IMPACT OF THE INVASIVE ALIEN SPECIES, *LANTANA CAMARA* (L). ON NATIVE VEGETATION IN NORTHERN GONAREZHOU NATIONAL PARK, ZIMBABWE

by

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ABSTRACT

This study assessed the impact of *Lantana camara* invasion on native vegetation in Northern Gonarezhou National Park (GNP), Zimbabwe. Stratified random sampling was used with three categories; uninvaded, moderately invaded and heavily invaded. The distribution of *L. camara* in Northern Gonarezhou National Park was mapped using GIS. Soil properties and vegetation attributes were assessed in each category. *L. camara* was mainly distributed within the riparian vegetation and in the low-lying areas of Northern GNP. A total of 41 native woody species and 27 native herbaceous species were identified in the study area. Significant differences (ANOVA, $P<0.05$) in soil nitrogen, phosphorus, potassium and moisture among the three categories were noted. Soil nitrogen and phosphorus levels were highest in the heavily invaded category and lowest in the uninvaded category. Soil potassium and moisture levels were highest in the uninvaded category and lowest in the heavily invaded. For native vegetation attributes; basal area, canopy cover, herbaceous cover, woody plant density, species diversity (H') and species richness (S) varied significantly (ANOVA, $P<0.05$) among the categories of *L. camara* intensity. These variables were highest in the uninvaded category and lowest in the heavily invaded category. The uninvaded category was the most diverse (H'=1.875) while the heavily invaded category was the least diverse (H'=1.334). Edaphic factors influenced plant species structure and composition in northern GNP. The significant differences in soil and vegetation variables suggest that *L. camara* is altering soil properties and native vegetation structure and composition in GNP to the detriment of wildlife management. Active management of *L. camara* in Gonarezhou National Park is therefore urgently required for wildlife and biodiversity conservation in the area.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

1.0 INTRODUCTION

1.1 Background

Plant invasions are posing a great threat to biodiversity (Crowling, Richardson and Piece, 1997), which is already threatened by habitat destruction due to human population growth. Invasive species are broadly defined as those species that are not native to an area and that may displace or otherwise adversely affect native plant species (Drake, Weltzin and Parr, 2003). These species, according to Drake *et al*. (2003), often produce prolific seeds that may disperse widely and remain viable in the soil for long periods of time. Invasion is defined as the whole process from the arrival of a new species into a community, its establishment and maintenance in that community, to its further spread into neighbouring communities (Prieur-Richard and Lavorel, 2000).

Invasive alien plant species have become a major threat to global plant biodiversity (Crowling *et al*. 1997; Meffe *et al*. 1997; Holmes *et al*. 2000; Prieur-Richard and Lavorel, 2000; Willis *et al*. 2000; Sharm and Raghubanshi, 2005), second only to habitat destruction (Holmes *et al*. 2000; Willis *et al*. 2000). Plant invasions pose a serious threat to natural and managed ecosystems globally (Collingham *et al*. 2000; Viisteensaari *et al*. 2000) with Zimbabwe not an exception. According to Crawley (1997), alien plants are the biggest single threat to plant conservation in nature reserves in many parts of the tropics and subtropics. However, Meffe *et al*. (1997) emphasized that maintenance of biological diversity is now recognized in many circles as the single highest conservation priority of our time because biological diversity is our living natural resources base, our biological capital in the global bank.

Case studies from around the world have shown that alien plants can increase carbon assimilation rates, change soil nutrient status, increase flammability, threaten native plant species and change habitat suitability for native animal species (Gentle and Duggin, 1997b; Stohlgren *et al*. 1998;

Higgins *et al*. 1999; Thomas and Ellison, 2000; Ehrenfeld, 2003; Hiremath and Sundaran, 2005; Sharm *et al*. 2005).

Invasives are thought to be one of the main causes of biodiversity loss worldwide, and native species and habitats are continuously put at risk of displacement and extinction from invasion by these non-native plants (BEST Commission, 2003). Higgins *et al*. (2000) recognised biological invasions as a widespread phenomenon that threatens the integrity and functioning of natural ecosystems whose effects are so widespread and significant that they are a recognised component of global change. Heffernan (1998) recognised invasive plants as a threat to natural areas, parks, forests and other sites in a more or less natural state. The non-native plant invasions produce a marked change in composition and structure of communities as well as ecosystem processes (Crowling *et al*. 1997).

One of the most invasive alien plant species is *Lantana camar*a (L), which is widely distributed worldwide. According to Sharm *et al*. (2005), the distribution of *L. camara* species indicates a severe threat for the ecosystems in hotspot areas. In South Africa, invasive alien species are threatening both the floristically distinctive fynbos vegetation and water resources (Holmes *et al*. 2000). The moist evergreen rain forests of the Eastern Highlands of Zimbabwe are being threatened by alien invasive plant species such as *L. camara*, wattle (*Acacia mearnsii*), Mauritius thorn (*Caesalpinia decapetala*) and eucalyptus species (Timberlake and Musokonyi, 1994), to the detriment of biodiversity of the forests. The invasions have increased globally due to the expansion in the trade of goods and services, increased mobility of people, liberalisation of markets and the use of exotic species for ornamental and horticultural purposes (BEST Commission, 2003).

Though national parks and natural reserves are protected from anthropogenic habitat destruction, high herbivore population densities are threatening species diversity in these areas. In addition to herbivore pressure, plant invasions by alien invasives such as *L. camara*, are posing a great threat to species diversity in these areas. Several woody species (e.g. *L. camara*, *Jacaranda mimosifolia*, *Melia azendarach*, *Nerium oleander* and *Sesbania punicea*) introduced for horticultural purposes have become invaders (Crowling *et al*. 1997).

In Zimbabwe *L. camara* has invaded areas such as Zambezi Valley; unbuilt areas of the cities of Harare, Masvingo and the Eastern Highlands, among other places, and is spreading so fast that it is becoming a threat to livestock paddocks in areas such as Chipinge and Chimanimani where it has developed into large monospecific stands (Pers. Observ.). *L. camara,* according to Day *et al.* (2003), is a major weed that invades natural and agricultural ecosystems in palaeotropics. The species is widely distributed throughout southern Africa (Simelane, 2002), including Zimbabwe.

1.2 Origin of *Lantana camara*

L. camara is a significant weed with some 650 varieties in many regions where it is established and is expanding in range, with 29 of them occurring in Australia and reportedly up to 40 in South Africa (Day and Neser, 2000; ISSG, 2006). *L. camara* was introduced by Dutch explorers into Netherlands in the late 1600s from Brazil and it was then grown in glasshouses in Europe before its importation to other countries as an ornamental (Day *et al*. 2003; ISSG, 2006).

The species was introduced as an ornamental into many parts of the tropical and subtropical world during the nineteenth and early twentieth century (Mack and D’Antonio, 1998). Having originated from South America (Fensham *et al*. 1994), *L. camara* is now naturalised in approximately 60 countries or island groups, between 35°N and 35°S (Day *et al*. 2003). *L. camara* is native only to the tropical and subtropical zones of the Americas (Neotropics) (Day *et al*. 2003). Introduced for horticultural purposes, *L. camara* has become a major invader of agricultural and natural ecosystems (Crowling *et al*. 1997). Currently, *L. camara* has been nominated as among the 100 of the "World's Worst" invaders (Lowe *et al*. 2004); ISSG, 2006).

1.3 Description of *L. camara*

The taxonomic classification of *L. camara* is given below:

Kingdom	Plantae
Phylum	Embryophyta
Class	Magnoliopsida
Order	Lamiales
Family	Verbenaceae
Genus	*Lantana*
Species	*L. camara* (L).
Common name	Lantana

Lantana camara is a multi-stemmed, perennial woody shrub with multi-coloured flower clusters (Fensham *et al*. 1994). It is low, erect and vigorous, with stout recurved prickles and a strong odour of black currents (Day *et al*. 2003). On average, the species grows to a height of between 1.2 and 2.4 meters, but can grow up to 10 meters (ISSG, 2006). It has a very strong but shallow root system, and it gives out a new flush of shoots even after repeated cuttings. The leaves are egg-shaped, pointed, with serrated margins, and have heart-shaped bases (Gentle and Duggin, 1997b). The flower, which is small, is usually orange, sometimes varying from white to red in various shades and having a yellow throat (Gentle and Duggin, 1997a). Inflorescences are produced in pairs in the axils of opposite leaves and in almost all colour forms. The flower opens yellow and changes to pink, white and red depending on the variety (Gentle and Duggin, 1998). Each compact flower head contains 10 to 40 flowers, and each flower has about four lobes (Gentle and Duggin, 1997b).

The plant bears fruits, which are small, greenish-blue black, blackish, with two nutlets each, almost throughout the year. Seed dispersal is primarily by fruit-eating birds, and to a lesser extent, by rodents, foxes and other vertebrate foragers (Day *et al*. 2003). The seed germinates very easily (ISSG, 2006). Having been subject to intense horticultural improvement in Europe since the sixteenth century, the species now exists in many different varieties throughout the world (Gentle and Duggin, 1998). Plants differ in growth rates and toxicity, chromosome number and DNA structure (Gentle and Duggin, 1997b). *L. camara* can grow individually in clumps, or as dense thickets which, in disturbed native forests, can become the dominant understorey, crowding out native species and disrupting succession. This leads to decline in biodiversity (Day *et al*. 2003; Drake *et al*. 2003).

1.4 Problem statement

L. camara has invaded the northern part of Gonarezhou National Park (GNP). This may result in the extinction of some native plant species and subsequent shortage of forage and habitats for animals in the park. *L. camara* invasion in GNP may alter the vegetation structure and species composition to the detriment of wildlife management in the Park. Furthermore, since *L. camara* is poisonous to ungulates, its invasion can adversely affect wildlife in the Park. The spreading and subsequent formation of monospecific *L. camara* stands may adversely affect the beautiful scenery of the Park.

1.5 Justification

Following the encroachment of the invasive alien species *L. camara* in the northern part of Gonarezhou National Park, there is need to establish its impact on native plant species in order to put in place management strategies in the Park. Biological invasions have been relatively well studied in some parts of southern Africa but poorly studied in others (Crowling *et al*. 1997). Several studies have investigated changes in vegetation in GNP (e.g. O'Connor, 1982; O'Connor and Campbell, 1986; Tafangenyasha, 1997; Clegg, 1999; Gandiwa, 2006) but no studies have considered the effect of invasive species on the vegetation in the Park.

One of the objectives of National Parks and Wildlife Management Authority is to prevent the introduction of exotic species in parks and to make every practical attempt to actively eliminate these when detected (DNPWLM, 1998). Such a study in GNP will lead to management strategies to control *L. camara* in the Park. Drake *et al*. (2003) emphasised the need for additional research focused on the general effects of individual invasive species on individuals, populations, communities and ecosystems.

A number of studies have documented the variable effects of a given alien invasive species in different environments such as decrease, increase or no effect in soil properties following alien plant invasions (Gentle and Duggin, 1997b; Stohlgren *et al*. 1998; Higgins *et al*. 1999; Thomas and Ellison, 2000; Ehrenfeld, 2003; Hiremath and Sundaran, 2005; Sharma *et al*. 2005). Given the frequency with which site-specific results have been reported, more research is needed to assess the generality of the observed impact of a given species across a variety of environments (Ehrenfeld, 2003). Based on these findings, it is imperative that the impact of *L. camara* invasion in Gonarezhou National Park be assessed. This will contribute to a better understanding of the impact of the species on the environment.

1.6 Aim

This study aimed at assessing the impact of *L. camara* invasion on native plant species in Northern Gonarezhou National Park.

1.7 Objectives

- To map the spatial distribution of *L. camara* in the northern part of GNP.
- To determine the effects of *L. camara* invasion on native vegetation composition and structure in northern GNP
- To determine other key factors that affect plant composition and structure in Northern GNP.
- To assess the effects of *L. camara* invasion on soil physical and chemical properties in Northern GNP.

1.8 Research questions

1. What is the spatial distribution of *L. camara* in the northern part of GNP?
2. Does *L. camara* have an impact on native vegetation composition and structure in Northern GNP?
3. What other key factors affect plant species composition and structure in GNP?
4. Does *L. camara* have an impact on soil physical and chemical properties in GNP?

1.9 Working Hypotheses

a). *L. camara* invasion has an effect on soil physical and chemical properties.

b). *L. camara* invasion affects native vegetation species composition and structure.

2.0 LITERATURE REVIEW

2.1 Pattern of Invasion by Invasive Species

Introduced alien species vary in their invasive behaviour in different regions (MaClaran and Anable, 1992). Plant invasions are mostly associated with disturbed habitats. Trees and other woody species in disturbed areas feature predominantly as invaders, often as a result of horticultural practices (Viisteensaari *et al*. 2000). Klink (1996) observed that introduced African grasses are the major invaders in the Brazilian savannas where the grasses are particularly good colonizers of disturbed sites. An invasive species can colonise an area with the same climate as its native place but the success depends on its ability to compete with indigenous species and colonise new habitats (Honing *et al*. 1992).

In Canada, it was found that the chances of establishment of alien plants increased with increase in amount of light reaching the ground, and amount of exposed mineral soil (Reader and Bricker, 1994). According to Prieur-Richard and Lavorel (2000), bare ground created by disturbance facilitates the recruitment phase of the invasion, and fertilization further promotes the growth and reproduction of successfully established invaders. Once alien plants have established, they grow faster and taller than indigenous species, and after one or two fire cycles, form closed stands with reduced light penetration and altered nutrient cycling patterns, litter fall and functional properties (Holmes *et al*. 2000).

Increasing disturbance of natural areas, such as through altered fire regimes and increased grazing pressure, increases the susceptibility of vegetation to invasion (Crawley, 1997). Ticktin *et al*. (2006) considered the removal of native plant parts as opening up space for light-loving alien seedlings to germinate, thereby facilitate their spread. Closed forests are, in general, rather resistant to invasion by alien plants, but natural or man-made disturbance increases the risk of invasion (Reader and Bricker, 1994; Viisteensaari *et al*. 2000). Fensham *et al.* (1994) found that mechanical disturbance was an agent for the proliferation of exotic plants. Viisteensaari *et al*. (2000), however, highlighted that invasive plants such as *Maesopsis eminii,* have proven to be an exception to the rule that closed tropical forests are resistant to invasion. Alien species might more easily invade areas of low species diversity than areas of high species diversity (Stohlgren *et al*. 1998).

2.2 Characteristics of Invasive Species

An invasive species must be capable of establishing self-sustaining populations in areas of natural or semi-natural vegetation and produce a significant change in terms of vegetation composition, structure or ecosystem processes (Viisteensaari *et al*. 2000). Studies in South Africa indicated that many successful alien invaders have high shoot to root ratios than native plants, which they displace (Macdonald *et al*. 1991). In a study in Brazil, Klink (1996) found that the invader species *Andropogon gayanus* had a higher and faster germination rate than the native species.

Other characteristics of invaders among others, given by Meffe *et al*. (1997), are high reproductive rates, short generation time, long-lived high dispersal rates, vegetative reproduction, high genetic variability, phenotypic plasticity, broad native range and habitat generalist. Invasive species are often prolific seed producers with seeds that may disperse widely and that may remain in the soil for long periods of time (Heffernan, 1998).

2.3 Invasive characteristics of *L. camara*

Being an invader, *L. camara* possesses a number of biological attributes that characterize it as an invader. The species has a wide geographic range. *L. camara* has a widespread distribution (35°N-35°S) beyond its native range, becoming naturalized in approximately 60 countries (Day *et al*.

2003). The wide distribution of *L. camara* indicates a severe threat for the ecosystems including hotspot areas (Sharm *et al*. 2005).

Homeostatic fitness and phenotypic plasticity also increase the invasiveness of *L. camara.* Homeostatic fitness describes the ability of an individual or population to maintain relatively constant fitness over a range of environments, while phenotypic plasticity is the ability of a genotype to modify its growth and development in response to changes in the environment (Sharm *et al*. 2005). Broughton (2003) found that *L. camara* compensates for defoliation through increasing its growth, thereby exhibiting its invasiveness potential. Fensham *et al*. (1994), in their study in Forty Mile Scrub National Park in Queensland, found that the foraging activities of vertebrates promote *L. camara* proliferation through enhanced vegetative propagation. According to Sharm *et al*. (2005), such plastic responses in vegetation structure are thought to promote survival and propagation of *L. camara* in new heterogeneous environments.

