody plant invasion may lead to a relatively rapid conversion of grassland to woodland, resulting in a loss of understorey productivity and diversity (Archer *et al.*, 1988; Briggs *et al.*, 2005). In the United Arab Emirates, the growing of *P. juliflora* shrubs has resulted in significant reductions in both species diversity and abundance of understory species, compared to the native species and *Acacia arabica* (El-Keblawy & Al-Rawai, 2005). Studies have shown that *P. juliflora* plants could produce allelopathic substances that would inhibit the growth of associated species, (Al-Humaid & Warrag, 1998; El-Keblawy & Al-Rawai, 2007). Alternatively, woody plants may have little effect or even enhance productivity and diversity of understorey species (Schade *et al.*, 2003; Whittaker *et al.*, 1979).

This study hypothesized that there would be no significant differences in the plant species richness of indigenous plants between the factors.

4.2 Materials and Methods

4.2.1 Plant Sampling

Plant sampling was carried out within a total of 75 modified Whittaker plots that were 0.1 ha (50 m x 20 m) each. A measuring tape was stretched lengthwise across the plot to create a central axis. The centre of the plot was broken up into ten adjacent 1m^2 plots marked along one side of the central axis. Each species within the ten quadrats was noted. Then, two 1 x 5m^2 quadrats were measured on the other side of the central axis and examined for other species not already noted in the 10 small quadrats. This provided two 2m x 5m = 10m^2 plot. Only the new species were recorded. A single 10m x 10m plot (=100m^2) placed around the 10m^2 plot was searched for more new species. The rest of the 20m x 50m plot (=1000m^2) was examined thereafter for species not previously recorded at smaller spatial scales. By adding the number of species to the previous (smaller) area, this provided a cumulative species-area curve with 1m^2 (10 replicates), 10m^2 (2 replicates), 100m^2 (1 replicate) and 1000m^2 (1 replicate) (Ward, et al., 1993).Twenty five plots were laid within each of three sampling sites (Kampi ya Samaki, Endau and Loboi). Kampi ya Samaki is situated near Lake Baringo (00:36:28N, 00:36:01E) a fresh water lake, Loboi is situated next to Lake Bogoria (00:26:28N, 36:00:90E), a salt water lake, while Endau lies between the two sites (00:31:42N, 035:59:28E) (Fig. 1).

The Modified-Whittaker plot design can be used for assessing plant communities at varying scales. Plots were placed parallel to the major environmental gradient in order to encompass heterogeneity and recover greater species richness. Nested plots allow sampling of the vegetation at multiple scales, making visible the mean cumulative species richness per unit area within the different factors. Using these plots to estimate species richness is important because multi-scale plots provide far more detailed information on plant richness than single-scale plots by capturing more locally rare, native and exotic plant species (Stohlgren *et al.*, 1998).

The factors constituted high density, low density and *P. juliflora* -free plots. This categorization of sampling factors was done following what was observed to be a uniform establishment of *P. juliflora* thickets. The spread of *P. juliflora* species is known to follow periods of high rainfall (Zimmerman, 1991), possibly due to improved conditions for germination and establishment or increased seed dispersal by water. This leads to the establishment of even-aged *P. juliflora* stands. Each tree with diameter at breast height (DBH) of more than 5 cm was measured. Ten plots were laid out in an area with more than 200 *P. juliflora* trees and were considered high-density stands. Plots with more than 200 individuals had what we observed to be impenetrable thickets that may possibly hinder solar radiation as well as stifling the growth of associate vegetation. Another ten plots in a low-density area contained less than 200 individuals of *P. juliflora* species. Areas considered to be *P. juliflora*-free mostly had no trace of the tree. Five plots at each site were laid in areas that were *Prosopis*-free. Few samples were taken here because cumulatively, all the samples were sufficient to do the soils analysis, and it was statistically acceptable.

In each plot, all plants (annual and perennial) were sampled and identified. Plants that could not be identified immediately were taken to Jomo Kenyatta Univerity of Agriculture and Technology GK laboratory for detailed identification. The number of *P. juliflora* trees and *Acacia* spp. were also counted in each plot (appendix four). Mean species richness was calculated as the mean number of species in the Whittaker plots within the same *P. juliflora* density class.

The mean species richness between high, low density *P. juliflora* stands and *P. juliflora*-free areas and mean species richness along each of the sites' factors was analysed. The correlation between the densities of native *Acacia* and the introduced *P. juliflora* was also assessed. This is because the *Acacia* species are the dominant woody species in this area, and they are also in the same family as the invading species.

4.3 Results

The highest mean species richness from all the three sites was obtained in the areas with low *P. juliflora* density (Fig 4.1). The mean species richness in areas with high density of *Prosopis* was 69.3 while areas with low density of *Prosopis* had a mean species richness of 93.7. *Prosopis*-free areas had a mean species richness of 47.3. Data from Kampi ya Samaki (next to the fresh water Lake Baringo) revealed higher species richness in the area that was *Prosopis*-free. This site also had the highest overall species richness of 156 species. Loboi (adjacent to the saline Lake Bogoria) had lowest species richness in factors that were *Prosopis*-free. The factors with the high density of *P. juliflora* had the highest species richness of indigenous species. Loboi also had the lowest species richness of the three sites with a species richness of 92 species. Endau lies between the previous two showed species richness being highest in areas with low *P. juliflora* density and lowest in areas with high *P. juliflora* density (Fig 4.2).

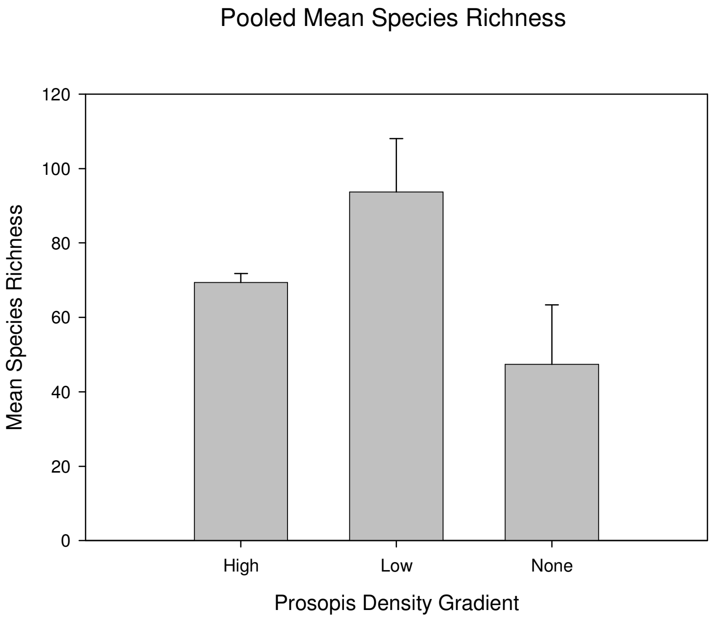

Figure 4.1: The mean species richness between different *P. juliflora* density factors for the three sampling sites

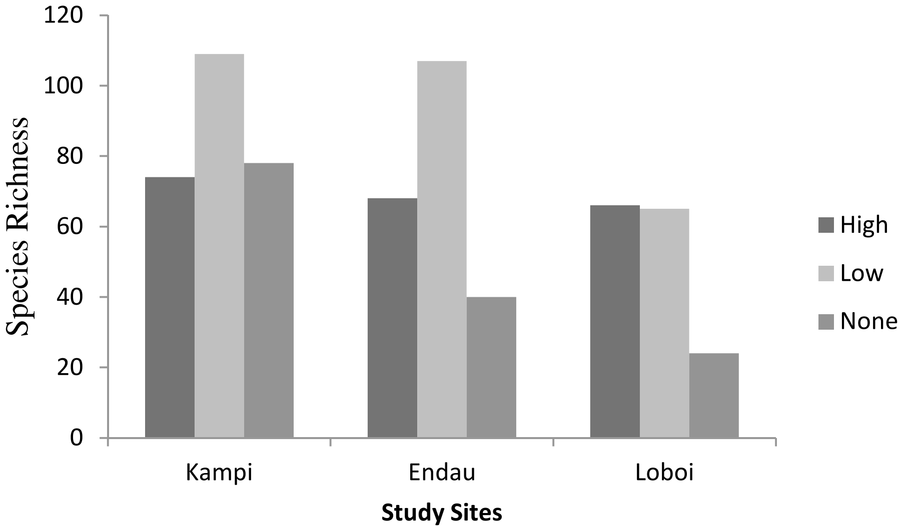

Figure 4.2: Comparison of species richness between the study sites

There was a negative correlation between the density of *Acacia* spp. and *P. juliflora*. (r^2=-0.409) (Fig 4.3).

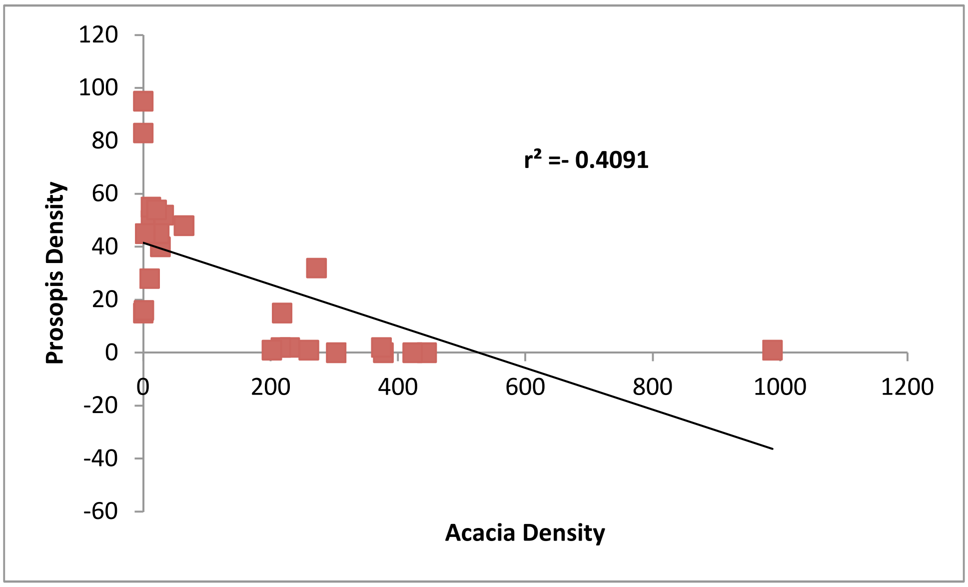

Figure 4.3: The correlation between *Acacia* spp. and *Prosopis* sp. density in the three sampling sites.

4.4 Discussion

As predicted, when all the three sites were analysed together, there was lower mean indigenous species richness in plots containing high *P. juliflora* densities and those that were *Prosopis*-free meaning that the invasive tree has an effect on indigenous species richness. Some site-specific uniqueness was revealed when each site was analyzed separately. Loboi, which was the site that was next to the saltwater lake revealed the opposite relationship where the highest indigenous species richness was in the areas with the highest density of the invasive species (Fig 4.2). It would however be important to note that, overall, Loboi had the lowest native species richness.

Elsewhere, high densities of *P. juliflora* species have been observed to suppress grass growth and reduce understory species diversity (Brown & Archer, 1989). Studies have shown that understory species production increases following control of *P. juliflora* (Bedunah & Sosebee, 1984; Dahl, et al., 1978).

This study revealed a negative correlation between *P. juliflora* and *Acacia* densities in the study sites. *Acacia* species are also nitrogen fixers and their existence in this area long before the arrival of the invasive. A strong negative correlation in density between the introduced species and the indigenous *Acacia* species may either indicate that *P. juliflora* is slowly replacing the indigenous *Acacia* species, or that the established stands of *Acacia* in non-disturbed conditions are a good deterrent to the encroaching *P. juliflora.* The latter is more likely because the indigenous *Acacia* species also have nitrogen-fixing ability, and at higher established densities, they may have a competitive superiority to an incoming invader because they have long been established here. A study carried out in a semi-arid savanna of southern Africa established that the contribution of N-fixation to the N budget decreased with increasing N supply and this effect was more pronounced on tree seedlings when there was decreased competition from grasses (Kambatuku *et al.*, 2013). Dommergues (1995) also reported a similar inhibition of nitrogen-fixation by available N.

Studies carried out on other nitrogen-fixing species in an arid savannas in Namibia (Wiegand, et al., 2005) have shown that the transformation from bush-encroached area into a mature *Acacia* stand and eventually into an open savanna again appeared to be dependent upon the plant-soil interactions as well as rainfall events affecting *Acacia* germination and establishment. In another study in a desert ecosystem, Munzbergova and Ward (2002) showed a combination of positive and negative effects of *Acacia* trees on other forms of vegetation, as a result of a combination of higher soil nutrients and high soil salinity, the last-mentioned of which may act negatively to recruiting plants. The effects of tree canopies on nutrient availability may be confounded by indirect interactions with animals because trees provide perches for birds and shady habitat for ungulates (Dean *et al.*, 1999). Animals that are attracted to trees often spend disproportionally large amounts of time near them and defecate there more often than in open environments, transporting nutrients from the surrounding open, treeless areas to understory habitats (McNaughton, 1983).

Minimal increase in nitrogen from nitrogen fixers such as *P. juliflora* may fail to mitigate against the loss of species and soil fertility, especially after severe disturbance events. A disturbed, nutrient-poor area with no vegetation may provide fertile ground for the invasion of *P. juliflora*. This is because *P. juliflora* may get established easily in disturbed areas. There is a need for more research that would attempt to manipulate densities of the different species and observe the resultant changes in soil quality and species richness and diversity.

The low herbaceous plant species richness observed under high densities of *P. juliflora* could be attributed to the canopy geometry, which influences the intensity and duration of light received by the understorey plant species. Frost and Edinger (1991) noted that the shading effect of the evergreen woody species, such as *P. juliflora,* might limit herbage production under their canopies. Weltzin and Coughenour (1990) observed that shading by tree canopies might be the most important factor affecting understorey herbage production and composition in African savanna. Pieper (1990) argued that apart from reduced light intensity at higher canopy densities, competitive interactions for water and nutrients between trees and herbaceous plant species, could partly account for the low biomass production.

The observation by Nakano *et al.* (2001) that *P. juliflora* is alellopathic in nature may also partly explain the relatively species richness of herbaceous plant species obtained in factors with high density of *P. juliflora*. Phytotoxic effects of leaves, shading and competition for soil moisture are some factors that might also have contributed to the low species richness under the highest density of *P. juliflora*. Other studies have also observed that the understorey plant species composition is generally different from that of the area immediately outside the canopy of trees in savanna habitats (Kinyamario *et al.*, 1995; Munzbergova & Ward, 2002) They attribute the differences to changes in shade density, water stress, and grazing tolerance among the herbaceous species.

4.5 Conclusion

This study revealed that *P. juliflora* plants pose significant negative impacts to other species at the community level. Hence, the hypothesis that there would be no significant differences in the plant species richness of indigenous plants along the *P. juliflora* density factors was rejected. The study revealed that the magnitude of the impacts of the invasive species is very variable and even the direction of the ecological impact is context-dependent. The presence of *P. juliflora* in this ecosystem can only be useful to the diversity of other species if it can only be managed at low densities and the presence of the undisturbed stands of native *Acacia* spp. acts as a buffer against the invasive species.

CHAPTER FIVE

5.0 THE EFFECT OF *Prosopis juliflora* ON THE DIVERSITY OF POLLINATORS OF INDIGENOUS *Acacia* SPECIES

5.1 Introduction

The invasion of ecosystems by non-indigenous species is one of the greatest threats to biodiversity and community structure (Gurevitch & Padilla, 2004; Vitousek, et al., 1997). As invasive species integrate into recipient communities, the number and type of species interactions are predicted to increase (Pearson & Callaway, 2003; Vermeij, 1996). Exotic invasions are particularly likely in habitats disturbed by human activities (Burke & Grime, 1996). Several studies show that alien invasions reduce the local diversity of plant communities (Levine, et al., 2003; Meiners *et al.*, 2002). Invasive species often produce highly nutritive nectar and/or pollen and are highly attractive to pollinators (Brown *et al.*, 2002; Grabas & Laverty, 1999).

Studies on mechanisms leading to reduced diversity after invasion by alien species have focused primarily on how the aliens competitively displace native species through direct competition for abiotic resources (Keane & Crawley, 2002; Levine, et al., 2003). However, exotic species may affect native species indirectly in several ways, including how natives interact with mutualist partners, an interaction that has large consequences for the ecology and evolution of plant species (Ashman *et al.*, 2004). Invasive species rely on mutualisms in their new habitats to overcome barriers that may hinder their establishment. Mutualisms involving pollination often facilitate invasions and indeed the spread of many alien plants, particularly woody ones (Richardson *et al.*, 2000).

Ecosystem services are functions provided by nature that improve and sustain human wellbeing (Kremen *et al.*, 2007). A key ecosystem service that has the potential to be interrupted by the arrival of novel species is pollination and therefore large-scale parallel declines of plants and pollinators reinforce the concern that pollination as an important ecosystem service is at risk (Potts *et al.*, 2010). Pollinators and their host plants form keystone mutualisms making them essential to maintaining the biodiversity and hence the integrity and sustainability of most terrestrial ecosystems (Holden, 2006; Kearns & Inouye, 1997; Kearns *et al.*, 1998; LaSalle & Gauld, 1993; Losey & Vaughan, 2006). Insufficient pollination can have serious implications for the population dynamics of plant species (Holden, 2006; Losey & Vaughan, 2006; Nabhan & Buchmann, 1997). In fact, some rare and endangered plant species rely solely on pollinators, especially bees, for their continued reproductive success (Buchmann & Nabhan, 1996; Cunningham, 2000; Gabriel & Tscharntke, 2007; Ingram *et al.*, 1996; Kevan & Viana, 2003; Klein *et al.*, 2007; Pauw & Hawkins, 2011; Winfree *et al.*, 2009).

Plant–pollinator interactions are essential for ecosystem species diversity and composition because they ensure that plant reproduction and long-term maintenance of genetic diversity of plant populations is upheld. This results in novel combinations of traits that may contribute to species survival (Kearns, et al., 1998). Invasive species are likely to interfere with pollination of native species by attracting pollinators away from the native species, and/or by lowering reproductive output due to increasing the likelihood of the deposition of foreign pollen on the stigmas of the native flowers species (Brown & Mitchell, 2001; Kaiser-Bunbury & Müller, 2009;

Memmott & Waser, 2002). On the other hand, invasive species might enhance pollination by attracting larger numbers of pollinators into the area. Bees are arguably the most important pollinator group and threats to wild bees have been more widely studied than impacts on other pollinator taxa (Brown & Paxton, 2009; Kenis *et al.*, 2009).