The success of *L. camara* may be attributed to the presence of a range of pollinators, accounting for the high percentage of fruit-set (Sharma *et al*. 2007). Once formed in high numbers, the seeds of *L. camara* are dispersed efficiently through the participation of a variety of animal dispersal agents that feed on its fruit (Sharm *et al*. 2005) such as birds, foxes, rodents and other vertebrate foragers (Simelane, 2002). The processes of invasion are further improved by nutrient additions, with animal droppings, canopy removal and soil disturbance, creating a good seed-bed (Gentle and Duggin, 1997b; Fensham and Cowie, 1998; Duggin and Gentle, 1998). Fensham *et al*. (1994) found that the foraging activities of vertebrates promote *L. camara* proliferation through enhanced vegetative propagation.

Once established, the rapid vegetative growth of *L. camara* facilitates the formation of large, impenetrable clumps and high seed production (Sharm *et al*. 2005). According to Swarbrick *et al*. (1995), the more common means of vegetative spread is through layering, where horizontal stems produce roots whenever they come in contact with soil but suckering also occur and prostate stems can root if covered by moist soil, fallen leaves or debris. Furthermore, *L. camara* stems and leaves can develop roots and grow into plants and eventually flower (Day *et al*. 2003).

L. camara is fire tolerant and this enables it to withstand moderate fires. Fensham *et al*. (1994); Reader and Bricker (1994); Gentle and Duggin (1997a) and Sharm *et al*. (2005) indicated that although *L. camara* burns readily during hot, dry conditions, even when green, moderate to low fire intensities can promote the persistence and spread of *L. camara* thickets, rather than reduce them. Gentle and Duggin (1997b) in their study of *L. camara* allelopathy in three Australian forests also described the removal of competing neighboring plant species and increase in soil nutrients after burning as factors that increase its germination. Its establishment is encouraged following mechanical or chemical control of mature plants (Sharm *et al*. 2005).

The high competitive ability of *L. camara* enables it to displace and replace native species. Mortality rate of mature *L. camara* in its naturalized range is very low under conditions of high light, soil moisture and soil nutrients (Sahu and Panda, 1998). Duggin and Gentle (1998) described the ability of *L. camara* infestations to be persistent, having the potential to block succession and displace native species, with subsequent reduction in biodiversity in forest communities. *L. camara* is a very effective competitor with native colonizers and is capable of interrupting the regeneration processes of other indigenous species by reducing germination, reducing early growth rates and increasing mortality (Sharm *et al*. 2005). It competes strongly for moisture and nutrients, thereby reducing productivity of the native plants (Day *et al*. 2003).

The allelopathic effect of *L. camara* is well documented, and results in severe reductions in seedling recruitment of nearly all species under its cover. Zero growth or only stunted growth have been observed for other species growing close to *L. camara* (Achhireddy and Singh, 1984; Achhireddy *et al*. 1985). According to Sharm *et al*. (2005), as many as fourteen phenolic compounds are present in *L. camara* that can reduce seed germination and growth of young plants. Experimental studies have verified that *L. camara* can have an allelopathic effect on a range of plant species- (Achhireddy and Singh, 1984; Fensham *et al*. 1994).

Potential allelopathic chemicals such as triterpenes have been isolated from *L. camara.* These compounds have been implicated in allelopathic responses (Fischer *et al*. 1994). Gentle and Duggin (1997b), in their study of the allelopathic effects of *L. camara* in three Australian forests, found a significant increase in seed germination and seedling biomass with removal of *L. camara* thickets. Gentle and Duggin (1998), also found that suppression of native species increased with increase in the density of *L. camara* due to allelopathy. Allelochemicals promote or inhibit the plant growth based on their concentration, which increases from root, stem to leaf, making the leaf toxic to grazing animals (Achhireddy and Singh, 1984).

2.4 Management of *L. camara*

Mechanical, chemical and biological control methods have been employed to control *L. camara* in different areas worldwide. Mechanical control can be achieved by physical removal of *L. camara* from initially, small gaps, accompanied by planting fast growing species that increase the shade at disturbed sites to prevent the reestablishment of the weed (Thomas and Ellison, 2000). Hot fires can also be used to control the plant. According to Day *et al*. (2003), chemicals such as glyphosate, 2,4-D, fosamine, dichlorporp and triclopur at standard rates can be used for the control, but glyphosate is most effective as an overall foliar spray (Stock, 2005). In many areas such as national parks, mechanical clearing, use of chemicals or fire would be uneconomic or environmentally damaging, resulting in biological control being the only viable option (Day and Neser, 2000).

Biological control has been widely used to control alien plant species. The method has been used against 38 alien plant species in South Africa. The most intensive biological control programme has been that against *L. camara*, on which 17 insect species have been released (Crowling *et al*. 1997). Biological control continues to play a major role in the management of invasive alien plants and six of the agents have become established in South Africa and contribute substantially to control the weed (Day and Neser, 2000). However, *L. camara* comprises a complex of 50 genetically distinct taxa and it remains a problem in many areas (Crowling *et al*. 1997; Day *et al*. (2003).

Thirty-six agents have been released on *L. camara* in 33 countries with the resulting control ranging from inadequate to good (Day and Neser, 2000). A number of these agents have been released in Australia, South Africa, Hawaii and other countries but with limited success (Baars and Heystek, 2003; Simelane, 2002; Stock, 2005). The insect agents released include *Uroplata girardi, Ophlomyla lantanae, Lantanophaga pusillidactyla, Teleonemia scrupulosa, Aceria lantanae, Octotoma scabripennis, Ophiomya lantanae, Calycomyza lantanae*, among others, while fungal agents include *Mycovellosiella lantanae, Puccinia lantanae-camarae, Prospodium tuberculatum*, among others (Thomas and Ellison, 2000; Baars and Heystek, 2003; Day *et al*. 2003). Limited success of biological control, according to Day *et al*. (2003), is because *L. camara* is found in a wide range of climatic regions, often occurring where biocontrol agents are not adapted.

Maintaining at least 75% shading can help reduce the success of *L. camara* encroachment (Stock, 2005). Although preventing introductions is the surest way to prevent the negative impact of invasions, it is often too late for this to apply (Day *et al*. 2003). The key to good management of *L. camara* is constant vigilance and repeated control of regrowth, and control of new infestations should be a priority (Simelane, 2002; Day *et al*. 2003).

2.5 *L. camara* Habitat Description

L. camara is found from sea level to 2000 meters above sea level. It occurs in diverse habitats and on a variety of soil types (Day *et al*. 2003; Sharm *et al*. 2005; ISSG, 2006). It grows in a variety of coastal and subcoastal areas, thriving in high rainfall areas of the tropical, subtropical and warm temperate climates (Simelane, 2002). *L. camara* occurs in agricultural areas, coastland, disturbed areas, natural forests, planted forests, range/grasslands, riparian zones scrub/shrub lands, urban areas and wetlands (Thomas and Ellison, 2000). Though the plant can tolerate prolonged dry periods, it prefers conditions where soil moisture is available throughout the year but not waterlogged or saline (Gentle and Duggin, 1997a).

Disturbed areas are favorable for the species since it generally grows best in open unshaded localities (ISSG, 2006). Gentle and Duggin (1997a) observed that invasion of *L. camara* significantly increased following disturbances associated with fire and grazing. The study by Timberlake and Musokonyi (1994) revealed that *L. camara* has invaded the disturbed margins of the evergreen rainforest of the Eastern Highlands of Zimbabwe. Macdonald *et al*. (1991) also documented correlation between successful invasion and increase in disturbance levels in their study on effects of alien plant invasions on native vegetation in India.

The plant can tolerate shade, but does not flower readily under these conditions. *L. camara* grows under a wide range of climatic conditions but seldom occurs where temperatures frequently fall below 5°C because new shoots are frost sensitive (Sharm *et al*. 2005). In South Africa it is found in areas with a mean annual surface temperature greater than 12.5°C (Simelane, 2002).

The diverse and broad geographic distribution of *L. camara* is a reflection of its wide ecological tolerances (ISSG, 2006). The plant grows well in rich organic soils, well-drained clay soils, and volcanic soils derived from basalts but also tolerate poor soils and almost pure sands, as long as moisture is available (Thomas and Ellison, 2000). In cases of reduced herbivory by natural enemies, original habitat restrictions, such as climate and soil type, may become less significant and *L. camara* can expand into previously marginal habitats (ISSG, 2006). *L. camara* forms dense thickets in forest gaps and increasing levels of disturbance favor successful invasions by the species (Macdonald *et al*. 1991). Shading plays a greater role as a limiting factor than any other, while surface soil macronutrient levels are also important, particularly when combined with canopy disturbances that increase light availability (Gentle and Duggin, 1997a). In Northern Queensland, Fensham *et al*. (1994) found a negative correlation between *L. camara* density and native vegetation canopy cover.

Tilman (1997), Stohlgren *et al*. (1998) and Davis *et al*. (2000) consider species rich communities as resistant to invasions but Rodgers and Parker (2003) describe the possibility of a positive association between species richness and alien invasibility. However, Fensham *et al*. (1994) found a negative correlation between species richness and *L. camara* density. In Australia alien invasions were found to be associated with more fertile soils (Gentle and Duggin, 1997a) and this according to Davis *et al*. 2000) implies that the physically harsh habitats had limited alien invasions because of poor availability of resources. On the Tiwi Islands of Australia *L. camara* was found to invade both less disturbed and severely disturbed sites (Gentle and Duggin, 1997a). According to Tilman, (1997), *L. camara* is exceedingly efficient at nutrient uptake and use enabling it to grow on highly impoverished soils and this gives it an advantage over native species in low fertility environments.

2.6 Distribution of *L. camara*

L. camara has established and spread in its introduced range worldwide at the cost of native species and habitats so much that the International World Conservation Union (IUCN) considers it to be among the world's 100 most invasive species (Lowe *et al*. 2004). Having been subject to intense horticultural improvement in Europe since the sixteenth century, it now exists in many different varieties throughout the world and invades pastureland in Australia, East Africa, Fiji, Hawaii, India, the Philippines, South Africa, Zimbabwe and Zambia, among others (Thomas and Ellison, 2000). The species was ranked the most significant weed of non-agricultural areas in southeastern Queens land (Day *et al*. 2003). In India, it is among the most widespread terrestrial invasive species today, particularly in dry-to-moist deciduous forests (Hiremath and Sundaran, 2005).

In Africa it is also widespread south of the Sahara Desert and particularly severe in South Africa, Kenya, Uganda, Tanzania, Zambia, Zimbabwe and Mozambique but also occurs in Ghana, Nigeria and Angola (Day *et al*. 2003). *L. camara* is currently rated the fourth most widespread invasive alien plant in South Africa occupying some 2.2 million hectares of forest and plantation margins, watercourses and savannas where it out competes and replaces other native vegetation (Simelane, 2002). In Zimbabwe it is threatening the moist evergreen rain forests of the Eastern Highlands (Timberlake and Musokonyi, 1994).

According to Day *et al*. (2003) and Sharm *et al*. (2005), the distribution of *L. camara* is still increasing, with many of the countries and islands that were listed in 1974 as not having *L. camara* being infested more recently (e.g. Galapagos Islands, Solomon Islands, Palau, Saipan, Tinian, Yap and Futuna Islands). They also highlighted that even in areas such as South Africa, India and larger islands such as New Zealand, where *L. camara* has been established for long periods of time, there is evidence that it is still spreading. Day *et al*. (2003) also pointed out that not only is the geographic range of *L. camara* still expanding in many areas, but also the density of infestations within its range is increasing and this has been recognized as a future threat to ecosystems in Australia, the Solomon Islands and Vanuata, and probably in many other countries.

2.7.0 General Effects of *L. camara*

2.7.1 Effects on Soils

Most changes in species composition reflect changes in soil water and nutrient availability and changes in availability of essential plant resources such as light, nutrients and water may result in a change in vegetation community composition (Clegg, 1999). Nutrient dynamics may become altered as a result of changes in the physical properties of the soil caused by the introduction of an alien species such as *L. camara* but it is not always the case that soil properties will be altered following alien species invasion (Ehrenfeld, 2003). *L. camara* population persistence also occurs through processes unrelated to allelopathy such as edaphic effects and changes in ecosystem functioning (Gentle and Duggin, 1997a). These processes may facilitate ongoing suppression of indigenous species by altering nutrient cycles and modifying microenvironments and disturbance regimes (van Wilgen and Richardson, 1985).

L. camara also has a negative effect on soil water supply (Hiremath and Sundaran, 2005). According to Day *et al*. (2003), dense stands of *L. camara* reduce the vegetation and the capacity of the soil beneath to absorb rain, which could potentially increase the amount of runoff and the subsequent risk of soil erosion in areas infected with *L. camara*. Ehrenfeld, (2003) found an increase in soil nitrate following *L. camara* invasion to the benefit of the *L. camara* and to the detriment of some native species and decline in other nutrients. In Australia, Gentle and Duggin (1997a) found that moisture content and pH were not significantly affected by *L. camara*. The allelochemicals produced by *L. camara* could alter the populations of soil microbial symbionts necessary for the early establishment of certain seedlings (Vranjic *et al.* 2000).

2.7.2 Effects on native plant species

Botanical species composition and structure is altered indirectly through the modified soil environment and directly through allelopathic means. Changes in environmental conditions generally lead to an increase in certain species at the expense of others (Clegg, 1999). Indirect changes in floral composition occur as a result of modification of factors such as the physical and chemical properties of soil, changes in competitive potential and light availability through the loss or introduction of new plants (Clegg, 1999).

Day *et al*. (2003) pointed out that *L. camara* could become the dominant understorey species in disturbed native forests, disrupting succession and decreasing biodiversity. Fensham *et al*. (1994) documented decline in native species richness with increasing levels of *L. camara* infestations in dry rainforest in north Queens land. Macdonald *et al*. (1991), in their study on Mascarene Islands, described the transformation of the semi-arid forest riparian vegetation and the replacement of forest patches by alien thickets of *L. camara*, *Rubus alceifolius* and *Boehmeira macrophylla*.

L. camara dense thickets reduce biodiversity through dominating understorey and excluding native species through smothering, reducing their recruitment and allelopathic effects (Simelane, 2002; Sharm *et al*. 2005). Allelopathy provides a potential explanation for its ability to form monospecific thickets (Gentle and Duggin, 1997b; Gentle and Duggin, 1998). Gentle and Duggin (1997b) provided evidence that *L. camara* is capable of interrupting regeneration processes by reducing germination, reducing early growth rates, and increasing mortality of indigenous species. They linked such changes to the ultimate disruption of community development because *L. camara* can aggressively compete with indigenous seedlings.

L. camara infestations have been so persistent in some areas that they have completely stalled the regeneration of rainforest for three decades (Day *et al*. 2003). Through shading and nutrient sequestration, *L. camara* also suppresses less competitive native vegetation and seedlings (Gentle and Duggin, 1997b; Gentle and Duggin, 1998). *L. camara* produces phytotoxins that suppress germination of native seeds (Fischer *et al*. 1994). Macdonald *et al.* (1991), in their study on Mascarene Islands, rated *L. camara* as the most threatening invasive alien species and found a decline in species richness with increase in *L. camara* density in forests.

According to Fensham *et al*. (1994) and Hiremath and Sundaran (2005), *L. camara*-climbing stems can reach up to more than 20 metres, getting into the forest canopy. This results in devastating crown fires when they burn. High *L. camara* density increases mid-storey fuel loads and intense fires kill the remaining canopy (Fensham *et al*. 1994), which subsequently promotes spread of *L. camara*. *L. camara* can greatly alter fire regimes in natural systems (ISSG, 2006). Day *et al*. (2003) indicated that *L. camara* competition may be responsible for the extinction of the shrub *Linium cratericola* and is a major threat to other endangered plants in the Galapagos Archipelago. Sharma *et al*. (2003) found that total diversity decreased with increase in *L. camara* density. Williams and West (2000) documented introduction of foreign genes into local plant populations by cross breeding. Higgins *et al*. (1999), in their prediction of plant invasion threats in South Africa, indicated that invasions can reduce native plant species richness by 50-86% and can increase the probability of recruitment failure of the dominant functional plant types found in fynbos by 40-80%.