Many invasive alien plants are visited by native pollinators and are mostly pollinated by them (Chittka & Schürkens, 2001; Huryn & Moller, 1995; Mitchell *et al.*, 2009; Moragues & Traveset, 2005; Morales & Traveset, 2009; Parker, 1997; Potts, et al., 2010; Pyšek *et al.*, 2011; Richardson, et al., 2000; Roulston & Goodell, 2011; Schweiger *et al.*, 2010; Stout & Morales, 2009). These plants are attractive to native pollinators for many reasons: some produce a massive floral display, have prolific nectar production, and often appear at high density or dominate the flower community in invaded sites (Bjerknes, et al., 2007; Ghazoul, 2002). In addition, many invasive alien plants fill a phenological gap of flower resources for pollinators, extending their foraging season. As a result, invasive alien plants have the potential to impact not only on individual foraging behaviour, but also on colony success of social species, population size and distribution of native pollinators, community structure and entire plant-pollinator networks (Aizen, et al., 2008). In addition, by affecting the native plant communities, invasive alien plants are likely to have indirect effects on native pollinator communities.

Prosopis juliflora flowers throughout the year (Andersson, 2005). Bjerknes *et al.* (2007) proposed that aliens with similar floral morphologies as the natives, and/or that are more attractive than the natives, have a competitive advantage in pollinator attraction. Corolla colour is one of the most important floral traits used by pollinators to discriminate among flowers (Menzel & Shmida, 1993; Neal *et al.*, 1998).

There is a general lack of knowledge as to the extent at which alien invasions affect population density of pollinator species, and about how alien invasions affect composition of pollinator communities at different spatial and temporal scales (Bjerknes, et al., 2007). Relatively little information exists on the status of pollinators or of pollination function (Kremen, et al., 2007). Understanding the balance between competition and facilitation in pollination dynamics is relevant to the conservation of plant–pollinator communities (Ghazoul, 2006). The genus *Acacia* is an important component of woody vegetation in the arid and semiarid parts of Africa (Sharma *et al.*, 1996). *Acacia* spp. commonly grow in mixed-species assemblages and several species flower together in space and time after seasonal rainfall (Ross, 1981). *Acacia* spp. have also shown highly synchronized anther dehiscence and daily peaks of pollen release (Stone *et al.*, 1998).

The effects of invasive plant species on pollinator faunas and on pollination of native *Acacia* spp. was studied by comparing insect visitation between them and the invasive *P. juliflora.* The hypothesis was that if *P. juliflora* is reducing the number of pollinators from the indigenous *Acacia* spp. (*Acacia tortilis, A. mellifera, A. etbaica* and *A. elatior*), then it was expected that there would be a higher diversity of floral visitors to the invasive species than to the indigenous *Acacia* spp. and also that the invasive *P. juliflora* will be highly dependent on the pollinators for reproduction. It was predicted that the negative effect of *Prosopis* sp. would cause a significantly higher diversity of floral visitors within *Prosopis* sp. stands than in the native *Acacia* spp. stands.

5.2 Materials and Methods

5.2.1 Study area

The study was conducted in Marigat (0° 28' 0" North, 35° 59' 0" East), in Baringo District south of Lake Baringo which is located at 50 km north of the equator (appendix one). The altitude of the study area ranges between 900 and 1200 m a.s.l. The climate is semi-arid (Owen, et al., 2004) and the average minimum and maximum temperatures are 20 °C and 30 °C respectively. The area has highly variable rainfall with a coefficient of variation of 36% (Rowntree, 1989) and a mean annual rainfall of 635 mm (Kassilly, 2002) accompanied by flash floods, erosion and potential evapotranspiration of over 2000 mm a^{-1} (Wijdenes & Bryan, 2001). The rainy season occurs from April to July while the peak dry season commences in November and ends in February of every year (Mala, et al., 2011).

5.2.2 Diversity of Floral Visitors

Two locations containing separate clusters of both *Acacia* species and *Prosopis juliflora* species were selected. The dominant *Acacia* species include *Acacia tortilis, A. mellifera, A. etbaica* and *A. elatior.* A 100 m^2 plot, on each location was permanently marked with wooden sticks and data collected at the same time during this survey, following the method by Kremen *et al.* (2004).

Observation of pollinators and floral visitors' diversity was carried out during seasons of overlapping flowering from 8.30 am to 4.30 pm daily both in September 2010 and June-July 2011. June-July 2011 was relatively wetter than September 2010 in Baringo County (pers. obs.). Floral visitors in the sampling plots were observed and captured under similar weather conditions per day as described by Gikungu (2006) for a period of two weeks in each year. All floral visitors on either plot (*Prosopis* sp. and *Acacia* spp.) were observed, recorded and captured using sweep nets. They were caught and put in killing jars containing ethyl acetate to inactivate or kill them. The collected floral visitors were pinned in boxes for preservation and identification.

Special attention was paid to discriminate between pollinators and ineffective floral visitor on both *Prosopis* and *Acacia* stands. Insects that were evidently carrying pollen and making contacts with the anthers and stigma were recorded as pollinators while all the others were recorded as floral visitors (Dafni, 1992; Fausto Jr *et al.*, 2001; Njoroge, 2005).

5.3 Results

The species diversity of floral visitors was much higher in the *Acacia* plot than in the *Prosopis* plot (Table 5.2). Evenness was however higher in *P. juliflora* than in the *Acacia* plot (Table 5.2).

In September 2010, only species in the order Hymenoptera were observed on both the flowers of *P. juliflora* and *Acacia* (Table 5.1). All were observed to be actively gathering pollen from the flowers. Only members of the species *Apis mellifera* were observed on flowers of *P. juliflora* (Table 5.1). The abundance (number of individual floral visitors) of this species was also much higher in the *P. juliflora* plot than in the *Acacia* plot. Species in the genus *Megachille, Lipotriches, Macrogalea, Amegilla,* and *Ceratina* were observed to be the only visitors of the *Acacia* spp. in September 2010 (Table 5.1).

When the experiment was repeated the following year (June-July 2011), abundance was higher than in September 2010 in both plots, but notably, there was a higher species diversity, species richness, and total abundance in the *Acacia* plot than in the *Prosopis* plot. *Bembix* sp., *Pinacopteryx eriphia* and *Megachile gratiosa* were found to be the only visitors of *P. juliflora* in June-July 2011 while species observed in the two tree species included*, Megachile discolor, Pseudapis* sp., *Lipotriches* sp., *Ceratina* sp. and a species from the family Syrphidae. At the same time, species that were observed only in the *Acacia* spp. included *Coryna sp., Mylothris sp., Hemipyrelia sp., Rhabdotis sobrina, Appias sp., Colotis eris., Eurema sp., Catopsilia florella., Zizeeria knysna.,* and *Lipotriches sp.* and species in the families Pentatomidae, Vespidae, and Zygaeidae.

Species found only in the *Acacia* but in both seasons included, *Macrogaela candida*., *Amegilla* sp., and *Ceratina* sp. Only the species *Apis mellifera* was observed on flowers of both the tree species across the two seasons.

Table 5.1: Diversity and abundance of *P. juliflora* and *Acacia* spp. floral visitors observed in June-July 2011 and September 2010.

Order	**Family**	**Species**		**June-July 2011**		**September 2010**	
				Acacia	*Prosopis*	*Acacia*	*Prosopis*
Coleoptera	Meloidae	*Coryna sp.*		3	0	0	0
Coleoptera	Scarabaeidae	*Rhabdotis*	*sobrina*	2	0	0	0
Diptera	Calliphoridae	*Hemipyrelia sp*		2	0	0	0
Diptera	Syrphidae			1	2	0	0
Hemiptera	Pentatomidae			1	0	0	0
Hymenoptera	Apidae	*Amegilla sp*		1	0	1	0
Hymenoptera	Apidae	*Apis*	*mellifera*	32	2	70	144
Hymenoptera	Apidae	*Ceratina sp*		2	2	1	0
Hymenoptera	Apidae	*Macrogalea*	*candida*	1	0	3	0
Hymenoptera	Apidae	*Xylocopa sp*		1	0	0	0
Hymenoptera	Halictidae	*Lipotriches sp.*	(a)	17	0	4	0
Hymenoptera	Halictidae	*Lipotriches sp.*	(b)	2	1	0	0
Hymenoptera	Halictidae	*Pseudapis sp.*	(a)	1	1	0	0
Hymenoptera	Halictidae	*Pseudapis sp.*	(b)	1	1	0	0
Hymenoptera	Megachilidae	*Coelioxys sp.*		1	0	0	0
Hymenoptera	Megachilidae	*Megachile*	*discolor*	6	4	0	0
Hymenoptera	Megachilidae	*Megachile sp.*		6	5	3	0
Hymenoptera	Megachilidae	*Megachile*	*gratiosa*	0	5	0	0
Hymenoptera	Sphecidae	*Bembix sp.*		0	1	0	0
Hymenoptera	Vespidae(a)			2	0	0	0
Hymenoptera	Vespidae(b)			2	0	0	0
Lepidoptera	Lycaenidae	*Zizeeria*	*knysna*	2	0	0	0
Lepidoptera	Pieridae	*Appias sp.*		1	0	0	0
Lepidoptera	Pieridae	*Belenois*	*aurota*	1	0	0	0
Lepidoptera	Pieridae	*Catopsilia*	*florella*	1	0	0	0
Lepidoptera	Pieridae	*Colotis*	*eris*	3	0	0	0
Lepidoptera	Pieridae	*Eurema sp.*		1	0	0	0
Lepidoptera	Pieridae	*Mylothris sp.*		1	0	0	0
Lepidoptera	Pieridae	*Pinacopteryx*	*eriphia*	0	1	0	0
Lepidoptera	Zygaeidae			1	0	0	0