2.7.3 Effects on Fauna

Apart from its negative impact on biodiversity, the *L. camara* plant is known to produce secondary compounds, which have been implicated in ungulate poisoning (Simelane, 2002; Hiremath and Sundaran, 2005). Sharma *et al*. (2007) indicated that ingestion of *L. camara* by grazing animals can cause cholestasis and hepatotoxicity, and both ruminants and non-ruminants are susceptible to the action of *L. camara* toxins, called lantadenes. Thomas and Ellison (2000) indicated that leaves and seeds of *L. camara* contain triterpernoids, which cause death through poisoning and photosensitivity.

In East Africa *L. camara* is known to harbour tsetse fly, which is an animal pest (Thomas and Ellison, 2000). Replacement of native vegetation by *L. camara* thickets may reduce the amount of available forage and habitat for native animals, which reduces the carrying capacity, and in Kenya; this is threatening the habitat of the sable antelope (Day *et al*. 2003). The spread of *L. camara* is seen as a threat to bird breeding populations and plant communities containing rare endemics (Thomas and Ellison, 2000). Simelane (2002) also documented the increase in wildfire intensity by *L. camara* thickets, which has disastrous effects on the native flora and fauna.

2.7.4 Other effects of *Lantana camara*

Removal of native plants could act to open up space for more light-loving alien seedling to germinate and thereby facilitate their invasion and spread (Ticktin *et al*. 2006). *L. camara* spoils scenery and has an adverse effect on recreation (Simelane, 2002). Malaria mosquitoes in India and tsetse flies in Rwanda, Tanzania, Uganda and Kenya shelter in *L. camara* bushes and are causes of serious health problems to humans (Day *et al*. 2003). In agriculture, it reduces crop productivity, interferes with harvesting and may affect economic viability of crops such as coffee, oil palm, coconuts and cotton (ISSG, 2006).

Dark (2004), documented the ability of alien invasive species to alter hydrological patterns, soil chemistry, moisture holding capacity and erodibility. They also change fire regimes. The subsequent loss in plant biodiversity results in alterations of soil chemistry, geomorphological processes, fire regimes, hydrology, levels of soil erosion, land transformation and disruption of ecosystem processes and functioning (Crowling *et al*. 1997). Day *et al*. (2003), considered loss of pasture as the greatest single cost of *L. camara* invasion in grazing areas in Queeensland. Reduction in environmental quality (Heffernan, 1998) may result from replacement of native vegetation by monospecific stands of *L. camara*. Whereas certain ecological functions can be regenerated through restoration ecology, there is no restoration biology to regenerate extinct species (Myers *et al*. 2000).

3.0 STUDY AREA

3.1 Location

The study was carried out in the northern part of Gonarezhou National Park (GNP). The Park is situated in the southeastern low veld corner of Zimbabwe, south of Chimanimani. Gonarezhou is Zimbabwe's second largest game reserve (after Hwange National Park), and, borders Mozambique's wildlife reserves and South Africa's Kruger National Park. The Park, which occupies the region 21°00'–22° 15'S and 30° 15'–32° 30'E, covers an area of 5053 km^2 (Mlambo (2007) and comprises two sections: Chipinda Pools, occupying three fifths of GNP in the north, and Mabalauta which occupies the remaining two fifths of the Park (Figure 1). In the southern and western directions, GNP borders Sengwe Communal Land and Malipati Safari Area respectively, while Gonakudzingwa Small-Scale Commercial Farming Area and Matibi No.2 Communal Lands lie in the northwest. To the north, GNP borders Sengwe Communal Lands and Malilangwe Trust, with Mahenye Ward of Ndowoyo Communal Lands lying to the northeast. To the east GNP borders Mozambique.

3.2 Relief

Gonarezhou is characterised by low relief, with altitude ranging from 162 m to 578 m above sea level. The Cretaceous sandstones form a plateau that is incised by the Save and Runde Rivers in the northeast, the Mwenezi River in the southwest, and to a smaller extent, the Guluene River in the centre. A number of scarp slopes, which rise more than 180 m above the river course, have been formed by river incision of the sandstones (DNPWLM, 1998). Sandstones on the north bank of the Mwenezi have been similarly, though less spectacularly incised to produce the Red Hills. Sandstone cliffs, together with the riparian woodlands on alluvial soils flanking the major rivers, form some of the most spectacular scenery in GNP.

3.3 Geology

The Jurassic basalt, being the major geological formation of the GNP, predominantly occurs along the northwestern boundary of the park with a small exposure in the Mwenezi Valley. The northern part of GNP is predominated by a variety of granophyres and granites of the late Jurassic. They form a minor exposure in the upper Guluene catchment area and a more extensive exposure in the Mwenezi Valley that extends into the Malipati Safari Area and most of the southern two-thirds of GNP is covered with cretaceous sandstones (DNPWLM, 1998).

3.4 Soils

The main soil categories are closely related to the surface geology in the park. On level sites, basalt weathers to produce moderately deep to shallow self-churning black clay soils that are highly calcareous and on hill slopes, basalt soils are lighter textured, reddish lithosols (DNPWLM, 1998). Granophyres and granite weather to produce moderately deep to shallow, dark, reddish grained and light to medium textured soils. These soils tend to be sodic in drainage depressions.

On level sites, the sandstones weather to form deep regosols with little or no profile differentiation. Regosols are highly permeable with low nutrient status, and high pH. Soil coloration varies with nature of parent sediments, the latter correlating with relief and elevation and in low-lying areas, along drainage lines; soils are largely derived from sandstones, and are heavily textured. At the base of scarp slopes, they are medium textured and gravely.

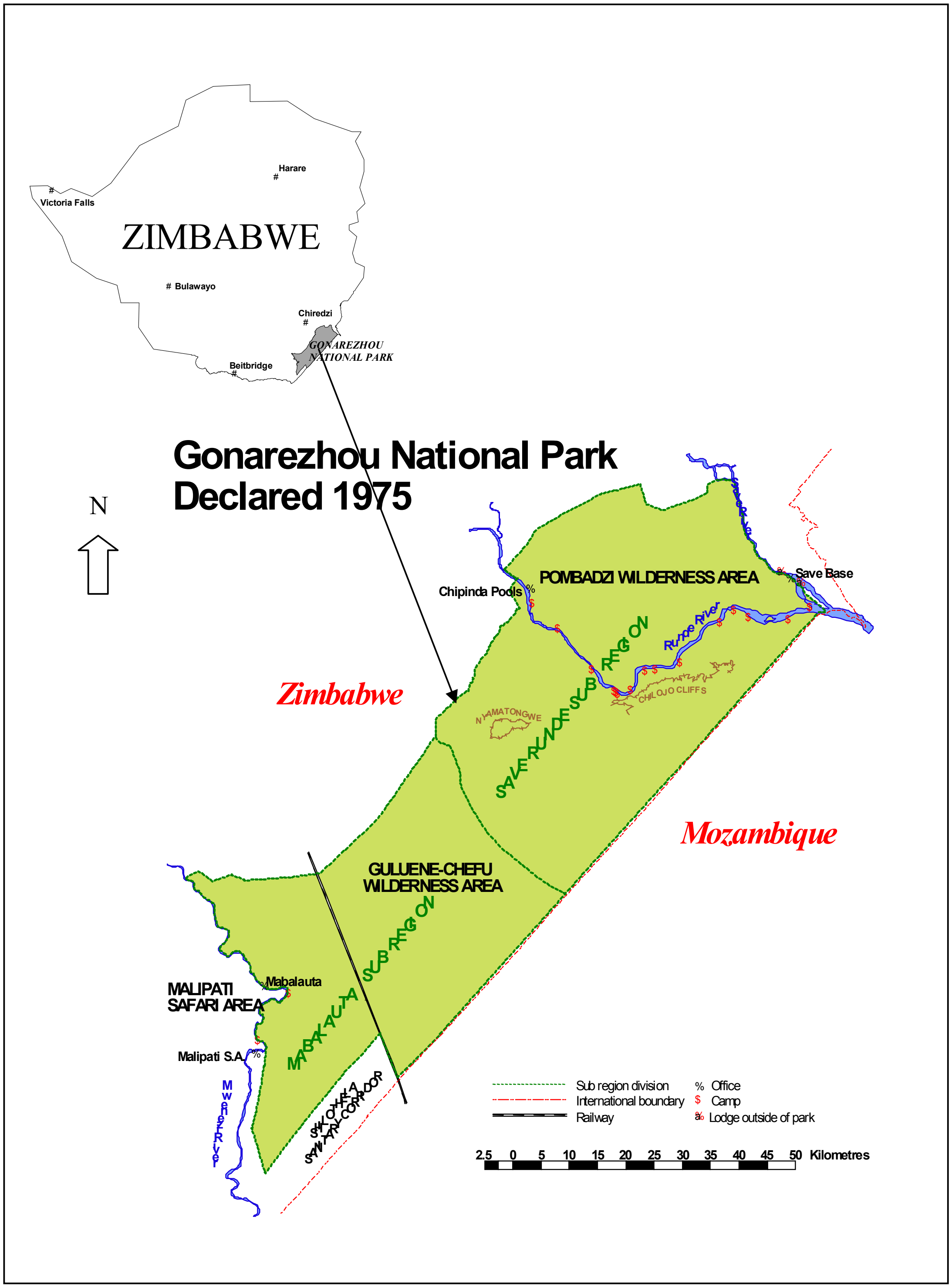


Figure 1: Map and location of Gonarezhou National Park

3.5 Climate

Mean annual precipitation for GNP (1972–2005) is 466.56 mm, and has varied between 92.3 mm in 1992 and 1114.6 mm in 2000 (Gandiwa, 2006). The climate of GNP therefore, may be regarded as semi-arid. Much of the rainfall falls between November and March. Droughts are a characteristic of GNP, and the most recent severe drought occurred in 1991/92 (DNPWLM, 1998).

Mean monthly maximum temperature ranges from 25.9°C in July to 36°C in January, with mean monthly minimum temperature ranging from 9°C in June to 24°C in January (1975–2005 Temperature records quoted from Gandiwa (2006)). The region has a short, dry winter season between May and July, and a hot wet summer season between November and April when daily temperatures frequently exceed 40^0C (DNPWLM, 1998).

3.6 Vegetation

A description of the vegetation of the northern part of Gonarezhou National Park was provided by Farrell (1968). The plant checklist for the GNP includes 924 species from 118 families and 364 genera, with 265 trees, 310 shrubs, 55 woody climbers and 137 grasses (DNPWLM, 1998). Figure 2 shows a remotely sensed false-colour composite species based vegetation map of the northern section of the GNP. The following vegetation types were recognized during surveys conducted in GNP (DNPWLM, 1998).

a) Mopane Woodland

This vegetation type is dominated by *Colophospermum mopane*, and covers approximately 40% of Gonarezhou. Mopane Woodland is mostly distributed along the larger river valleys, and is found in low altitude, low rainfall areas, that coincide with high temperature (Mapaure, 1994).

Mopane Woodland occurs on almost all soil types. Other species associated with this woodland type are *Grewia* spp., *Ximenia caffra* and *Euclea* spp.

b) Mopane Scrubland community

This woodland is characterized by multi-stemmed shrubs of *C. mopane* and patches of *Terminalia prunioides* with the dominant grass species including *Enneapogon cenchroides, Heteropogon contortus, Urochloa mosambicensis* and *Cenchrus ciliaris*. *C. mopane* sandveld ecotone complex (with *Combretum apiculatum*) occurs in broken, rocky country where *C. apiculatum* occurs frequently and in some areas dominates the *C. mopane*.

c) *Julbernadia globiflora* woodland

Occurring on the Cretaceous sandstone, the *Julbernadia globiflora* Woodland includes discrete patches of *Combretum* shrub savanna. Annual grasses and forbs in years of high rainfall dominate the herbaceous layer.

d) *Brachystegia glaucescens* Woodland

This woodland type has dense thickets occurring on the granophyre on the southern slopes of Chionja Hills. The woodland includes a number of shrub species such as *Gardenia resiniflua, Vitex mombassae, Monodora junodii* and *Bauhinia petersiana*. Dominant grasses in the *Brachystegia glaucescens* Woodland include *Panicum maximum, D. eriantha* and *Pogonarthria patens.*

e) Dry deciduous sandveld woodland and scrub

This vegetation community is species rich and occurs predominantly on sandstone uplands with deep sandy loamy soils on the watershed between Mwenezi and Runde rivers. Important species associated with this woodland community include *Pteleopsis myrtifolia, C. collium, Strychnos madagascariensis, C. zeyheri, Ochna pulchra, Diplorhynchus condylocarpon, Cassia abbreviata, Xeroderris stuhlmanii, Terminalia sericea, Acacia burkeii* and *Afzelia quanzenzis*. *U. mosambicensis* is the common grass associated with this vegetation type.

f) *Guibourtia conjugata* complex woodlands

The *Guibourtia conjugata* woodland is almost entirely restricted to the cretaceous sandstone and reaches a height of 12-15m tall. Understorey species include *Albizia anthelmintica, Vitex mombassae* and *Monodora junodii*. This woodland grades into *C. apiculatum-Strychnos innocua* woodland. The *Guibourtia conjugata-Baphia obovata* thickets occur with the following species: *Pterocarpus antunesii, Strychnos innocua, Pteleopsis myrtifolia* and *Monodora junodii.*

g) Mixed woodlands

The woodland, which is frequently associated with the *C. mopane* woodland on gravelly basalt, includes *Kirkia acuminata, Commiphora* spp. and *Adansonia digitata* open woodlands that occur with the following species: *Cassia abbreviata, Sclerocarya caffra, Pterocarpus rotundifolius* and *Commiphora pyracanthoides. Combretum fragrans-Terminalia stenostachya* open woodland is found together with *Pseudolachnostylis maprouneifolia* species among others. *Acacia nigrescens-A. welwitchii* tree savanna is widespread in the GNP. Common grasses include *Panicum maximum* and *Sorghum versicolor.*