Table 5. 2: Diversity measures of floral visitors between *P. juliflora* and *Acacia* spp. in 2011

	Acacia	***Prosopis***
Shannon-Wiener Diversity	2.60	2.19
Species Richness	27	11
Total Abundance	94	25
Evenness	0.79	0.91

Table 5. 3: Diversity measures of floral visitors in 2010

	Acacia	***Prosopis***
Shannon-Wiener Diversity	0.7	0.00
Species Richness	7	1
Total Abundance	83	144
Evenness	0.35	N/A

5.4 Discussion

The results indicate that in September 2010, which is usually a relatively drier month than June and July in this area (Rowntree, 1989), there was a higher diversity of pollinators on *Acacia* species (Table 5.2 and 5.3)than in *Prosopis* species. However, of *Apis mellifera* was more abundant in the *P. juliflora* stand. Hymenoptera, especially *A. mellifera,* are arguably the most important pollinator group (Murray *et al.*, 2009). Percentage pollination in *P. juliflora* is always low, due to poor pollen viability, short periods of pollen release or stigma receptivity, lack of synchronisation between pollen release and pollen reception, few pollinating insects or too few at times of maximum receptivity, flower sterility or high rates of ovary abortion(Pasiecznik, et al., 2001). Goel and Behl (1996) found *P. juliflora* pollen viability to be 79-96%, but maximum pollen production occurred at midday, and insects are less mobile during the high temperatures found at this time.

When the same study was repeated the following year at the onset of a wetter season (June-July 2011), the species richness, species diversity and total abundance were still higher in the *Acacia* species stand (Table 5.2). It was therefore clear that despite the potential of the invasive species to act as refuge for important native pollinators species during periods of drought, it was not evident that the pollinators were distracted from the *Acacia* species at the onset of a relatively wetter season. These results agree with the analysis of long-term data from Illinois, (1895-1916) by Memmott and Waser (2002) who found significantly more flower visitor species associated with native plants than with invasives. Memmott and Waser (2002) and later Tepedino *et al.* (2008) concluded that most of the insects that visit the flowers of abundant invasives are generalists. The open, accessible structure of *Acacia* flower heads makes them accessible to a wide variety of visitors.

The visit by a solitary wasp, *Bembix* sp., (Sphecidae) and *Pinacopteryx eriphia* (Lepidoptera) exclusively on *P. juliflora* in during the June-July 2011 period may have been coincidental. *Bembix* sp. thrives in habitats that are moderately disturbed (Bonte, 2005). *P. eriphia* recorded here, has been used as an indicator species for savannas (Larsen, 1994). Solitary bees have been known to be important pollinators of *Acacia* especially the Megachilidae, Colletidae and Halictidae families. In Kenya, important solitary genera include *Xylocopa, Amegilla* and *Megachile*. *Bembix* sp. has especially been known to visit the Acacia flowers probably in search of insect prey, such as the caterpillars of butterflies (Stone *et al.*, 2003). However, the presence also of *Megachile gratiosa* exclusively on *P. juliflora* is significant. This is because *Megachile* is a group of solitary bees that are also found on *Acacia* flowers (Tybirk, 1993). The foraging behaviour of some megachilid solitary bees, particularly *Megachile* species indicate that they may be specialist pollinators of mimosoids with densely packed flower heads such as *Acacia* or *Prosopis* species (Stone, et al., 2003). Our data does not fully explain the presence of this bee exclusively on *Prosopis* and more studies needs to be done to find out why this was the case. Species that were observed exclusively on *Acacia* spp. were mainly beetles, butterflies and flies in the genera *Hemipyrelia* (Diptera), *Coryna and Rhabdotis* (Coleoptera), *Mylothris, Appias, Colotis, Eurema, Catopsilia, and Zizeeria* (Lepidoptera). These family groups have earlier been found on different species of

Acacia elsewhere in Africa (Krüger & MCgavin, 1997), and hence this find was not unique.

The study has revealed that a more rich or diverse pollinator assemblage during wetter weather conditions might lead to a greater availability of pollinators. Thus, our results contribute to a growing literature showing that the presence of an alien invasive species may not always have a significant negative influence on pollinator visitation (Memmott & Waser, 2002). A study conducted in Acadia National Park in Maine found that the invasive Japanese barberry (*Berberis thunbergii*) and glossy buckthorn (*Frangula alnus*) may benefit native co-flowering lowbush blueberry (*Vaccinium angustifolium*) and wild raisin (*Viburnum nudum*), respectively, by attracting more pollinators to them. This same study indicated the invasive plants may benefit native bee populations by providing them with additional food resources (Pisanty & Mandelik, 2011). Another study in the Chilean Andes of invasive dandelion (*Taraxacum officinale*) and native *Hypochaeris thrincioides* and *Perezia carthamoides* had mixed results - at low densities the presence of the invasive had either neutral or positive effects on pollinator services available for native species. At higher densities the presence of the invasive negatively affected pollinator service of the native plants (Muñoz & Cavieres, 2008). Another study in Mediterranean Spain also had mixed results when examining two invasive plants, balsam (*Carpobrotus affine acinaciformis*) and erect prickly pear (*Opuntia stricta*). The balsam facilitated the visits of pollinators to native species in the same community, while the erect prickly pear competed with native species for pollinators (Bartomeus, et al., 2008).

Alien species may not show a direct potential to take away pollinators from the native *Acacia* species, however an indirect threat on the pollinators may occur as a result of the invasive species having the potential to actively replace the indigenous species. This study has documented a plant species that serves as alternative floral resources for bees during a drier season. When both *Acacia* and *Prosopis* were flowering, *Acacia* species registered a higher abundance and diversity of pollinators compared with *Prosopis* during this study. *P. juliflora* is a mass flowering plant that flowers throughout the year (Masilamani & Vadivelu, 1997). Knock-on effects of changes in plant community composition could have dramatic implications for native pollinators, particularly specialist species which are not able to utilize the invasive alien plant because of temporal, morphological or nutritional restrictions. For them, loss of their native host plants (assuming this occurs due to alien plant invasion) may severely reduce their fitness. A negative feedback would then operate whereby the decline of these specialist pollinator species may result in pollination limitation of the specialised native plants they pollinate (Waser *et al.*, 1996). Generalist native pollinators such as *Apis mellifera* that are able to utilize the resources of invasive alien plants may support native alien communities (Memmott & Waser, 2002) and promote further invasion of the alien plant species (Stout, 2007).

This potential of the invasive species serving as an alternative resource during the dry season may be of significance to the communities living in Baringo where honey has become an alternative source of livelihood for a number of residents. (Mwangi & Swallow, 2005).

5.5 Conclusion

The results supported the predictions that there would be significant differences in the floral visitors diversity between the invasive *Prosopis juliflora* and the native *Acacia* spp. This study established that the presence of the invasive *P. juliflora* is a threat to the pollinators of the indigenous *Acacia* spp during the dry season. However, this study also established that the invasive species is a good refuge for important pollinators during the relatively dry seasons.

CHAPTER FIVE

6.0 GENETIC DIVERSITY OF *Prosopis juliflora* IN KENYA, AND THE ROLE OF MULTIPLE INTRODUCTIONS

6.1 Introduction

Genetic diversity studies and the potential for rapid evolution of invasive species may provide useful insights into what causes species to become invasive (Sax *et al.*, 2007). Information about the genetics and evolution of invasive species or native species in invaded communities, as well as their interactions, can then lead to predictions of the relative susceptibility of ecosystems to invasion, and predictions of the subsequent effects of removal (Dlugosch & Parker, 2008). Among the factors that have been identified to cause invasions, such as the adaptations for dispersal and the competitive ability of the species, the character of invaded habitats and communities, the presence or absence of predators and pathogens, the success of invasive taxa may also depend on the genetic variability of introduced populations (Sakai, et al., 2001).

High genetic variability in non-native species is advantageous while invading new areas, because in sexual species it allows more rapid evolution and adaptation to changing environmental conditions (Lambrinos, 2001; Sakai, et al., 2001). Many studies have examined genetic diversity as a factor that affects non-native species in their introduced range (Novak & Mack, 2001; Sax, et al., 2007; Vitousek, et al., 1997; Waloff & Richards, 1977). Theory predicts that plants in their introduced range will have diminished within-population genetic variation and increased among-population genetic differentiation relative to their native range (Barrett &

Richardson, 1986; Husband & Barrett, 1991) because founder effects and genetic drift tend to reduce heterozygosity and lead to interpopulation differentiation when introduced population sizes are small. However, colonizations that stem from multiple introductions or involve large founding populations may not exhibit large reductions in genetic variation (Dlugosch & Parker, 2008). Separate introductions from multiple parts of the native range may result in intermingling of genotypes that increase sampled genetic diversity (Novak & Mack, 1993).

In plants, individuals that are geographically close tend to be genetically more similar than individuals that are far apart. This limited dispersal has important consequences on the spatial distribution of genetic variation. If dispersal distances are small, a pattern of spatial autocorrelation emerges in the distribution of genetic variation: individuals that are close to each other are likely to be more related, and therefore genetically more similar, than individuals that are farther apart. Therefore, within populations, and by extension, at larger geographic scales, a positive relationship is expected between relatedness and geographic distance (Meirmans, 2012).

Many studies have compared molecular genetic diversity of invaders to that of either conspecifics in the native range or related noninvasive species. Reviews of this work (Barrett *et al.*, 1990; Bossdorf *et al.*, 2005; Gray *et al.*, 1986; Lambrinos, 2004; Lee, 2002; Marshall & Brown, 1981; Merilä & Crnokrak, 2001; Novak & Mack, 2005) have highlighted the variety of outcomes observed. Many invasive species exhibit reduced genetic variation in their introduced ranges, while many others maintain a high genetic variation. For instance *Clidemia hirta* (DeWalt *et al.*, 2004), and *Epipactis helleborine* (Squirrell *et al.*, 2001), revealed increased genetic diversity as a result of multiple introductions, (Bossdorf, et al., 2005) while species such as *Alliaria petiolata* (Durka *et al.*, 2005), *Bromus tectorum* (Novak & Mack, 1993) revealed a decreased genetic variation.

Although many studies have examined the potential determinants of invasibility, few have simultaneously investigated the relative importance of multiple invasion mechanisms (Holle & Simberloff, 2005).

Multiple introductions seem to be common in invasions (Bossdorf, et al., 2005; Ellstrand & Schierenbeck, 2000; Novak & Mack, 2005) and they can bring together unusually large amounts of variation and novel genetic combinations. This leads to the hypothesis that many invasions might be successful as a direct result of influxes of genetic variation from multiple introduction events (Allendorf & Lundquist, 2003; Bossdorf, et al., 2005; Dlugosch & Parker, 2008; Ellstrand & Schierenbeck, 2000; Facon *et al.*, 2006; Frankham, 2005; Genton *et al.*, 2005; Lockwood *et al.*, 2005; Novak & Mack, 2005). However a general association between multiple introductions and variation in invasions has never been quantified. The idea that increased genetic diversity contributes to invasion success presupposes that evolution enhances invasions, and that bottlenecks during invasion limit the adaptive evolution of fitness-related traits. Genetic variation and evolution might play an important role in the success of invading species. A growing number of studies show that putatively adaptive traits have evolved in introduced populations (e.g. (Blair & Wolfe, 2004; Bossdorf, et al., 2005; Huey *et al.*, 2000; Stockwell *et al.*, 1996), and sometimes quite rapidly (e.g. (Daehler & Strong, 1997; Reznick & Ghalambor, 2001; Thompson, 1998).

The analysis of genetic variation in introduced populations has been done with DNA markers or allozymes (Schaal *et al.*, 1991). Molecular markers are important tools for studying plant invasions because they provide information about invasion pathways and the amount of genetic variation introduced (Barrett, et al., 1990; Marshall & Brown, 1981). Allozymes, random amplified polymorphic DNA (RAPD), Restricted Fragment Length Polymorphisms (RFLP), Amplified Fragment Length Polymorphism (AFLP), and microsatellite markers have been widely used to study genetic variability in populations (Kalia *et al.*, 2011). Single nucleotide polymorphisms (SNPs) have recently also become popular in the study of genetic variation because of their high potential for automated analysis (Sehgal *et al.*, 2008).

Allozymes, RAPD, RFLP, AFLP, SNPs and microsatellites all have advantages and limitations. Microsatellites can generate a relationship of more accurate clustering than the other methods when the evolutionary relationships of closely related populations are examined. However, they are quite expensive (Karp, 1997). The RAPD method is simple but has low reproducibility (Zhang *et al.*, 2002). Allozyme analysis is a classical assay used in the study of population variability and although they are rarely used today due to their limitation in the number of informative loci (Schlötterer, 2004), they have a higher capacity for reproducibility than RAPDs (Zhang, et al., 2002). Gel electrophoresis of proteins coupled with histochemical visualization of locus-specific allozymes offers a relatively cheap, fast method of analyzing single locus variability too (Zhang *et al.*, 2007). RAPD markers are ‘anonymous’ DNA fragments amplified using single short primers, generally 10 bases long, of ‘arbitrary’ (also termed ‘random’ or non-specific) sequence. Individual primers operate in both forward and reverse directions, thus amplifying between inverted repeats of the binding sequence, if repeats are close to each other. A single primer is usually able to amplify simultaneously fragments from around 5 to 20 sites in the genome. Although there have been only a few studies comparing the markers directly, most qualitative comparisons have shown that RAPDs and allozymes are not so different in how they reveal patterns of genetic diversity (Aagaard *et al.*, 1998; Liu & Furnier, 1993; Peakall *et al.*, 1995; Zhang, et al., 2007). Molecular markers are important tools in the context of biological invasions because they provide information about pathways of introduction and the amount of genetic variation introduced (Kalia, et al., 2011; Sakai, et al., 2001; Shore, 1989).

In this study, genetic diversity was analysed using allozymes in four Kenyan populations in order to reveal the genetic distances between them and reveal whether the studied rate of reproductive effort and invasion in Kenya is related to either geographical distances or introduction events. We predicted that the genetic distances will be correlated with geographic distances between different parts of Kenya. However, since it is less than 40 years from the time of introduction (Jama & Zeila, 2005), it is predicted that adaptive evolution of distinct populations would not have occurred.

6.2 Materials and Methods

6.2.1 Sampling of populations

To estimate differentiation among *P. juliflora* populations, four populations were sampled: Garrisa, Bura, Loboi in Bogoria, and Endau near Lake Baringo. The four populations were selected because they are among the sites where *P. juliflora* was introduced in Kenya. They are also among the sites where the invasive species is spreading fast. Two of the sites in Baringo are separated by a distance of 30 kilometers while Garissa and Bura are separated by a distance of 100 kilometers. These two regional populations are separated by a distance of more than 500 kilometers which would offer a geographical barrier, and hence in line with our hypothesis, we would expect a positive correlation between the genetic and geographical distances (appendix one). Fifteen maternal parent trees were randomly sampled in each population (appendices two and three). We selected trees with adequate seed crop and the different target trees had to be separated from each other by at least 50 m (Saidman *et al.*, 1993). At least 20 seedlings from each tree were soaked in petri dishes for 24 hours and the cotyledons obtained used for protein extraction. Horizontal cellulose acetate electrophoresis was used for the genetic analyses as described in (Hebert & Beaton, 1993). Stuber's extraction buffer (Stuber *et al.*, 1988) was used to extract the proteins where the tissue was crushed in 0.5 ml of grinding buffer using pestle and mortar. The extracts were centrifuged at 15,000 rpm (21924g) for two minutes. The supernatant was absorbed onto double-thickness filter paper wicks and immediately subjected to horizontal starch gel electrophoresis.

6.2.2 Allozyme Electrophoresis

Three buffer systems were used for the electrodes and the gels: Poulic (Selander *et al.*, 1971), Ridgeway (Ridgeway *et al.*, 1970) and Tris-Citrate 7.5 (Soltis *et al.*, 1983). The gel was covered with a polythene sheet to prevent desiccation during electrophoresis, which was carried out at 4^{o}C for 8 hours at a constant current of 50 mA and voltage of 250 V. The electrophoresis was stopped when the bromophenol blue marker had migrated to the edge of the gel. Most of the enzymes did not show sufficient activity for routine screening and therefore only seven of them were included for the analyses: AAT, EST, GDH, GPI, IDH, MDH and PER. Eleven enzyme loci were finally selected for further analyses because they showed clear movement of the proteins on the gels.

6.2.3 Data Analysis

Enzymes with more than one band were considered to be polymorphic. Each monomeric band was scored either as (1,1), for homozygotes, (1,0) for heterozygotes or left blank if it was not clear what was on the band. Allellic frequency was determined by counting the total number of times the allele was present in the sample and divide by the number of alleles in the sample (Bessega *et al.*, 2005; Saidman & Biológicas, 1990). The mean over all loci which was a function of the proportion of polymorphic loci, the number of alleles per locus, and the evenness of allele frequencies, was thus a measure of the genetic information in the populations. In order to assure reliability of data matrix, photo interpretations were made by two different members of the laboratory. Allelic frequencies from allozyme markers were used to estimate Nei's (1978) genetic identities, mean heterozygosity (Nei, 1978), using the program TFPGA (Miller, 1997). Analysis of Molecular Variance (AMOVA) was also done in GenAlEx program (Peakall & Smouse, 2006). Nei's (1972) original genetic distance matrices (GDM) were estimated from allelic frequencies of the allozyme data. The correlation between genetic and geographical distances was tested through a (Mantel, 1967) test. Cluster analysis was carried out with the genetic distances matrix of the populations using PHYLIP's Neighbor-Joining method (Felsenstein, 1993) as the grouping algorithm because it does not assume standard evolutionary rates between populations. An ANOVA was performed for the differences between the mean population codominant genotypic genetic distances between the four populations.