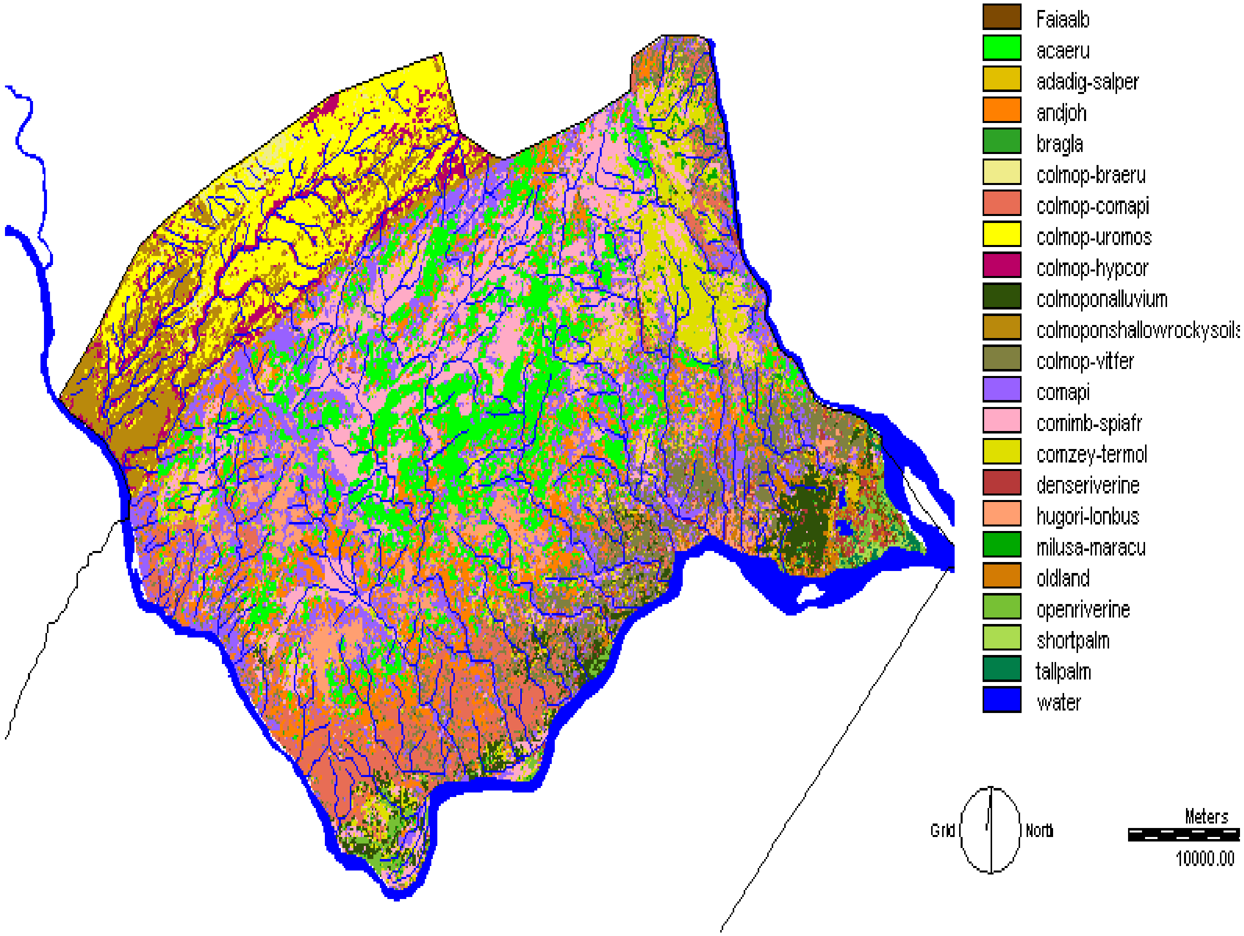
h) Riparian and alluvial woodlands

Riparian and alluvial woodlands are found along major river courses such as Save, Runde and Mwenezi, and other small streams. The dominant tree species in these woodlands include

Trichilia emetica, Cordyla africana, Kigelia africana, Combretum imberbe, Lonchorcarpus capassa, Albizia glaberrima, Acacia albida, A. tortilis, A. robusta, Ziziphus mucronata, and occasionally *Adansonia digitata*. In the understory of riverine and alluvial woodlands are *Croton megalobotrys, Grewia* spp., and *Combretum microphyllum. Maytenus senegalensis, C. imberbe, L. capassa* and *Acacia tortilis* dominate the alluvial deposits. Dominant grasses include *Panicum maximum, Urochloa mossambicensis* and *Digitaria* spp.

i) Other woodlands

Other woodlands in GNP include *Spirostachys africana-Terminalia prunioides, Milletia stuhlmannii, Phragmites* reed beds and *Ficus capreifolia* on sand bars and riverbanks.



Faidherbia albida
Acacia erubescens
Adansonia digitata-Salvadora persica
Androstachys johnsonii
Brachystegia glaucescens
Colophospermum mopane-Brachiaria eruciformis
Colophospermum mopane-Combretum apiculatum
Colophospermum mopane-Urochloa mosambicensis
Colophospermum mopane-Hyphaene petersiana
Colophospermum mopane on alluvium
Colophospermum mopane on shallow rocky soils
Colophospermum mopane-Vitex ferruginea
Combretum apiculatum
Combretum imberbe-Spirostachys africana
Combretum zeyheri-Terminalia mollis
Dense riverine
Hugonia orientalis-Lonchocarpus bussei
Millettia usaramensis-Markamia acuminate
Old cultivation land
Open riverine
Short palm
Tall palm
Water

Figure 2: Detailed vegetation map of the northern GNP (source Clegg, 2003)

3.7 Fauna

Gonarezhou National Park has a diverse vertebrate fauna that consists of 89 species of mammals, 400 species of birds, 76 species of reptiles, 28 species of amphibians and 50 species of fish (DNPWLM, 1998). The mammal fauna includes both large herbivores and carnivore species with the large herbivore community being dominated by elephant (*Loxodonta africana*) which makes up approximately 80% of the total biomass). Other dominant herbivores include buffalo (*Syncerus caffra*), giraffe (*Giraffa camelopardalis*) and impala (*Aepyceros melampus*). Elephant numbers in GNP decreased during the mid-1950s as part of the Tsetse Control Programmes (Clegg, 1999), and during the 1991/92 drought (DNPWLM, 1998). Elephant numbers however, have increased in recent years.

3.8 Land use History

Gonarezhou National Park was established in 1934 as a protected area, and designated a National Park in 1968 (DNPWLM, 1998) after numerous changes in land designations. Prior to 1934, most of what is now GNP was unoccupied. Small groups of the Shangaan people occupied part of the park along the Mwenezi, Save and Runde rivers. The Shangaan people depended on hunting, gathering, fishing, crop production and trading but frequent droughts limited crop production. When GNP was designated a national park in 1975 other tribes were resettled in the adjacent Matibi No.2 Tribal Trust Lands.

3.9 Recent Human settlements in GNP

The establishment of illegal human settlement in year 2000 has influenced the ecology of GNP. About 16,000 ha (3.2% of GNP) of land in the northwestern part of GNP are now illegally settled. Anthropogenic activities in the area have led to increased woodland destruction and altered animal distributions in Northern GNP (Gandiwa, 2006).

4.0 METHODS

4.1 Experimental design and demarcation of plots

A field reconnaissance survey was done in the Northern part of Gonarezhou National Park to establish areas with *L. camara* occurrences. Stratified Random Sampling (Mueller-Dombois and Ellenberg, 1974) was used in this study with three categories. The area of *L. camara* occurrences in the northern part of Gonarezhou National Park was stratified into 3 categories: heavily invaded (*L. camara* cover ≥50%), moderately invaded (0%<*L. camara* cover<50%) and uninvaded (no *L. camara*) areas.

After the reconnaissance of the area, a total of 20 sampling plots were randomly selected using computer generated random numbers based on GNP topographical map grid square intercept system. Each plot, measuring 10mx10m, was located at least 30m from rivers and roads to avoid possible river and road effects. Six plots were sampled from the heavily invaded category and seven in each of the moderately invaded and the uninvaded categories. The seventh plot in the heavily invaded category was not sampled because an accident occurred that resulted in withdrawal from the field. The ″crosses″ (×s) on Figure 3 show the location of sampling sites in Northern GNP.

The plots were pegged on the ground with four metal pegs using a 50m tape measure, laid around the plot perimeter to assess tree floristic composition and structure. Within each plot, a subplot of 4mx4m was randomly demarcated for shrub component assessment. For herbaceous species, five 1mx1m quadrats were randomly thrown and assessed within each 10mx10m plot. Random throws were used for randomisation of the smaller plots and quadrats. Explanatory variables were also assessed in each plot. These plot sizes were adopted from Mueller-Dombois and Ellenberg (1974).

In each plot, altitude and location from a global positioning system were recorded using a Geographical Positioning system (GPS) unit.

4.2 Vegetation Assessment

Both woody and herbaceous vegetation components were assessed at the end of the rainy season (April-May 2007) when species composition was best represented (Walker, 1976). The woody vegetation comprised trees and shrubs. In this study, trees were defined as rooted, woody, self-supporting plants ≥ 3 m high with one or a few definite trunks (≥ 6cm in basal stem diameter) while shrubs were defined as rooted, woody, self-supporting plants <3 m high and < 6cm in stem basal diameter (Brown *et al*. 2005).

All plant species encountered in each plot were identified in the field using field identification guides (Linley and Baker, 1972; S.C.N.V.Y.O. 1972; Palgrave, 1983; Plower and Drummond, 1990; Carruthers, 1997); and those not identified were plant pressed for later identification at the National Herbarium, Harare. All woody plants rooted within the plot were recorded and measured. Woody plants occurring along plot margins were included if at least half of the rooted system was inside the plot (Walker, 1976).

4.2.1 Woody species attributes

Woody species in the plots were identified using field identification guides and species richness was determined by counting the number of different species present. Woody vegetation heights were measured using a ranching rod. Height is the vertical distance from the ground to the highest living part of a plant (Anderson and Ingram, 1993). For multi-stemmed plants, only the height of the tallest stem was recorded.

Crown diameter method (Mueller-Dombois and Ellenberg, 1974) was used to estimate canopy cover. Two greatest crown diameters (D1and D2) of each woody plant, perpendicular to each other were measured to the nearest 0.1m and averaged to get the mean diameter (D). The mean diameter was used to estimate canopy cover using the formula:

$$\textbf{Canopy cover} = \Pi(D/2)^2$$

Where D is the mean crown diameter

Circumference of each plant stem was measured at breast height to the nearest centimeter. A flexible 10m tape was used to measure the stem circumferences. From the stem circumferences, basal area was calculated using the formula:

$$\textbf{Basal area} = (C^2/4\pi)$$

Where C is stem circumference.

For multi-stemmed species, stems were treated individually and then added to get total basal area for the plant.

Density (e.g. plants per ha) for each plot was calculated using the formula:

$$\textbf{Density (plants/ha)} = \textbf{Number of plants} \frac{\times 10{,}000\ m^2}{\text{Plot area } (m^2)}$$

4.2.2 Herbaceous species attributes

1mx1m quadrats were randomly thrown and sampled for herbaceous species attributes within each plot, with each species encountered being identified using field identification guides. Five quadrats were assessed in each plot for species presence/absence. Percentage herbaceous cover was also estimated in each quadrat and averaged to give mean cover for each plot.

Percentage *L. camara* cover was estimated for each plot by estimating the proportion of the plot under *L. camara* cover.

4.3 Soil Properties

4.3.1 Physical and chemical properties.

The method used by Stohlgren *et al.* (1998) was adopted. Five soil samples from the top 15cm of the soil were collected from the four corners and center of each plot using a soil auger. The soil samples from the same plot were thoroughly mixed and bulked into a composite sample in an air-proof polythene bag. The samples were analyzed for texture, moisture content, pH, nitrogen, phosphorus and potassium as outlined in (Anderson and Ingram, 1993; Okalebo *et al.* 2002). The analyses were carried out with the assistance of Analytical Services Laboratory, Department of Soil Science and Agricultural Engineering, University of Zimbabwe.

4.3.2 Soil Depth

Soil depth was measured by hammering a metal rod into the ground until the bedrock was encountered (Burke, 2001) at all portions of soil sample collection in each plot. The depths were averaged to get the mean depth for the plot.

4.4 Data Analysis

Analysis of variance (ANOVA), classification and ordination were used for data analysis. Geographic Information Systems (GIS) were used to map the spatial distribution of *L. camara* in Northern Gonarezhou National Park. Soil Adjusted Vegetation Index (SAVI) for GNP was calculated from the Moderate Resolution Imaging Spectrometer (MODIS) satellite image of March 17, 2007. This is the period when woody vegetation is at the peak of its greenness in Zimbabwe. The MODIS satellite images are provided every 1 to 2 days for the entire earth's surface by The National Aeronautics and Space Administration (NASA) Earth Science Enterprise (ESE) (Jensen, 2005). SAVI and all the measured variables were subjected to Linear Regression Analysis. SAVI is a vegetation index that accounts for and maximises, the effect of soil background conditions (Gilabert *et al*. 2005).

GIS refers to a system used for storing, manipulating, and retrieving spatially referenced data, which includes systems designed to capture spatial and non-spatial information and to process it (Mironga, 2004). Data in GIS are its database, usually composed of data planes derived from different data sources, and this combination of data sets allows data interpretation. According to Mironga (2004), models can be created that describe existing relationships among landscape components, predict future plant distributions and assist in making ecologically sound management decisions. Ground truthing was done to affirm the validity of the model that was used to map the distribution of *L. camara* in Northern GNP.

Variables included in data analysis were number of species per plot (S), Shannon Index of Diversity (H'), species evenness (E), herbaceous cover, woody plant height, basal area, density, canopy cover and species frequency. *L. camara* cover, altitude, soil pH, texture, nitrogen, phosphorus, potassium, depth and moisture were also included as explanatory variables.

Shapiro-Wilks W test for normality was performed on both vegetation and explanatory data to test for the normality assumption of ANOVA using STATISTICA version 7. One-way ANOVA was used to test for significant differences in both vegetation and explanatory variables among the three categories of *L. camara* intensity, using STATISTICA version 7 package. Significant differences in height and basal area size class distributions among the three categories were also tested using χ^2 tests available in MINITAB. Descriptive statistics (means and standard errors) were calculated using STATISTICA for all the measured variables. The Shannon Index (H') was calculated using the formula:

$$H' = -\sum pi \ln pi$$

Where p_i is the proportion of species **i** and ln is the natural logarithm (Ludwig and Reynolds, 1988).

Evenness was calculated using the formula:

$$E = \frac{H'}{\ln S}$$

Where S is species richness (Ludwig and Reynolds, 1988).

Vegetation species data and explanatory data from the 20 plots were subjected to cluster analysis and ordination (ter Braak and Smilauer, 1998) to explore the relationship between composition and structure of vegetation and the measured explanatory variables. Hierarchical Cluster Analysis (HCA) using the average linkage method was performed on a matrix of plots by species, using species presence/absence data as described by Anderson and Ingram (1993) in MINITAB. This was done to produce a classification identifying similarities among the plots based on species composition. Hierarchical Cluster Analysis was also used to classify the plots with respect to soil properties (soil pH, depth, texture, N, P, K and moisture).

Ordination collectively describes the multivariate techniques that arrange sites along axes on the basis of data on species composition (Jongman *et al*. 1995). Ordination arranges the points such that the points that are close together correspond to sites that are similar in species composition and points that are further apart correspond to sites that are dissimilar in species composition (Gauch, 1982; ter Braak and Smilauer, 1998). The aim of canonical ordination is to detect the main pattern in the relations between the species and the observed explanatory variables (ter Braak, 1995). Cluster analysis (CA) classifies sites, species or variables with respect to similarity or dissimilarity (Anderson and Ingram, 1993; van Tongeren, 1995), and a common goal in community ecology is to identify homogeneous communities from samples taken over diverse environments (Ludwig and Reynolds, 1988).

Both species and explanatory data were analysed using ordination: Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). Detrended Correspondence Analysis (DCA), an indirect gradient analysis technique, was performed on basal area, abundance, height and presence/absence data to explore relationships among various plant species and the underlying explanatory variables. DCA is used when environmental variables are not available and relationships are detected indirectly with species data only (ter Braak and Smilauer, 1998). DCA is capable of handling large, complex data sets, and uncovering extremely long ecological gradients (McGarigal *et al*. 2000). Unlike Principal Components Analysis, DCA is not subject to arch and compression effects and it performs particularly well when the data have non-linear and unimodal distributions (McGarigal *et al*. 2000) and most ecological data are often non-linear and unimodal. However, the most important limitation of DCA is its sensitivity to outliers and discontinuities in the data.

CCA is a technique that integrates regression and ordination techniques into a method of multivariate direct gradient analysis that is used to detect unimodal relationships between species and explanatory variables (ter Braak and Smilauer, 1998). The relationships can be shown in an ordination diagram by vectors for the explanatory variables, with lengths proportional to their importance in explaining the variation and directions showing their correlation with each axis (Mapaure and McCartney, 2001). The explanatory variables are represented by arrows that point in the direction of maximum variation (Velazquez, 1994).

CCA detects patterns of variation in the species data that can be explained best by the observed explanatory variables (McGarigal *et al*. 2000). Since comparison of results will provide information beyond what DCA or CCA analysis alone can provide, McGarigal *et al*. (2000) recommended that DCA be used whenever CCA is performed. Both DCA and CCA were carried out using the programme package CANOCO for Windows (version 4) (ter Braak and Smilauer, 1998). The statistical significance of the ordination was tested using an unrestricted Monte-Carlo permutation test available in CANOCO (ter Braak, 1995).