6.3 Results

This investigation established that the average expected heterozygosity (H_e) within the different populations was low (Bura 0.3718; Garrisa. 0.4124; Loboi 0.3949; Salabani 0.4216.

The average observed and expected heterozygosity within the different populations is shown in Table 6.1. The genetic distance was also low with values ranging between 0.0049 and 0.0161. Molecular variance within individuals was (99%) while between populations it was only (1%). Mantel's test of correlation between genetic distance and geographical distance matrices including all populations was not significant ($r = -.7845$, $p = 0.07$)

Analysis of variance comparing differences in heterozygosity values between the four populations did not show significant differences (p=0.90, F=0.25).

Table 6.1: The average expected and observed heterozygosities within different populations

Population	Average expected heterozygosity	Observed heterozygosity
Bura	0.459	0.444
Garrisa	0.372	0.356
Loboi	0.0395	0.378
Salabani	0.0.422	0.402

The analysis of molecular variance (AMOVA) for populations showed significant differentiation (p<0.001), with 99% of the differentiation attributed to within populations and 1% attributed to among populations (Table 6.1).

Table 6.2 Analysis of molecular variance (AMOVA) between individuals and populations

Table 6.2: Analysis of molecular variance (AMOVA) between individuals and populations

AMOVA Results

Source of Variation	df	Est. Var.	%
Among Pops	3	0.006	1%
Among Indiv	56	0.000	0%
Within Indiv	60	0.575	99%
Total	119	0.581	100%

Nei's original (1972) genetic distance showed minimal genetic distance between populations (Table 6.3). The genetic distance between Bura and Salabani was the highest while the genetic distance between Loboi and Salabani was the lowest.

Table 6.3: Nei's original (1972) genetic distance between populations

Population	1	2	3	4
1	*****			
2	**0.0077**	*****		
3	**0.0080**	**0.0102**	*****	
4	**0.0161**	**0.0141**	**0.0049**	*****

1 (Bura); 2(Garissa); 3(Loboi); 4(Salabani)

Table 6.4: Tested enzymes, their abbreviation and Enzyme Commission numbers

Enzymes Tested	**Enzyme Commission Number**
Aspartate aminotransferase	AAT, EC 2.6.1.1
Acid phosphatise	ACP; EC 3.1.3.2
Alcohol dehydrogenase	ADH, EC 1.1.1.1
Adenylate kinase	AK, EC 2.7.4.3
Catalase	CAT, EC 1.11.1.6
Diaphorase	DIA; EC 1.8.1.4
Esterases	EST, EC 3.1.1.1
Fumarate hydratase	FUM, EC 4.2.1.2
Glucose dehydrogenase	GDH, EC 1.1.1.47
Glucose-6-phosphate dehydrogenase	GPD EC 1.1.1.49
Glucose-6-phosphate isomerise	GPI, EC 5.3.1.9
Hexokinase	HK, EC 2.7.1.1
Isocitrate dehydrogenase	IDH, EC 1.1.1.42
Leucine aminopeptidase	LAP; EC 3.4.11.1
Lactate dehydrogenase	LDH, EC 1.1.1.27
Mannose phosphate isomerase	MPI, EC 5.3.1.8
Malate dehydrogenase	MDH, EC 1.1.1.40
Malate dehydrogenase	NADP+ ME, EC 1.1.1.40
Menadione reductase	MNR, EC 1.6.99.2
6-phosphogluconate dehydrogenase	PEP, EC 3.4.11
Peptidases	PGD, EC 1.1.1.44
Phosphoglucomutase shikimate dehydrogenase	PGM, EC 5.4.2.2
Sorbitol dehydrogenase	SDH, EC 1.1.1.1
Superoxide dismutase	SOD, EC 1.15.1.1

PHYLIP's Neighbor-Joining method did not reveal any clustering of regional populations. (Fig. 6.1).

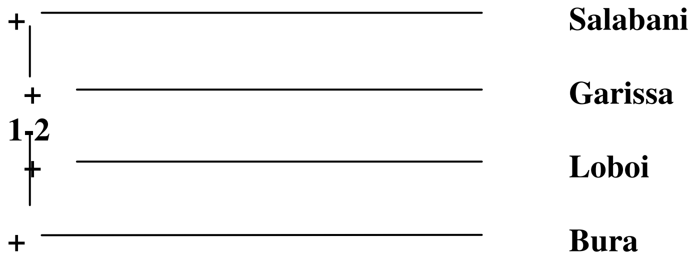

Figure 6.1 : Neighbour-joining method showing clustering between populations

Table 6.5: Analysis of variance comparing differences in heterozygosity values between the four populations

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*
Between Groups	0.005427	4	0.001357	0.253378	0.905852
Within Groups	0.208839	39	0.005355		
Total	0.214266	43			

6.4 Discussion

The average heterozygosity values were well above what has been found previously for *Prosopis juliflora* in Sudan (0.218) or even isoenzyme loci of other species such as *Pinus oocarpa,* $H_e = 0.27$ by Millar *et al.*, (1988). Saidman and Vilardi (1987) studied isoenzymes with seven enzymatic systems in populations of seven native Argentinean species of *Prosopis* and found a mean percentage of polymorphic loci (P) of 45%, with maximum values of 50% for *P. flexuosa* and a minimum of 38% for *P. ruscifolia*. These authors determined the heterozygosis mean values by locus and by individual (H) of 18%. These results, based on a study of 20 to 23 loci, demonstrated a high genetic variability in several of these species.

Nei's original (1972) genetic distance also showed minimal genetic distance between populations considering their separation by distance with values ranging between 0.0049 and 0.0161 and high molecular variance within individuals (99%) as opposed to between populations (1%). Mantel's test of correlation between genetic distance and geographical distance matrices including all populations was nonsignificant (r = -0.7845, p = 0.07) with no clustering of populations in close proximity. Some of the studied Kenyan populations are more than 500 km apart so there is no actual interaction between them. However, *P. juliflora* was introduced in Kenya only recently. The first documented introduction of the tree was in 1973 (Jama & Zeila, 2005), and it therefore may not have had time to evolve independently. The high inter-individual variation is not surprising. Genetic variation is usually introduced into a population by (i) outcrossing, thus maintaining genetic heterozygosity, (ii) hybridisation with subsequent backcrossing and, (iii) mutation of alleles in the duplicate set of chromosome (Solbrig & Orians, 1977). Genetic variation has been found to be quite low within some *Prosopis* species populations. Solbrig and Bawa (1975) attributed the low genetic variation found in some *Prosopis* species to: (i) partial self-compatibility, (ii) severe genetic depletion following extreme reduction in population, or (iii) extreme directional selection following population expansion.

Genetic variation was low both within and between populations of *P. juliflora* in isolated valleys of Colombia and Venezuela (Solbrig & Bawa, 1975). This result was assumed (like the current study in Kenya) to be due to recent establishment or isolation of the populations, lack of gene flow between populations and inbreeding within populations (Solbrig & Bawa, 1975). Genetic variation has been seen to be low in recently introduced populations (less than 50 years old). In expanding populations in Brazil, low genetic variation was assumed to be based on the initial introduction of only four trees (Kageyama, 1990).

Population biology is useful in identifying the point where containment rather than eradication efforts would be more practical (Allendorf & Lundquist, 2003). The genetic structure of populations affects the efficacy of invasive plants control (Müller-Schärer, et al., 2004). Furthermore, the control of a population with a genetically homogeneous structure, due to asexual mode of reproduction, can be easier for matching a biological control agent to the host genotype, where it is vulnerable to its biological enemies (Hoddle & Van Driesche, 1996). However, in sexually reproducing trees, as in our case, the greater genetic variation may lead to fast adaptive evolution and may mean escape from the biological control agents (Sakai, et al., 2001). This study indicates that, although we may have had multiple introduction events in Kenya (Paetkau, 1980), the introduced provenances did not have distinct genetic identities. Control strategies are therefore not expected to be different among the four populations at this point. Sakai *et al.* (2001) suggested that if the eradication of invasive populations is impossible, then setting control strategies to alter the population genetic structure in order to reduce adaptive variation is important.

Introductions of *P. juliflora* to Africa are thought to have had a small genetic base (Hughes, 1991). Other *Prosopis* populations arising from recent invasions such as *P. glandulosa* in the USA and *P. ruscifolia* in Argentina, were also found to have low genetic variation (Solbrig & Bawa, 1975). Thus it is assumed that many introductions of *Prosopis* species have started with only a few seeds and thus a low genetic base, and rapid expansion reinforces this low variation. Gene flow in Kenyan populations of *P. juliflora* may therefore be geographically restricted, with the likelihood that long-distance dispersal is not sufficiently common to prevent isolation by distance.