5.0 RESULTS

5.1 Distribution of *L. camara*

Regression Analysis revealed that *L. camara* cover was negatively correlated with Soil Adjusted Vegetation Index (SAVI). A regression model was, therefore, generated with SAVI as a predictor to predict *L. camara* spatial distribution in the park. The following regression model was generated and used for the prediction:

***L. camara* cover =110.262 –336.910(SAVI)**

Where SAVI is the Soil Adjusted Vegetation Index. The coefficient of determination was 37.832% (Appendix 7).

A map of the distribution of *L. camara* in Northern Gonarezhou National Park (Figure 3) was then generated in a GIS environment using the regression model at 5% level of significance. Ground-truthing revealed that the model was about 87% (13 out of 15 sites visited had *L. camara*) reliable in predicting the occurrence of *L. camara* in the park. Figure 4 is the verification map showing the location of sites used for ground-truthing in the study area.

L. camara was found to be most prevalent in the riparian vegetation and in the low-lying areas, especially along Save, Mwenezi and Runde Rivers as shown on figure 3.

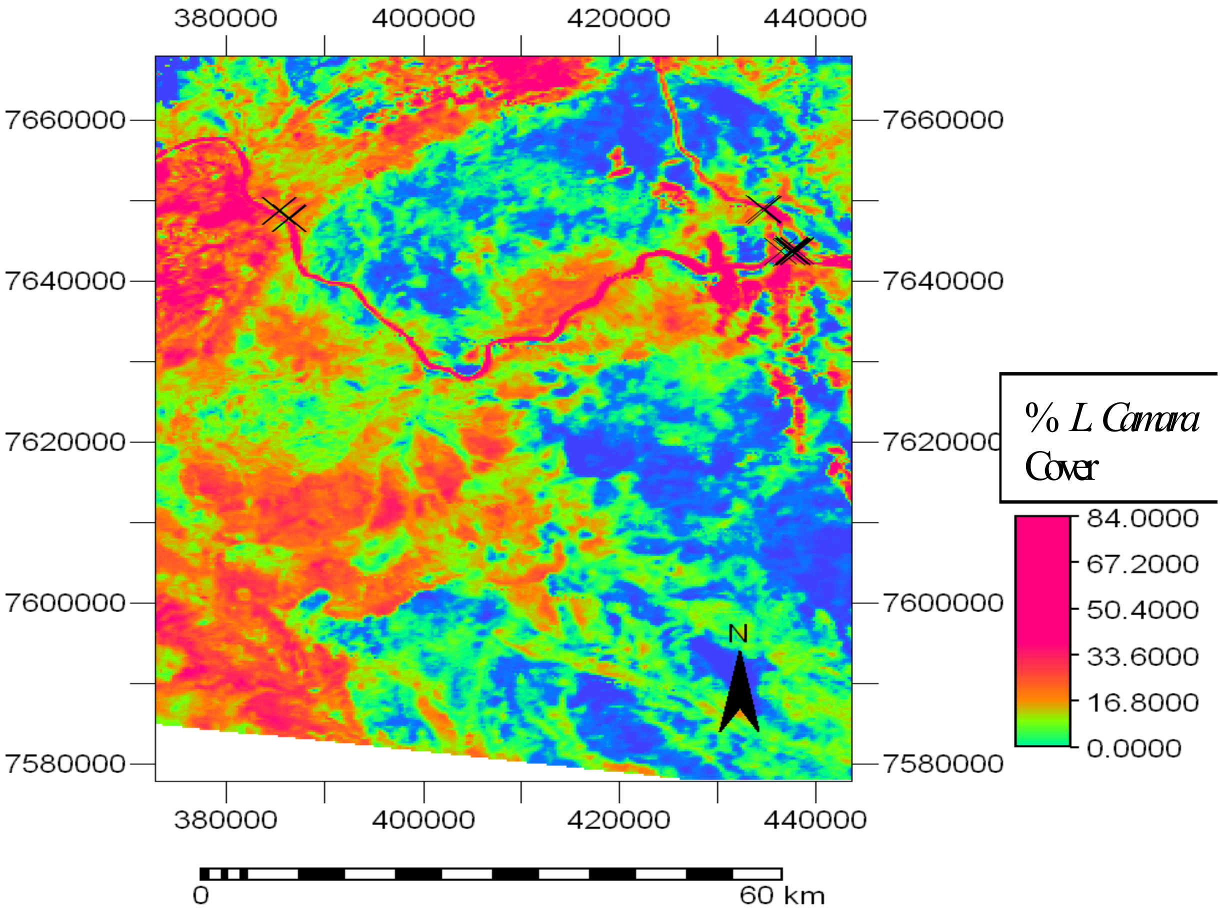


Figure 3: Modelled Spatial Distribution of Percentage *L. camara* cover in Northern Gonarezhou National Park.

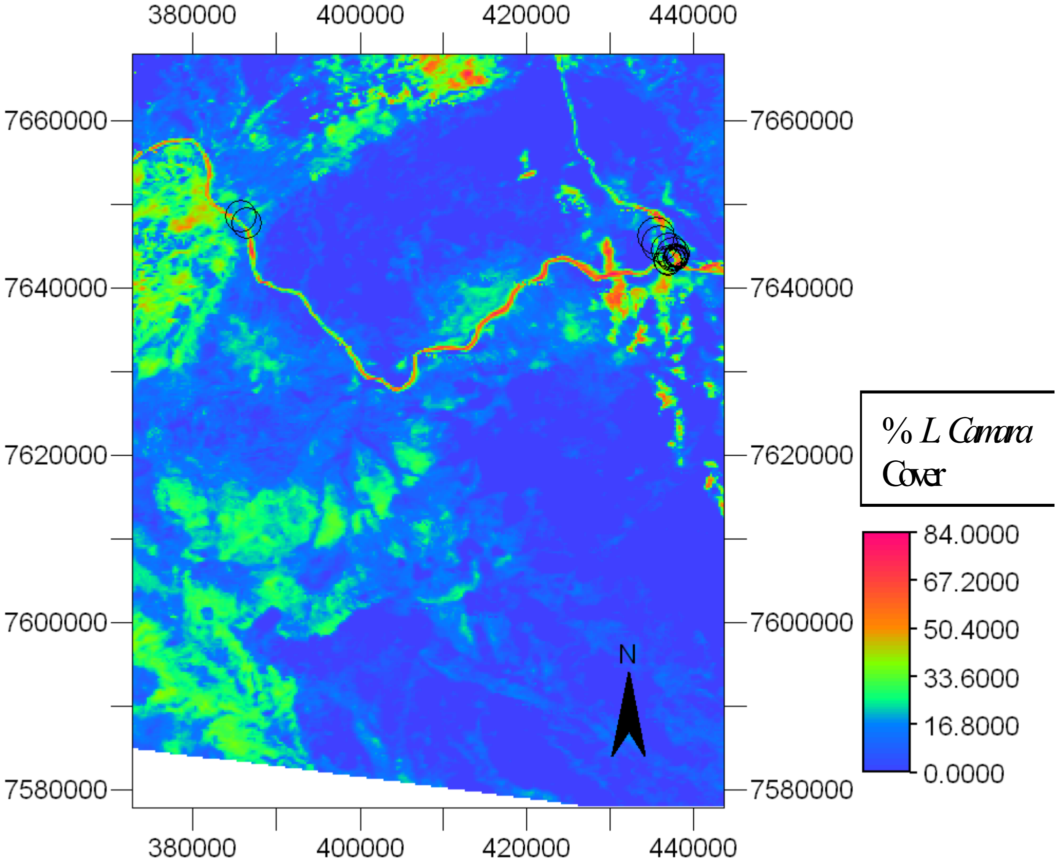


Figure 4: Location of sites used for ground-truthing the occurrence of *L. camara* (%) in Northern Gonarezhou National Park.

5.2 Vegetation Classification

A total of 41 woody and 27 herbaceous plant species were identified in the twenty plots assessed during this study (Appendix 3). The most common woody species identified in the study area were *Lonchocarpus capassa, Dichrostachys cinerea, Tabernaemontana elegans, Diospyros mespiliformis* and *Grewia monticola* in decreasing order of dominance. Hierarchical cluster analysis separated the plots into three distinct groups with respect to species presence/absence data (Figures 5 and 6) and explanatory variables (Figure 7). The three clusters corresponding to plots from the uninvaded (Group 1), moderately invaded (Group 2) and heavily invaded (Group 3) categories (Figures 5 and 7) were produced based on differing floristic associations and explanatory variables.

Distinct groups of the floristic associations were produced when woody species frequency was used (Figure 5). These groups were however distorted with the inclusion of herbaceous species. The categories of *Lantana camara* intensity could not be clearly defined when herbaceous species frequency was included in the clustering (Figure 6).

However, The heavily invaded category was dominated by *Lonchocarpus capassa, Dichrostachys cinerea, Tabernaemontana elegans, Grewia monticola* and *Phyllanthus reticulates*. While *Panicum maximum* dominated the herbaceous layer followed by *Achyranthes aspera var. sicula* and *Setaria incrassata, Achyranthes aspera var. sicula* was most dominant in the heavily invaded category followed by *Panicum maximum*. *Panicum maximum* was present in almost all the sampled plots except in two plots from the heavily invaded category.

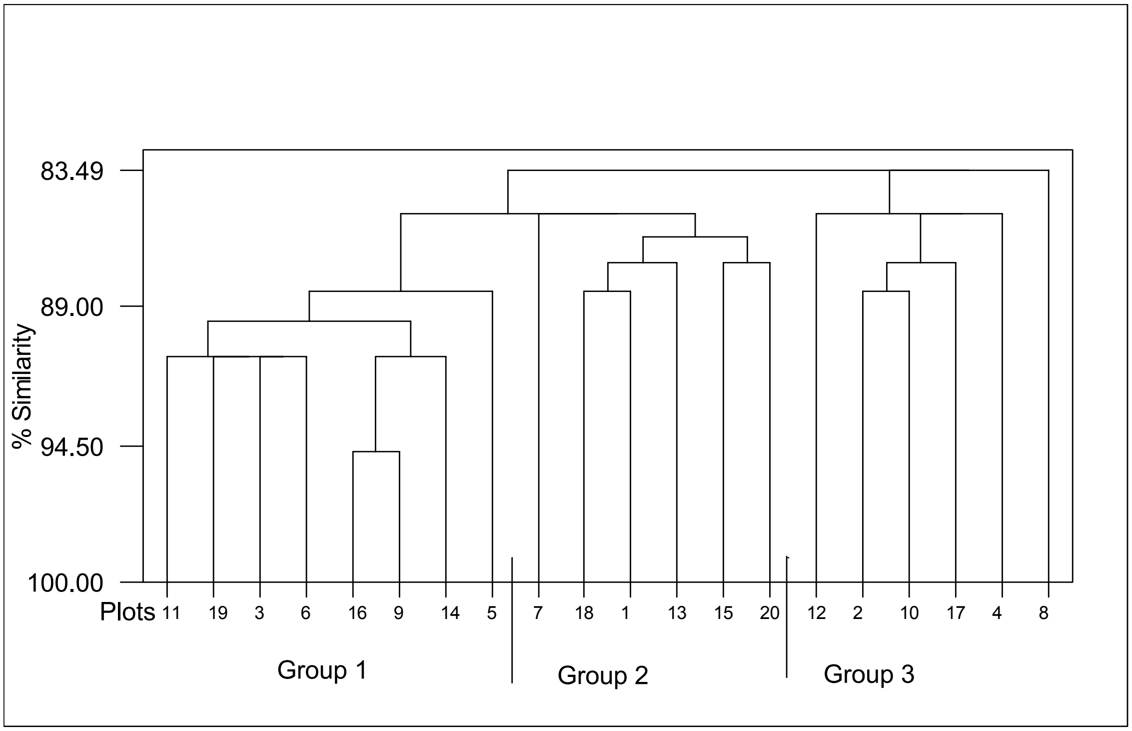


Figure 5: Hierarchical Cluster Analysis dendrogram of plots based on woody species presence/absence in Northern GNP.

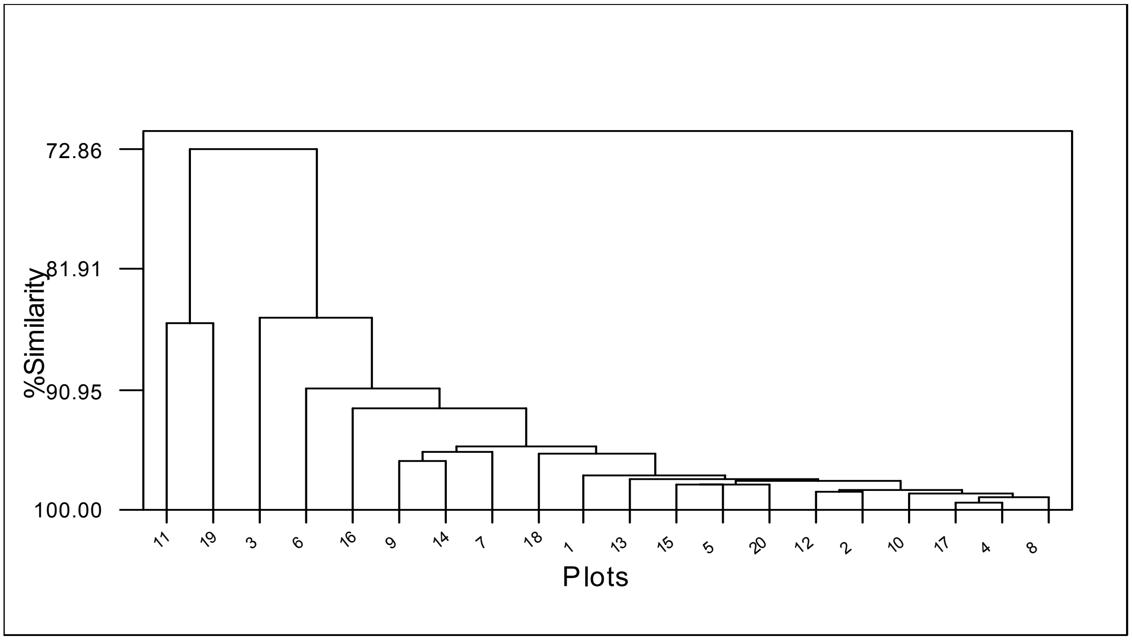


Figure 6: Hierarchical Cluster Analysis dendrogram of plots based on woody and herbaceous species presence/absence in Northern GNP.

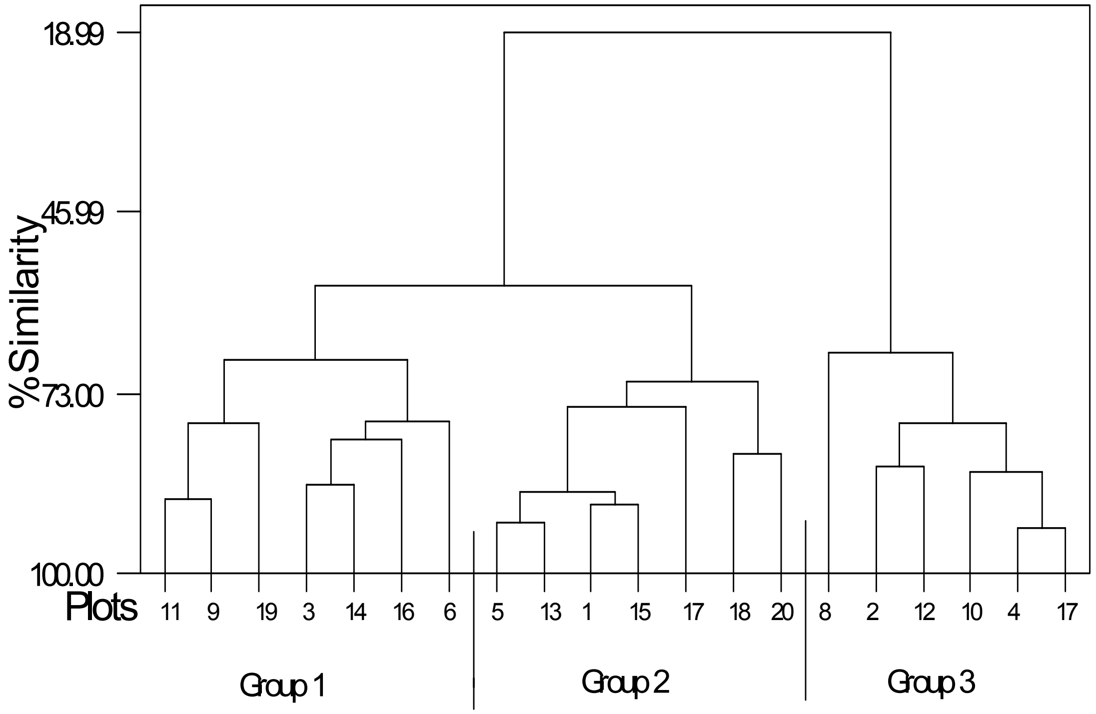


Figure 7: Hierarchical Cluster Analysis dendrogram of plots based on explanatory variables in Northern GNP.

5.3 Basal Area

There were significant differences in mean woody vegetation basal area among the three *L. camara* intensity categories (F=8.5026, P<0.05). The uninvaded recorded the highest mean basal area followed by the moderately invaded and the heavily invaded recorded the least mean basal area (Table 1). The χ^2 tests showed significant differences in size class distributions of woody species basal area among the three categories (χ^2 =14.513, Df =6, P =0.025) (Appendix 4). The uninvaded recorded the highest frequency of the smaller size class woody plants (<100 sq cm) with the heavily invaded recording the lowest frequency (Figure 8). However, the smallest size class (<100 sq cm) dominated in all the three categories (Figure 8). The basal area size classes showed a reverse-J shape in all the three categories. The larger size class (>1000 sq cm) was dominated by *Trichilia emetica*, *Lonchocarpus capassa, Diospyros mespiliformis* and *Combretum imberbe*.

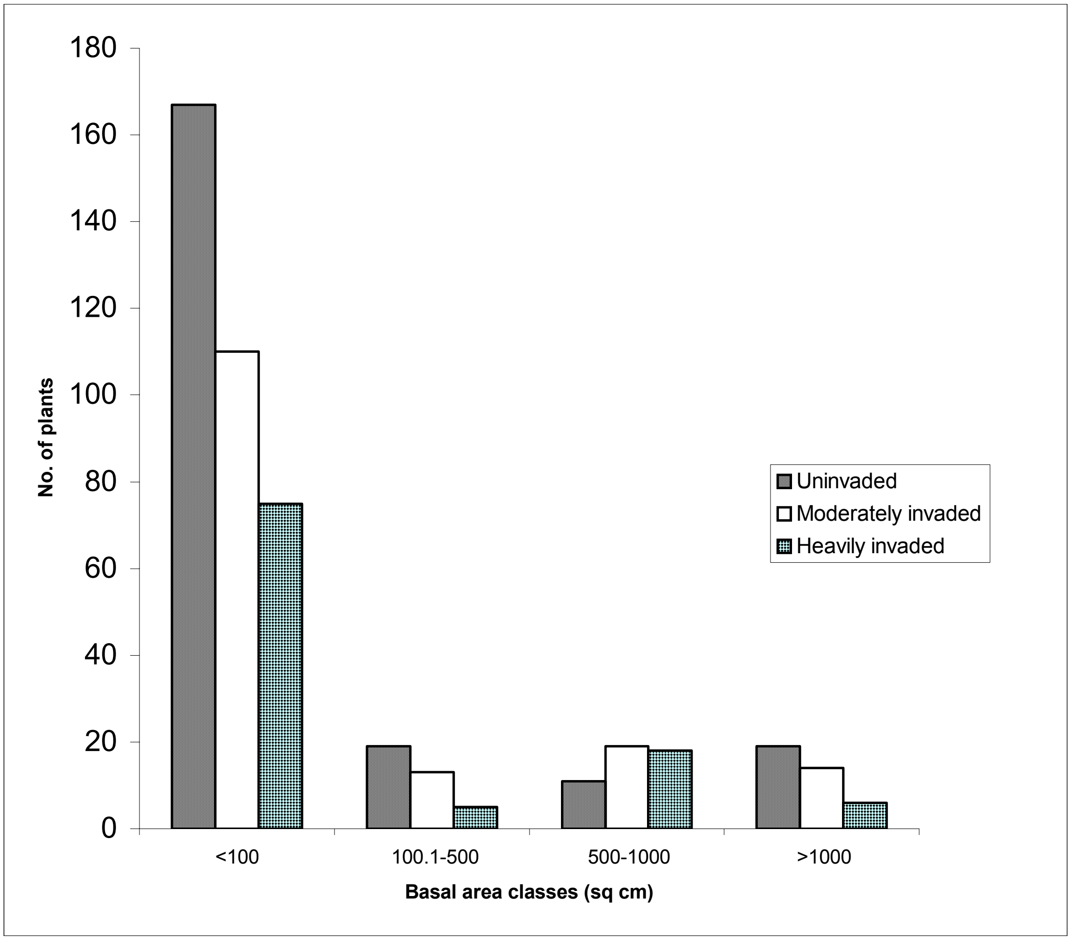


Figure 8: Basal area size class distribution of woody species in the three levels of *L. camara* invasion in Northern GNP.

5.4 Woody plant Height

Both mean tree and shrub heights were not significantly different among the three levels of *L. camara* invasion. However, height classes differed significantly among the three levels of *L.*

camara invasion with the uninvaded recording the highest frequencies of plants less than 2m in height (χ^2 =26.738, Df =8, P =0.001) (Appendix 4). The heavily invaded recorded the lowest frequencies of plants less than 2m in height (Figure 9). *Faidherbia albida, Trichilia emetica, Diospyros mespiliformis, Ficus capensis, Lonchocarpus capassa* and *Combretum imberbe* dominated the size class greater than 20m. Height size class distributions also revealed a reverse-J shape in all the categories.

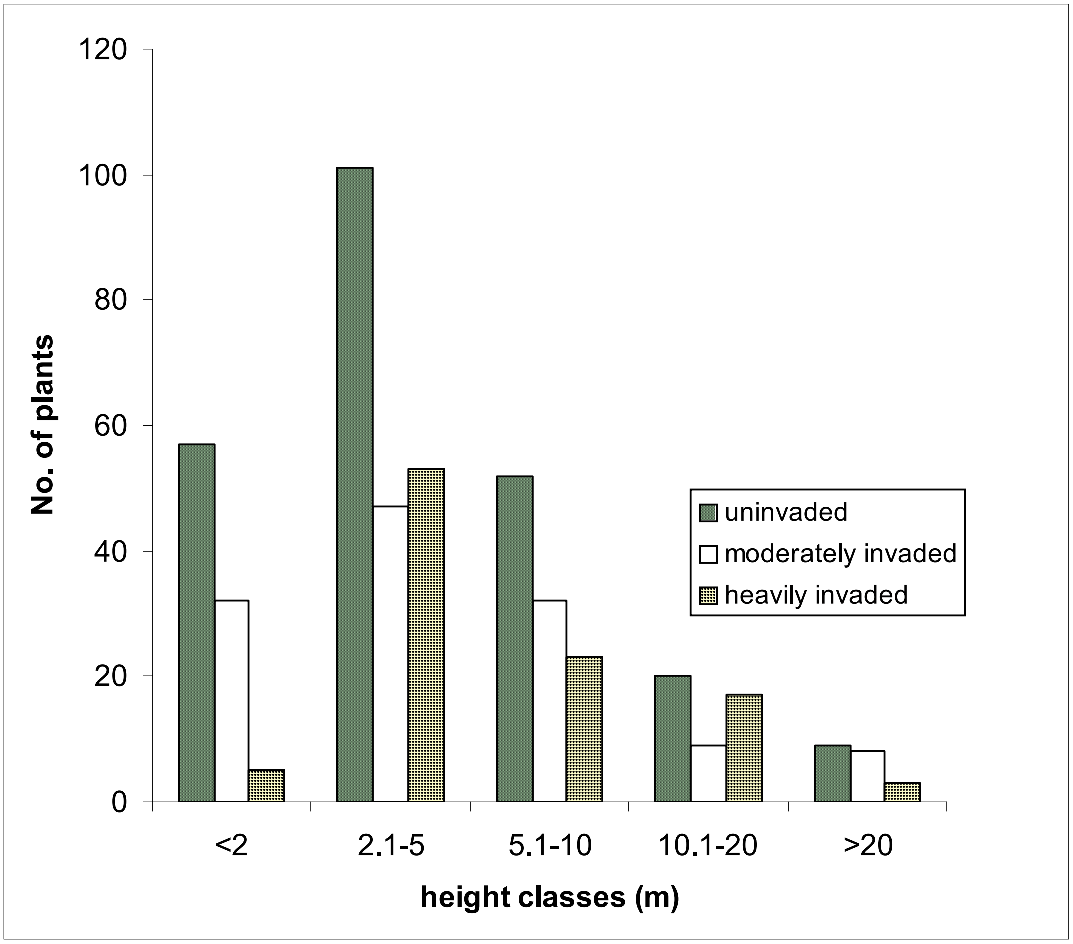


Figure 9: Height size class distribution of woody species in the three levels of *L. camara* invasion in Northern GNP.

5.5 Species Diversity and Richness

Species diversity and richness varied significantly among the three levels of *L. camara* infestation as revealed by the Shannon-Winner Index of Diversity (H') and species richness (S) (F= 9.616, P< 0.05; F=22.1083, P<0.05, respectively). The uninvaded category had the highest species diversity and species richness followed by the moderately invaded, and the heavily invaded was the least diverse amongst the three categories (Table 1). Species evenness showed no significant differences among the categories.

5.6 Woody Plant Density

Analysis of variance on both mean tree density and mean shrub density showed significant differences among the *L. camara* levels (F=6.9241, P<0.05; F=10.1400, P<0.05 respectively). The heavily invaded category recorded the lowest mean densities with the uninvaded recording the highest densities of woody plants (Table 1).

5.7 Canopy Cover and Herbaceous Cover

Mean canopy cover and mean herbaceous layer cover decreased with increase in *L. camara* invasion (Table 1). The two variables showed significant differences with change in *L. camara* cover (F=12.7283, P<0.05; F=40.860, P<0.05 respectively). In the uninvaded categories canopy cover was well more than 200%, and slightly more than 100% in the moderately invaded but was below 100% in the heavily invaded category.

Table 1: Means and standard errors of the vegetation attributes in the different intensities of L. camara in Northern GNP.

Variable	Uninvaded	Moderately Invaded	Heavily Invaded
H'	1.875 ± 0.084	1.621± 0.084	1.334 ± 0.090
S	14.571 ± 0.670	9.571 ± 0.700	8.167 ± 0.756
E	0.707 ± 0.035	0.723 ± 0.035	0.636 ± 0.0382
Tree Density/ha	857.143 ± 69.065	542.857 ± 69.065	533.333 ± 74.598
Shrub Density/ha	4375.000 ± 237.712	3482.143 ± 237.712	2812.500 ± 256.758
Herb cover	70.114 ±2.612	48.229 ± 2.612	36.150 ± 2.821
Tree height (m)	10.016 ± 1.188	9.487 ± 1.188	9.331 ± 1.283
Shrub height (m)	2.363 ± 0.098	2.128 ± 0.098	2.302 ± 0.106
Basal area	1.380 ± 0.174	0.896 ± 0.174	0.322 ± 0.188
Canopy cover	254.271 ±26.254	105.415 ± 26.254	76.016 ± 28.358

5.8. Explanatory Variables

Significant differences in soil nitrogen and phosphorus levels were recorded amongst the three levels of *L. camara* infestation (F=183.825, $P<0.05$; F=146.200, $P<0.05$ respectively). The heavily invaded category recorded the highest mean soil nitrogen and phosphorus followed by the moderately invaded with the uninvaded recording the lowest levels (Table 2). The three levels of *L. camara* invasion recorded significant differences in soil potassium (F=5.4183, $P<0.05$). The highest soil potassium levels were recorded in the uninvaded category and the lowest in the heavily invaded category (Table 2). Mean soil moisture varied significantly among the three levels of *L. camara* infestation (F=17.3547, $P<0.05$). Mean soil moisture was highest in the uninvaded category followed by the moderately invaded and was lowest in the heavily infested category (Table 2). However, there were no significant differences in altitude, soil texture (clay, silt and sand content), pH and depth among the three categories.

Table 2: Means and standard errors of the explanatory variables in the different intensities of *L. camara* in Northern GNP.

Variable	Uninvaded	Moderately Invaded	Heavily Invaded
Soil depth (cm)	37.143 ± 5.667	55.000 ± 5.668	52.833 ± 6.123
PH	6.729 ± 0.142	7.000 ± 0.142	6.767 ± 0.154
PpmP	3.129 ± 0.815	11.600 ± 0.815	23.617 ± 0.881
PpmN	25.914 ± 0.954	32.286 ± 0.954	51.983 ± 1.031
K (me%)	1.153 ± 0.127	1.129 ± 0.127	0.600 ± 0.138
% Clay	14.143 ± 1.923	11.286 ± 1.922	12.500 ± 2.076
% Silt	18.714 ± 3.111	17.429 ± 3.111	20.833 ± 3.361
% Sand	67.143 ± 4.439	71.143 ± 4.439	66.667 ± 4.795
% Moisture	13.917 ± 0.985	7.727 ± 0.985	5.900 ± 1.064
Altitude	208.309 ± 23.098	225.291 ± 23.098	194.157 ± 24.949
% *L. camara* cover	0.000 ± 2.906	30.714 ± 2.906	71.667 ± 3.139

5. 9 Main Gradients in Native Vegetation Composition

Detrended Correspondence Analysis (DCA) based on species basal area produced the summary output shown in Table 3. The four axes account for 37% of the species variance and have eigen values of 0.977, 0.944, 0.739 and 0.372 respectively. These eigen values that are greater than 0.5 imply a good separation among species, which is a turnover in ecological conditions along these axes. The first axis accounted for 97.7%, while axes 2, 3 and 4 accounted for 94.4%, 73.9% and 37.2% of the observed variation respectively. The first axis separated the species along a soil nutrient gradient while the second axis separated the species along the texture gradient. The plots and the species were separated by eye into three major groups (Figure 10). Similar plots, and species that respond to the same explanatory variables tend to be closer together on the ordination diagrams. The points that are close together correspond to plots that are similar in species composition, and points that are far apart correspond to plots that are dissimilar in species composition. The DCA results are in support of the cluster analysis results (Figure 5).

Group 1 comprises plots (3, 6, 9, 14, 16 and 19) from the uninvaded category and the associated species. However, plot 11 from the uninvaded category was classified in Group 3. Group 1 had the highest mean soil moisture, potassium level and Clay content. This group is associated with species such as *Colophospermum mopane, Acacia ataxacantha, Spirostachys africana, Diphorhynchus condylocarpon* and *Lecaniodiscus fraxinifolius.*

Group 2 is composed of plots (1, 5, 15, 18 and 20) from the moderately invaded category. Though plots 7 and 13 belong to Group 2, they were classified in Group 3. Species such as *Leucosidea sericea, Bridelia carthatica, Grewia monticola, Tabernaemontana elegans* and *Diospyros loureiriana* are associated with this group.

Plots (2, 4, 8, 10, 12 and 17) from heavily invaded category form Group 3. Associated with this group, are species such as *Lonchocarpus capassa*, *Diospyros mespiliformis, Dichrostachys cinerea, Thilachium africanum, Kigelia africana, Xeroderris stuhlmannii, Gardenia volkensii* and *Vitex payos.*

Table 3: Detrended Correspondence Analysis (DCA) summary output on the basis of basal area in Northern GNP.