The results of this study indicate that geographic proximity is not indicative of genetic similarity and hence, is not a guide for understanding the genetic structure of this species in the four populations in Kenya. There is no indication of significant genetic differentiation among populations and most of the genetic variation is within populations. The four studied populations can be therefore be considered a single panmictic unit. For a long time the expectation of invasion biologists has been that introduced populations should experience loss of diversity relative to native sources because of founder effects and post-introduction demographic bottlenecks (Dlugosch & Parker, 2008). However, empirical data on wild plant populations do not always demonstrate that reduced genetic variation accompanies reductions in population size or that reduced heterozygosity results in a decrease in fitness.

6.5 Conclusions

The study did not reveal a correlation between genetic and geographic distances and there was little molecular variation among populations of *P. juliflora*. This investigation therefore revealed that the multiple introductions that characterize the different populations in Kenya have not contributed to its invasive capacity.

CHAPTER SEVEN

7.0 GENERAL CONCLUSIONS AND RECOMMENDATIONS

- The study has revealed that *P. juliflora* trees have established in areas that have very low levels of N and P, most likely brought about by disturbance that created an empty niche which the invader can occupy.
- It is recommended that areas affected by disturbance that leads to removal of local plant species be given more emphasis in conservation efforts. Indigenous species should be used in the rehabilitation programs. More controlled experiments should be carried out to measure the direct contribution of disturbance to the invasion of *P. juliflora.*
- Local pastoralist communities should be cautioned against removal of local species as it may act as a deterrent to future invasions by alien species. The study indicates that at low levels, this plant can actually act as a facilitator to other local species but this changes as the density rises. It is therefore recommended that conservation efforts concentrate to keep *P. juliflora* at low levels where it is not detrimental to local species diversity. More research should be carried out to find the optimal density of the invading species that may be useful to local species.
- The study established that during a dry weather period there was a higher species abundance of the important pollinator *Apis mellifera* in

the *P. juliflora* stand. The results suggest that *P. juliflora* may be a preferred source of resources for *A. mellifera* during the dry season.

- It is recommended that further studies on the impacts of invasive alien plants and pollinators be extended to the landscape scale and should be long-term and observations should be carried out at the species and community level. The impacts on specialist versus generalist pollinators should also be considered in such studies.
- There was no relationship between genetic distances and geographical distances in four Kenyan populations. *P. juliflora* was introduced in Kenya only recently and it may not have had time to have the different populations evolve independently.
- It is recommended that a study where all populations in Kenya are sampled be carried out in order to test for the influxes of genetic variation from multiple introduction events and indicate whether the movement of genotypes within an invaded range is likely to enhance the fitness of invading species.
- Since invasive species are one of the leading causes of biodiversity loss, there is a need to generate interest in the scientific community by training more specialists in the area and organize meetings, workshops and conferences that will highlight the need to elevate this subject as a core discipline for emerging scientists

- There is a need for institutions in East Africa to embrace and incorporate invasive species biology as a core course in their curriculums right from the entry level where students can appreciate the importance of biodiversity conservation and ecosystem integrity even before they get into their narrower specializations.

- There is a serious need for policy makers and the scientific community to communicate the information that can be useful to local communities in a language that is easy and practical management strategies and policy framework based on sound empirical information are necessary. With such information, some benefit may accrue from the exploitation of these species.
- The government and other development agencies have the responsibility both at the national and the local level to provide funding and incentives for low and localized programs to control existing invasive species in order to protect the yet uninvaded ecosystems. Policy frameworks are needed that support alliances among the many interest groups involved in invasive species management.

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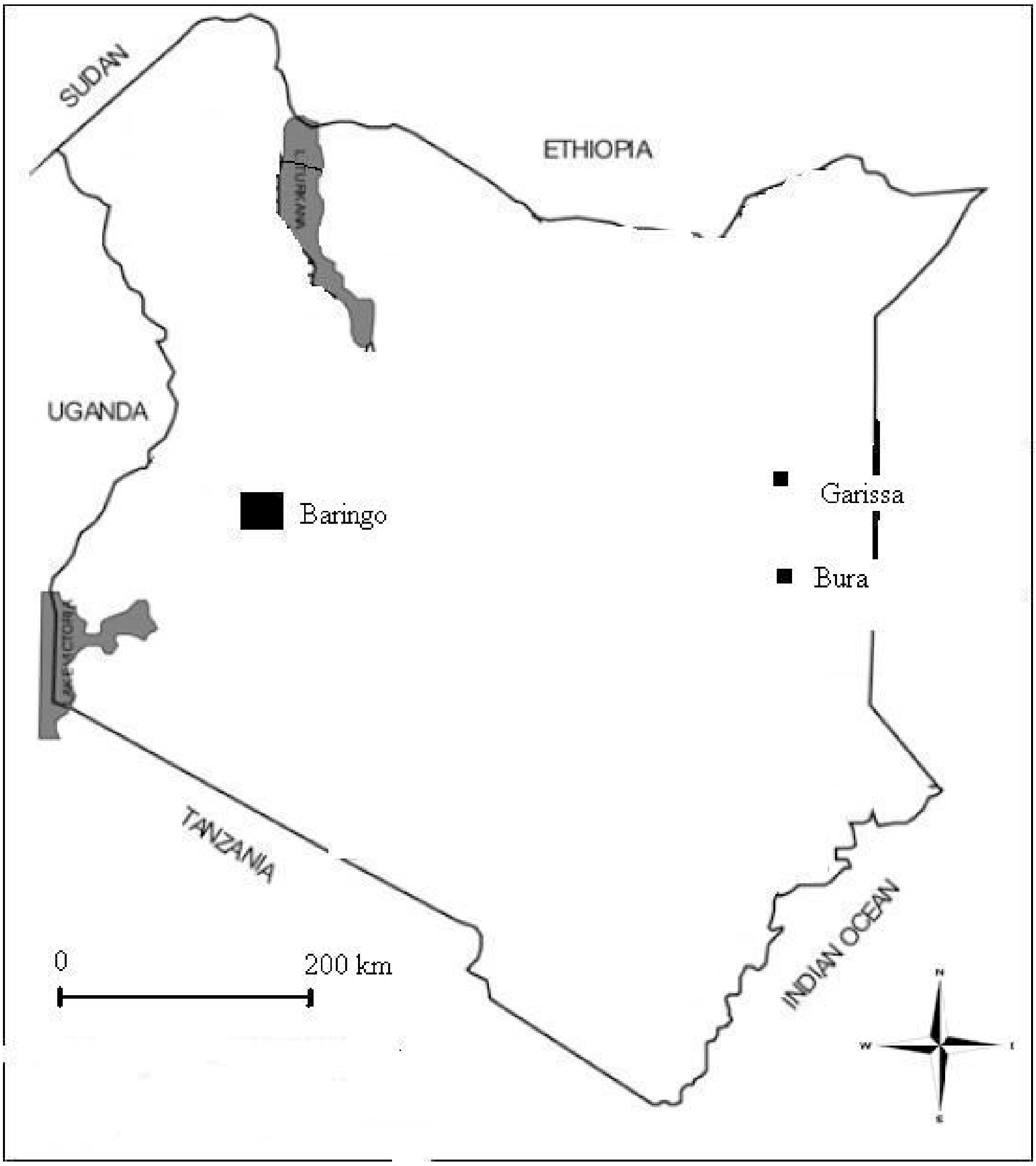
APPENDICES:

Appendix One: The Map of Kenya showing the location of the study sites



Appendix Two: Tree for Bura and Garissa

CODE NO	**SOUTH**	**EAST**

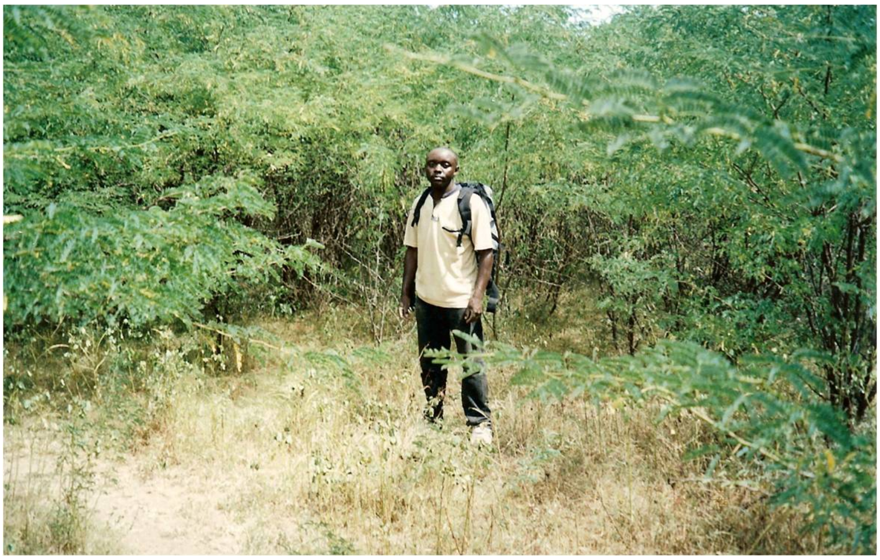
Bura1	01^{0}11.166’	039^{0}49.863’
Bura 2	01^{0}11.141’	039^{0}49.855’
Bura 3	01^{0}11.110’	039^{0}49.839’
Bura 4	01^{0}10.619’	039^{0}49.484’
Bura 5	01^{0}10.602’	039^{0}49.471’
Bura 6	01^{0}10.533’	031^{0}49.441’
Bura 7	01^{0}10.487’	039^{0}49.437’
Bura 8	01^{0}10.484’	039^{0}49.440’
Bura 9	01^{0}10.481’	039^{0}49.430’
Bura 10	01^{0}10.478’	039^{0}49.440’
Bura 11	01^{0}10.473’	039^{0}49.445’
Bura 12	01^{0}10.448’	039^{0}49.441’
Bura 13	01^{0}10.437’	039^{0}49.444’
Bura 14	01^{0}08.704’	039^{0}47.969’
Bura 15	01^{0}08.341’	039^{0}47.890’
Garrisa1	00^{0}27.760’	039^{0}37.912’
Garrisa2	00^{0}27.756’	039^{0}37.904’
Garrisa3	00^{0}27.727’	039^{0}37.876’
Garrisa4	00^{0}27.726’	039^{0}37.886’
Garrisa5	00^{0}27.723’	039^{0}37.858’
Garrisa6	00^{0}27.718’	039^{0}37.857’
Garrisa7	00^{0}27.700’	039^{0}37.860’
Garrisa8	00^{0}27.675’	039^{0}37.835’
Garrisa9	00^{0}27.635’	039^{0}37.857’
Garrisa10	00^{0}27.619’	039^{0}37.852’
Garrisa11	00^{0}27.575’	039^{0}37.851’
Garrisa12	00^{0}27.552’	039^{0}37.845’
Garrisa13	00^{0}27.541’	039^{0}37.843’
Garrisa14	00^{0}27.677’	039^{0}37.509’
Garrisa15	00^{0}27.761’	039^{0}37.371’