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.977	0.944	0.739	0.372	8.200
Lengths of gradient	:	4.873	6.657	4.716	3.027	
Cumulative percentage variance of species data	:	14.9	25.4	32.4	37.0	
Sum of all unconstrained eigenvalues						8.200

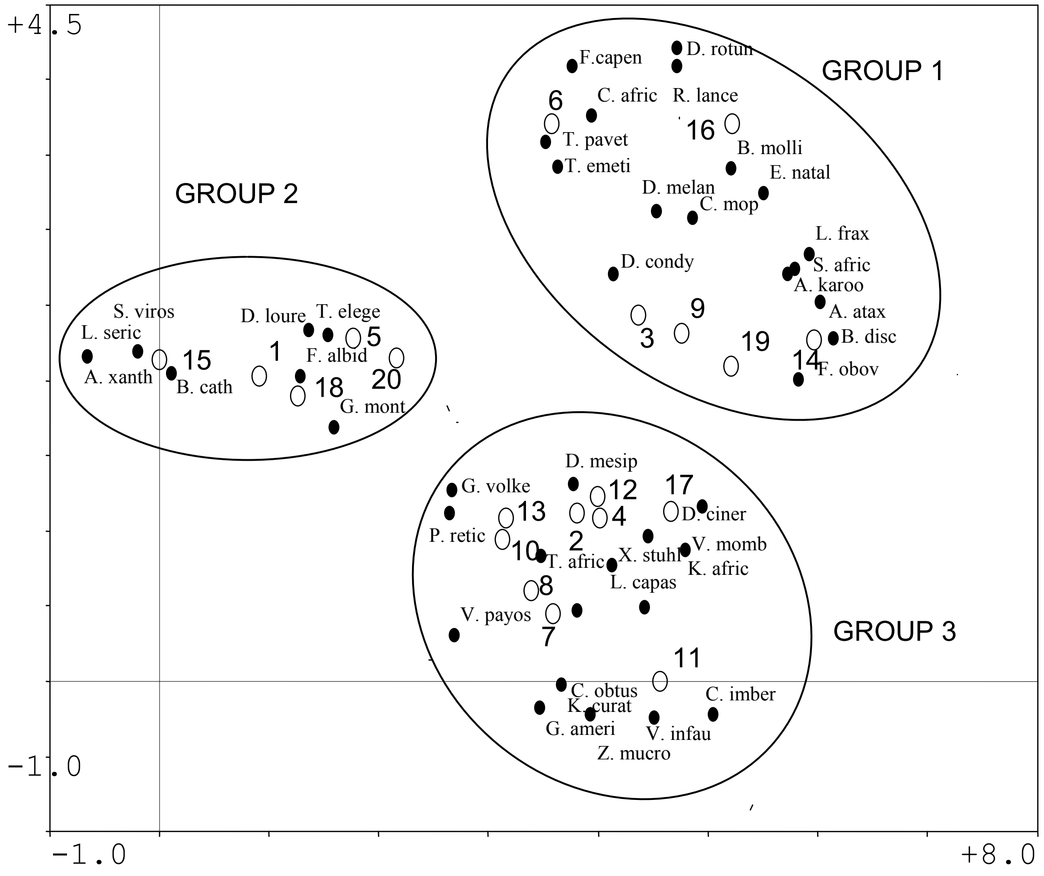


Figure 10: DCA ordination diagram based on basal area showing the separation of plots and species into three main groups.

5.10 Vegetation-explanatory variable Relationships

Canonical Correspondence Analysis (CCA) based on basal area and explanatory variables produced the summary output shown in Table 4. The first four axes of the species-environment plot account for 68.7% of the total variation. The main vegetation-environmental patterns are shown on the ordination diagrams in figures 11 and 12, which show the relationship between the sampling plots and the explanatory variables, and the relationship between the species and the explanatory variables, respectively. Axis 1 accounted for 93% of the observed variation in vegetation, whereas axes 2, 3 and 4 accounted for 83.4%, 75% and 60.9% respectively (Table 4).

The separation of the plots and species along the first axis was related to pH, clay content, soil depth, *L. camara* cover, phosphorus levels, nitrogen levels and potassium levels. These variables were important in explaining the variation observed. Along the second axis, the separation was related to sand content, silt content and moisture content. pH was negatively correlated with the first axis. Silt content and soil moisture were negatively correlated with the second axis. The smaller the angle between the arrow of the variable and the canonical axis the more correlated the variable is with the axis.

Table 4: Canonical Correspondence Analysis (CCA) summary output on the basis of basal area and the measured explanatory variables in Northern GNP.

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.930	0.834	0.750	0.609	8.200
Species-environment correlations	:	0.988	0.980	0.971	0.957	
Cumulative percentage						
variance of species data	:	11.3	21.5	30.7	38.1	
of species-environment relation	:	20.4	38.8	55.3	68.7	
Sum of all unconstrained eigenvalues						8.200

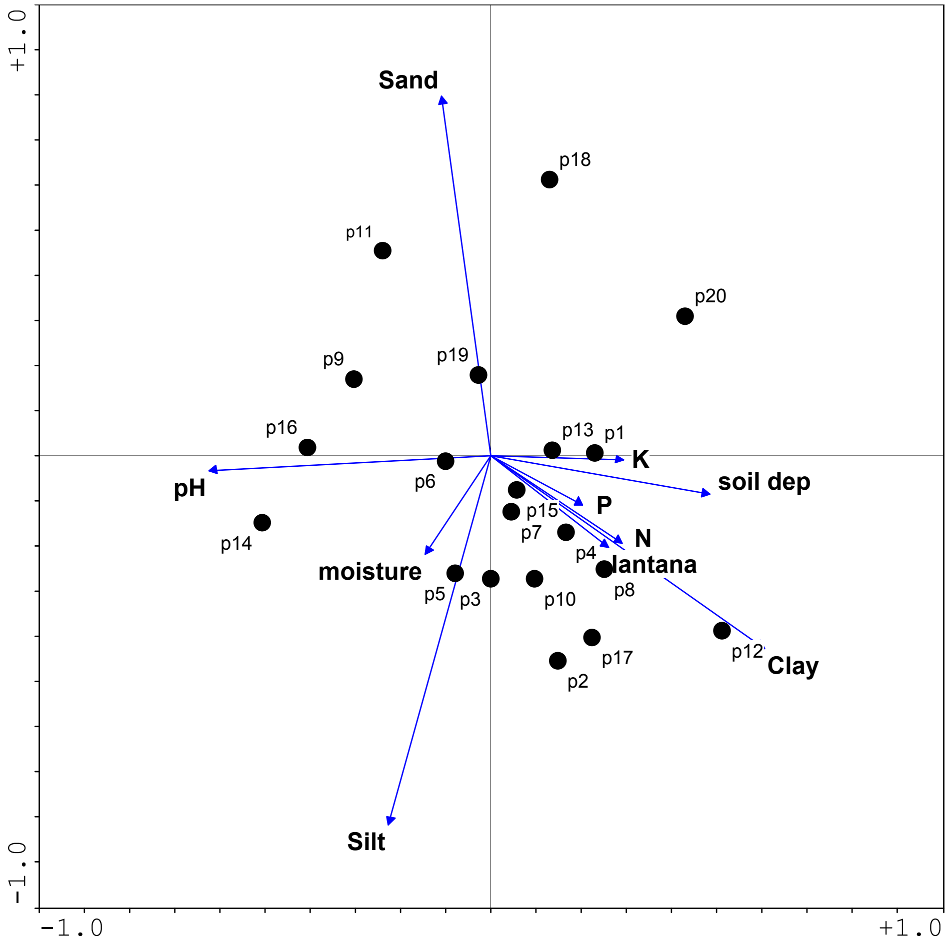


Figure 11: CCA ordination diagram based on basal area showing the separation of plots in relation to the measured explanatory variables.

The correlation between the plant species and the explanatory variables ranged from 0.957 to 0.988 on all the four axes (Table 4). These high correlation values show that positions of the plots and the species on the ordination diagrams are influenced by the explanatory variables measured. Each of the variables is at least correlated with one of the first two axes on the diagrams (Figures 11 and 12). Soil depth, potassium, nitrogen and phosphorus levels were negatively correlated with pH (Figures 11 and 12).

It can be observed from Figure 12 that the abundance of species such as *Grewia monticola, Xeroderris stuhlmannii, Combretum imberbe, Lonchocarpus capassa* and *Dombeya rotundifolia* is correlated with clay content, *L. camara* cover, soil depth, soil nitrogen, phosphorus and potassium levels. Species such as *Colophospermum mopane, Acacia ataxacantha, Spirostachys africana, Diplorhynchus condylocarpon* and *Lecaniodiscus fraxinifolius* and *Ziziphus mucronata* are positively correlated with sand but negatively correlated with *L. camara* cover and the associated variables.

From the permutation tests the influence of the variables along the first canonical axis was significant (F=1.151, P<0.05) and the overall test for all the canonical axes was also significant (F=1.125, P<0.05). Variables that significantly influenced species composition were pH (F=1.80, P<0.05), sand (F=1.65, P<0.05), clay (F=1.63, P<0.05), and potassium level (F=1.76, P<0.05). The results of the permutation tests are shown in Appendix 8. Soil moisture, nitrogen, phosphorus, altitude and soil depth had an insignificant influence on vegetation composition.

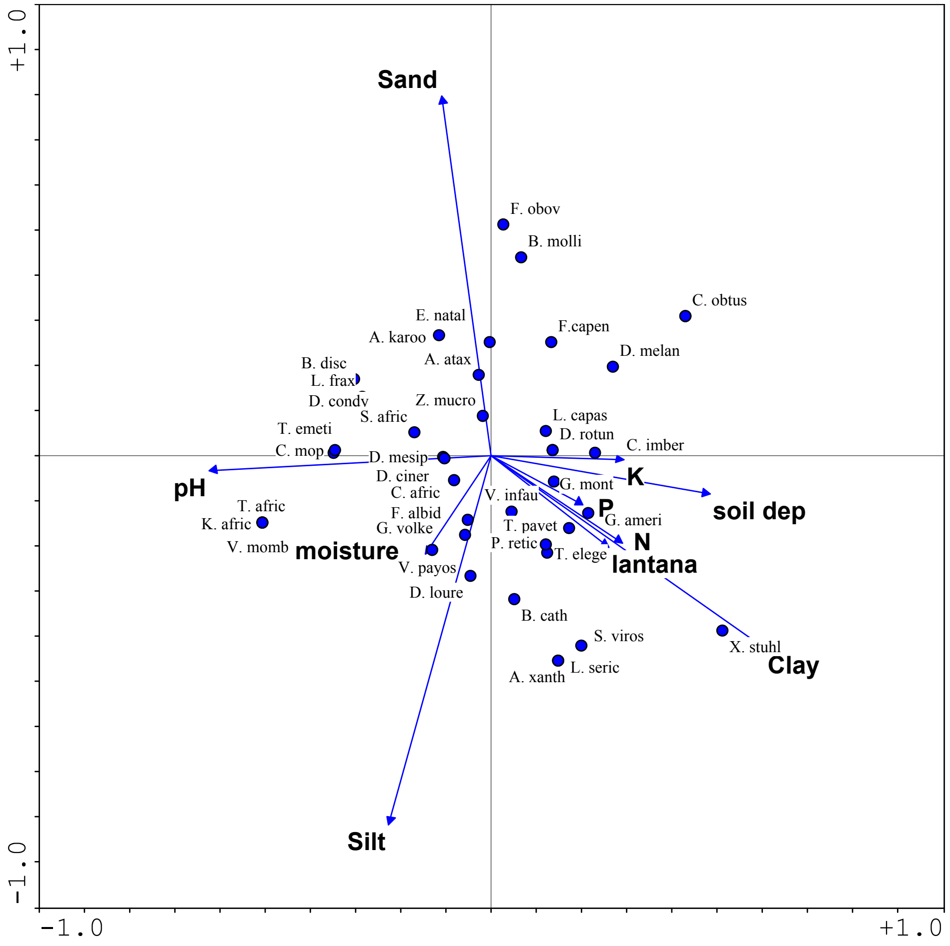


Figure 12: CCA ordination diagram based on basal area showing the separation of species in relation to the measured explanatory variables.

6.0 DISCUSSION AND CONCLUSION

6.1.0 Discussion

6.1.1 Distribution of *L. camara* in Northern GNP

Figure 3 shows that more than 50% of Northern Gonarezhou National Park has been infected by *L. camara,* which implies that the area is already threatened by the invasion to the detriment of wildlife management in the park. *L. camara* is mainly distributed within the riparian vegetation, especially along Save, Runde and Mwenezi Rivers and the low-lying areas. These findings are consistent with those by Thomas and Ellison (2000) who found that invasive species were mostly distributed in riparian areas.

The dispersal mechanism of *L. camara*, which is mainly through birds and floods (Day *et al*. 2003), could account for such a distribution since riparian areas in the park are associated with floods and high diversity of birds (DNPWLM, 1998). Furthermore, GNP has a dry and hot climate (section 3.5) and this makes the low-lying areas and riparian zones with high moisture levels, the most favourable habitats for dispersal agents and *L. camara* itself.

These results are consistent with findings by Stohlgren *et al*. (1998), who reported a higher degree of invasion in riverine habitats in Central Portugal. According to Crawley (1997), the periodic disturbances in the form of floods that disperse seeds, prepare them for germination, provide seedbed, and remove competing plants, are features of the riparian environment that promote invasions. Following the impact of *L. camara* implied by this study, the distribution of *L. camara* in northern GNP is to the detriment of ecosystems in the park. The distribution of *L. camara* in the park as indicated by this study would pose a severe threat to the riparian zones and aquatic ecosystems. Stohlgren *et al*. (1998) considered riparian zones as hot spots of biological diversity, rare habitats, with distinct plant and animal communities. *L. camara* invasion in riparian areas therefore puts many species at the risk of extinction.

Changes in the riverine vegetation can be translated into aquatic ecosystems, to the detriment of aquatic life. Changes in riparian vegetation results in changes in aquatic ecosystem processes such as self-purification, and the river continuum as a whole. Soil erosion will be increased with reduced plant diversity in riparian vegetation communities with subsequent reduction in water volume due to siltation. River hydrology can also be negatively affected following reduction in plant diversity in these communities. The riparian area is considered to be among the Special Conservation Areas of the park since it has a high diversity of bird and other wildlife species, contributing to the exceedingly beautiful scenery along the rivers bird watching and wildlife viewing (DNPWLM, 1998). The species rich vegetation, which is threatened by *L. camara*, dominates the low-lying and riparian areas in the park.

6.1.2 Vegetation Classification

A study of vegetation in Northern Gonarezhou National Park revealed clear-cut separation of vegetation associations according to intensity of *L. camara* invasion. Vegetation composition and abundance varied significantly along the *L. camara* intensity gradient from the uninvaded category to the heavily invaded category. Associated with each level of *L. camara* intensity, were three main vegetation groupings defined on the basis of species composition and abundance (Figures 5 and 10). Each group had different species composition and abundances, and also varied in explanatory variables (Figure 10). Separate groupings of the uninvaded plots 6 and 11 could be explained by the heterogeneity of the environment in which they are located. The distortion on the clusters with the inclusion of herbaceous species (Figure 6) could be explained by the fact that herbaceous species composition rapidly changes with any minor variations in edaphic factors.

The woody species that dominated the heavily invaded category were *Lonchocarpus capassa*, *Diospyros mespiliformis, Dichrostachys cinerea, Thilachium africanum, Kigelia africana, Xeroderris stuhlmannii, Gardenia volkensii* and *Vitex payos*, while *Achyranthes aspera var. sicula* was dominating the herbaceous layer followed by *Panicum maximum*. This indicates that these species could be resistant to *L. camara* invasion. On the other hand, it could be that *L. camara* favours the same conditions as these native species. *Colophospermum mopane, Faidherbia albida, Acacia ataxacantha, Spirostachys africana, Diplorhynchus condylocarpon* and *Lecaniodiscus fraxinifolius* were virtually absent from *L. camara*-infested sites and were found on the uninvaded sites, which could imply that they are displaced once *L. camara* invasion occurs. This is because growth of *Faidherbia albida* is limited by its intolerance to competition.