Appendix three: Tree Coordinates for Loboi and Salabani

CODE NO	SOUTH	EAST
Loboi 2.	00^{0}32..276	036^{0}01.379
Loboi 3.	00^{0}32.285	036^{0}01.719
Loboi 4.	00^{0}32.294	036^{0}01.752
Loboi 5.	00^{0}32241	-01.438
Loboi 6.	00^{0}32.256	-01.263
Loboi 7.	00^{0}32.287	-01.122
Loboi 8.	00^{0}32.307	-01.004
Loboi 9.	00^{0}32.442	-00.819
Loboi 10.	00^{0}32.499	036^{0}00.662
Loboi 11.	00^{0}32.170	00.208
Loboi 12.	00^{0}31.787	035^{0}29.608
Loboi 13.	00^{0}31.749	035^{0}29.538
Loboi 14.	00^{0}31.424	035^{0}59.283
Loboi 15.	00^{0}31.292	-59.255
Salabani1.	00^{0}31.144	-59.218
Salabani2.	00^{0}30.706	-59.178
Salabani 3.	00^{0}29.859	-58.974
Salabani 4.	00^{0}29.265	035^{0}59.997
Salabani 5.	00^{0}29.012	-59.010
Salabani 6.	28.8228	-59.006
Salabani 7.	00^{0}26.284	036^{0}00.090
Salabani 8.	00^{0}22.263	036^{0}02.477
Salabani 9.	00^{0}21.457	036^{0}02.975
Salabani 10.	00^{0}21.460	03.548
Salabani 11.	00^{0}21.403	03.701
Salabani 12.	21.110	03.853
Salabani 13.	20.817	03.978
Salabani 14.	20.696	03603.975
Salabani 15.	20.770	03.956

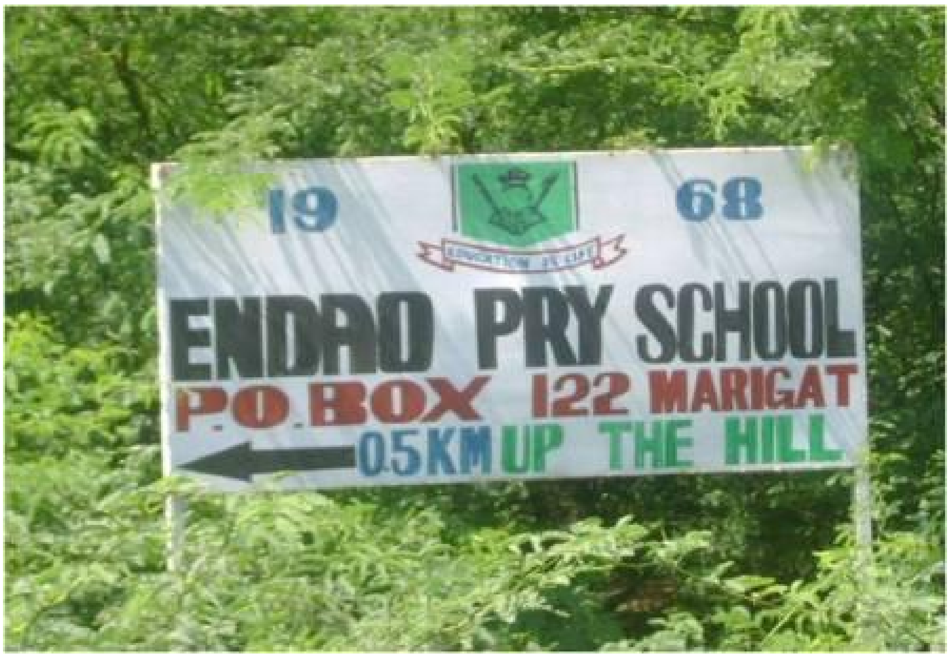
Appendix Four: *Prosopis juliflora* clogging the shores of Lake Baringo

Appendix Five: *Prosopis juliflora* trees at the edge of a high-density thicket



Appendix Six: *Prosopis juliflora* covering part of the road to Salabani

Appendix Seven: *P. juliflora* thicket at the entrance of Endau Primary School



Appendix Eight: Data used for scoring in allozyme analysis

BURA																																
Enzyme	Electrode Buffer																															
		LOCUS	B1		B2		B3		B4		B5		B6		B7		B8		B9		B10		B11		B12		B13		B14		B15	
GPI	P		1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0	1	1	1	1	0
EST	RW		0	1					1	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	0			1	1	1	0
MDH	TC		1	1	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1	1	1
PER	P		1	0	1	1	1	0	1	0	1	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0			1	1	1	1
GDH	P		0	1	0	1	0	1	1	1	1	1			1	1	1	1	1	1			0	1			0	1	0	1	0	1
AAT	P				1	1	0	1					1	1	0	1	0	1	1	1	1	0	1	1	1	1						
GDH	P						1	1													0	1	0	1	1	1	1	1	0	1	0	1

GARISSA																																
Enzyme	Electrode Buffer																															
			G 1		G 2		G 3		G 4		G 5		G 6		G 7		G 8		G 9		G10		G11		G12		G13		G14		G15	
GPI	P		0	1	1	1	1	1	1	0	0	1	0	1	1	1	1	0	0	1	0	1	0	1	1	1	0	1	1	1		
EST	R W		1	0	0	1	0	1	0	1	1	1					0	1	1	1	1	0	1	1	0	1	0	1	1	1	0	1
MDH	TC		1	1	0	1	0	1	0	1	1	1	1	1			1	1	1	0	1	1	1	0	1	0	1	0	1	0	1	1
PER	P		1	1	0	1	1	1	0	1	1	1	1	0			1	1	1	1	1	1	0	1	1	1			1	1	1	0
GDH	P		0	1	0	1	1	1	1	1	0	1	1	1	1	1							1	1					1	1		
AAT	P		0	1	0	1			1	1	1	0			1	1	1	1	1	1	0	1	0	1			0	1	0	1		
GDH	P		1	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1														

Loboi																																
Enzyme	Electrode Buffer																															
			L1		L2		L3		L4		L5		L6		L7		L8		L9		L10		L11		L12		L13		L14		L15	
GPI	P		0	1	0	1	1	1	1	1	0	1	1	0	0	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1	1	1
EST	R W		1	0	1	0	1	1	1	1	1	1	1	1					0	1	1	0	1	1	0	1	0	1	1	1		
MDH	TC				1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	0	1	0	1	1	1	0	1	1		
PER	P		1	0	1	0	0	1	0	1	0	1			1	1	1	0	1	0	0	1	1	1	1	1	0	1	0	1	1	1
GDH	P		0	1			1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	1	1
AAT	P				0	1	1	1	0	1	0	1	1	0	1	0			1	1	0	1	0	1	1	1						
GDH	P		0	1	1	1	0	1	0	1	0	1			1	1			0	1	1	1	1	1	1	1	0	1	0	1	0	1

SALABANI																																
Enzyme	Electrode Buffer																															
			S1		S2		S3		S4		S5		S6		S7		S8		S9		S10		S11		S12		S13		S14		S15	
GPI	P		0	1	1	0	1	0	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1			1	0	1	1	1	0
EST	R W		0	1	1	0	1	0	1	1	1	1					1	1	1	1	1	1					1	1	1	1	0	1
MDH	TC		1	0	1	0	1	1	1	1	1	1	1	1	1	0			1	1	1	0	1	1	1	0	1	0				
PER	P		1	0	1	1					1	1	0	1	0	1	1	0			1	1	1	1	1	1	1	1				
GDH	P		1	0	1	0	1	0	0	1	1	1																				
AAT	P						0	1			1	1			0	1					0	1	1	1			0	1				
GDH	P		0	1	1	1	1	1			0	1			0	1	0	1			1	1	0	1	1	0	1	0				