The main factor governing the occurrence of *Colophospermum mopane* is low availability of moisture in the soil (Nyamapfene, 1988). However, in this study, the effect of *L. camara* appeared to be outweighing the influence of moisture on occurrence of *C. mopane*. Species such as *Leucosidea sericea, Bridelia cathartica, Grewia monticola, Tabernaemontana elegans* and *Diospyros loureiriana* appeared to resist moderate levels of *L. camara* invasion but are displaced as invasion intensifies.

6.1.3 Impact of *L. camara* on Vegetation Structure

The evidence provided by this study show that *L. camara* invasion is negatively affecting elements of vegetation structure in Northern GNP. The principal elements of structure are growth form, stratification and coverage (Mueller-Dombois and Ellenberg, 1974). Basal area decreased with increase in *L. camara* intensity. Height size class distribution showed the dominance of the 2-5m size class. Though height was insignificantly different, the size class distribution showed significant differences among the three categories with frequency decreasing with increase in *L. camara* infestation.

The basal area size class distribution of woody species in Northern Gonarezhou National Park showed a reverse-J shape (dominance of the smaller size classes) in all the three categories, which is characteristic of communities with high recruitment (Figure 8). According to Chidumayo *et al*. 1996), small size class distribution dominance indicates the potential for high regeneration. Reverse-J shape is a characteristic for species with good rejuvenation and continuous replacement of themselves, whereas flatter distributions indicate lack of recruitment and may be species composition change (Lykke, 1998).

However, there were significant differences in basal area and height size class distributions among the three categories with the heavily invaded category recording the lowest frequency. This would imply that recruitment decreased with increase in *L. camara* intensity. During a study on the effects of alien plant invasions in India, Macdonald *et al*. (1991) found that alien plant invaders shade out indigenous species and reduce their recruitment. The present study gives strong evidence to show that *L. camara* invasion affect native vegetation recruitment and regeneration negatively as revealed by decreasing dominance of smaller size class distributions with increasing *L. camara* intensity. Furthermore, Duggin and Gentle (1998) documented the capability of *L. camara* to interrupt the regeneration processes of native species by reducing germination, reducing early growth rates, and increasing mortality.

Gentle and Duggin (1997b), in their study of the allelopathic effects of *L. camara* in three Australian forests, found a significant increase in seed germination and seedling biomass with removal of *L. camara* thickets. The allelopathic effects of *L. camara* result in severe reductions in seedling recruitment of nearly all species under its cover (Sharm *et al*. 2005). Both tree and shrub density of native species tended to decrease with increase in *L. camara* intensity. This reduction in density could be attributed to reduced recruitment and growth rates.

Canopy cover and herbaceous aerial cover differed significantly among the three levels of *L. camara* infestation. The heavily invaded category recorded the minimum of both cover variables. More than 250% canopy cover was recorded in the uninvaded category. According to Mueller-Dombois and Ellenberg (1974), the total cover of a plot may exceed 100% because of over layering of canopies of different heights. However, the heavily invaded plots recorded much less than 100% mean canopy cover. This could imply that reduction in recruitment by *L. camara* invasion results in decrease in woody vegetation density with subsequent low canopy cover. According to Fensham *et al*. (1994), *L. camara* increases mid-storey fuel loads and intense fires kill the vegetation canopy. This could be the case in GNP where according to Gandiwa, (2006), an average of 5.1 fires occur every year.

However, presence of *L. camara* in sites with low canopy cover could be due to open canopy cover promoting *L. camara* invasion and spread. Decrease in herbaceous aerial cover with increase in *L. camara* intensity could be due to recruitment reducing, smothering or allelopathic effect of *L. camara*. These findings support results by Fensham *et al*. (1994), in their study in Forty Mile Scrub National Park, Australia, who found that grass cover was negatively correlated with the abundance of *L. camara*, which reduces grass cover as its cover increases. Low soil moisture levels, which were found to be associated with *L. camara* invasion, could account for decrease in herbaceous cover with increase in *L. camara* intensity in this study. Chatanga (2003) found a decrease in herbaceous cover with decrease in soil moisture levels.

6.1.4 Impact of *L. camara* on Native Species Diversity and Richness

Species diversity and richness decreased significantly with increase in *L. camara*-infestation. The heavily invaded category was the least diverse and the poorest in species richness. The present findings support those by Moyo (2004) in his study in Zambezi/ Victoria Falls National park, Zimbabwe, who found a decrease in species richness and density with increase in *L. camara* invasion. The current results are also in agreement with those by Fensham *et al*. (1994) who documented a decline in plant species richness with increasing levels of *L. camara* infestation of dry rainforest, and accumulation of heavy fuel loads leading to significant canopy tree loss. In the Western Cape Province, in South Africa, Holmes *et al*. (2000) found significantly lower indigenous plant cover and density in invaded areas compared to controls.

The decline in species diversity and richness recorded in the current study is probably due to the fact that *L. camara* reduces recruitment of native species and subsequently reduces their establishment. Increase in fuel loads by *L. camara* dense stands also results in some species being burnt during fires. It could also be due to suppression of native species with increasing density of *L. camara* as was found by Thomas and Ellison (2000). Achhireddy and Singh (1984) and Achhireddy *et al*. (1985) observed no growth or only stunted growth for species growing close to *L. camara* due to allelopathic effects. In their study of the effects of alien plant invasions in India, Macdonald *et al*. (1991) found that alien thickets of *L. camara* had replaced patches of the Tevelave forest. However, the current findings contradict with findings by Stohlgren *et al*. (1998), Higgins *et al*. (1999) and Rodgers and Parker (2003) who found a positive correlation between level of invasion and species richness.

6.1.5 Vegetation-explanatory variable Relationships

The current study shows strong vegetation-explanatory variable relationships in Northern Gonarezhou National Park. Species were grouped into three distinct communities (Figure 10). *L. camara* appeared to be altering species composition and structure both directly and indirectly in Northern GNP. Plant species composition and structure can be altered indirectly through the modified soil environment and directly through allelopathic means (Clegg, 1999). The first axis on the DCA ordination diagram separates the species along the edaphic factors gradient (Figure 10). The same trend is also shown on the CCA ordination diagram (Figure 12).

The first CCA ordination axis, which was strongly associated with potassium, pH and soil depth, explained much of the variation in species composition in the study area. The CCA ordination diagram (Figure 12) shows that separation along the first axis is mainly along the edaphic factors gradient (depth, potassium and clay gradients). Species that are associated with deep soils, low clay content and more alkaline conditions are grouped on the right of the ordination diagram, while those associated with shallow soils, high clay content and more acidic conditions are on the left.

Vegetation groupings, which reflect the underlying environmental conditions, differed with respect to level of *L. camara* infestation, from uninvaded to the heavily invaded category. Nyamapfene (1988) documented the close relationship that exists between vegetation and soils that was recognised in some of the early soil classifications. More recent detailed studies by ecologists have shown that vegetation-soil relationships can express some very fine differences in edaphic conditions (Nyamapfene, 1988). Much of the variation in vegetation composition in Northern GNP is explained mainly by soil depth, soil texture, soil pH, and soil moisture and nutrients.

Monte-Carlo tests, however, showed that soil pH, potassium, sand and clay significantly influenced vegetation composition in Northern GNP (Appendix 8). Altitude, soil moisture, soil depth, nitrogen and phosphorus levels did not show significant contribution. Although these variables did not contribute significantly in this study, Tinley (1982) found that species composition was influenced by soil texture, nutrient status, pH and soil moisture. According to Scholes and Walker (1993), chemical and physical properties of soil influence plant species composition, morphology and aboveground biomass in semi-arid savannas. Subsequently, the effects of *L. camara* on the soil properties implicated by the current study are translated into plant species and composition and structure.

6.1.6 Impact of *L. camara* invasion on environmental variables

Soil moisture, potassium, nitrogen, and phosphorus levels varied significantly among the three levels of *L. camara* infestation. Soil nitrogen and phosphorus levels increased with increase in *L. camara* intensity while soil moisture and potassium levels decreased. Soil pH, depth, texture and altitude were not significantly affected by *L. camara* invasion.

Altitude, soil texture and soil depth are unlikely to change significantly following *L. camara* invasion. As a result, the insignificant difference in these variables among the three categories would indicate the homogeneity of the environment. Soil texture is a useful indicator of soil permeability, soil water retention capacity, and soil capacity to retain cations and influences plant available moisture and plant available nutrients (White, 1997). Scholes and Walker (1993) considered clay content as an index of nutrient availability. According to White (1997), the greatest influence of pH on plant growth is its effect on nutrient availability. Since the indices for moisture and nutrients (soil depth, pH and texture) did not vary significantly with increase in *L. camara* intensity, it follows that changes in nutrient levels observed could be attributed to *L.*

camara invasion effects. Differences in plant species composition reflect differences in soil water and nutrient availability (Scholes, 1990a), and changes caused by *L. camara* in the soil can be translated into plant species composition.

The increase in nitrogen and phosphorus levels with increase in *L. camara* intensity could be due to decrease in nutrient sequestration following native species displacement or reduction in their recruitment and growth rates. *L. camara* drops a lot of litter beneath it (Pers. Observ.), and this probably account for the elevated nitrogen and phosphorus levels when the litter decays. These findings are consistent with findings by Ehrenfeld (2003), who recorded an increase in soil nitrate following *L. camara* invasion, to the benefit of the *L. camara*, and a decline in other nutrients. Nitrogen mineralization and nitrification commonly increases in response to invasions (Ehrenfeld, 2003), which could explain the increase in available nitrogen that was observed in this study. This is to the detriment of native species since Thomas and Ellison (2000) noted a significant increase in level of suppression of native species by *L. camara* with increase in soil fertility.

The results of this study also agree with the findings by Stohlgren *et al*. (1998) who reported a positive correlation between level of invasion, and soil nitrogen levels and silt content. It has recently been suggested that invasibility is more closely related to resource availability (Davis *et al*. 2000). Hueneke *et al*. (1990) showed that the addition of nutrients on Serpentine soils of California elevated alien plant abundances. Therefore, inherent high nutrient levels could have promoted *L. camara* invasion in GNP instead of the high nutrient levels being a result of invasion (Davis *et al*. 2000). Davis *et al*. (2000) theory of invasibility states that whenever there are unutilized resources in an ecosystem, that ecosystem becomes susceptible to invasion.

In Australia, alien invasions have been shown to be associated with more fertile soils (Rodgers and Parker, 2003). Vranjic *et al.* (2000) observed that soil phosphorus concentration was the major difference between the invaded and the uninvaded regions, which is in agreement with the current results. The characteristic all year- prolific flowering and large seed number production by *L. camara* (Thomas and Ellison, 2000; ISSG, 2006), which exerts much demand for the nutrient could account for the decrease in potassium following *L. camara* invasion. Decrease in soil extractable nutrient pools may be associated with high uptake of these nutrients, which is driven, by large biomass or tissue concentrations (Ehrenfeld, 2003). Vranjic *et al.* (2000) documented the capability of invasive species to deplete the soil nutrient status directly through vigorous extraction of resources.

Decrease in soil moisture with increase in *L. camara* intensity shown by this study could be accounted for by the fact that *L. camara* is a short rooted plant, which maximises use of moisture on the top layers of the soil, from which soil samples were collected. Furthermore, *L. camara* is very efficient in moisture sequestration leading to reduction in soil available moisture. The current findings are in agreement with Ehrenfeld (2003) who documented that soil moisture can either increase or decrease following invasion. These findings where *L. camara* reduces moisture levels are also consistent with findings by Hiremath and Sundaran (2005) who found that *L. camara* affects water supply negatively. According to Day *et al*. (2003), dense stands of *L. camara* reduce the capacity of soil beneath to absorb rain with subsequent increase in the amount of run-off and risk of soil erosion.

Contrary to the results of the current study, Sharma *et al*. (2003) observed that different levels of *L. camara* increased available water by 3-6%. The current findings also contradict with those by Gentle and Duggin (1997b), who recorded insignificant changes in soil moisture and pH following removal of *L. camara* thickets. However, according to Ehrenfeld (2003), soil pools of nutrients and water often respond to exotic invasions, but the general direction of change cannot as yet be predicted because both increases and decreases have been observed in roughly equal numbers.

6.2 Conclusion

The present study has demonstrated that *L. camara* impact negatively on native vegetation structure and composition. The effects on native vegetation are direct, through smothering and allelopathic means, and indirect through changes in soil properties. The results of the current study has also revealed that *L. camara* alters soil properties such as nutrient status, pH, moisture levels, and the extent of change depends on the intensity of invasion. These changes in soil properties can be reflected in the vegetation composition and structure. *L. camara* invasion reduces native species diversity and richness to the detriment of ecosystems. This study has also revealed that edaphic factors influence plant species structure and composition in northern GNP. The present study also gives strong evidence to show that *L. camara* invasion affect native vegetation recruitment and regeneration negatively.

Much of the variation in vegetation structure and composition in Northern GNP is explained by soil depth, soil texture, soil pH, and soil moisture and nutrients. However, soil pH, potassium, sand and clay showed significant influence on the vegetation.

L. camara invasion has been shown to be mainly associated with riparian and low-lying areas in GNP, which threatens biodiversity since riparian areas are quite diverse in both plant and animal species. Changes in vegetation structure and composition following *L. camara* invasion may have important implications on wildlife habitat, biotic diversity and risk of future catastrophic disturbances. The effect of *L. camara* on vegetation affects the quality and availability of forage and cover for mammals and birds. Apart from its negative impact on biodiversity, *L. camara* also contains toxic compounds (triterpenoids) that have been implicated in the killing of animals such as buffalo, through poisoning and photosensitivity. Furthermore, the plant also harbours tsetse flies that affect animal health. Therefore alien plant invasions in GNP are to the detriment of wildlife management.

The present study has provided strong evidence that *L. camara* invasion is reducing biodiversity and negatively affecting other ecosystem processes in GNP and possibly in other areas of its occurrence in Zimbabwe. It has been shown by this study that *L. camara* is one factor that is significantly altering native vegetation structure and composition in Northern Gonarezhou National Park. Without timely action, the vegetation will totally be transformed by *L. camara* in the park. However, in the current study only one season assessment was done and the results suggest that a long-term study would provide a much more detailed understanding of the impact of *L. camara* invasion in the park. Furthermore, due to lack of resources a smaller area was sampled. This suggests that increasing the number of sampling plots would improve the sampling method.

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APPENDICES

Appendix 1: Sample Field Data Sheet

Researcher: **Chatanga Peter**. Study Area: **Gonarezhou National Park**
Period of fieldwork: April/ May 2007.
Category …………………… Site ……………… Plot Number ………………………Date ……………
GPS Coordinates: S…………E……………… Altitude………….. % *L. camara* cover…………….

Other site notes

………

………
……………………

Soil depth	**Depth 1**	**Depth 2**	**Depth 3**	**Depth 4**	**Depth 5**

Species Name	**Circumference at breast height** (1.3 m)					**Crown diameter**		**Height**	**Notes**
	Circ_1	**Circ_2**	**Circ_3**	**Circ_4**	**Circ_5**	**D_1**	**D_2**		

Appendix 2: Location of plots and level of *L. camara* invasion, and the dates of assessment in Northern GNP.

			GPS COORDINATES	
Plot	Category	Date of assessment	S	E
1	Moderately Invaded	2/5/2007	21° 18.452′	032° 24.034′
2	Heavily Invaded	2/5/2007	21° 18.486′	032° 24.024′
3	Uninvaded	2/5/2007	21° 18.470′	032° 23.044′
4	Heavily Invaded	3/5/2007	21° 18.493′	032° 23.804′
5	Moderately Invaded	3/5/2007	21° 18.506′	032° 23.810′
6	Uninvaded	4/5/2007	21° 18.490′	032° 23.720′
7	Moderately Invaded	7/5/2007	21° 18.484′	032° 23.668′
8	Heavily Invaded	7/5/2007	21° 18.406′	032° 23.696′
9	Uninvaded	7/5/2007	21° 18.543′	032° 23.542′
10	Heavily Invaded	8/5/2007	21° 15.698′	032° 22.131′
11	Uninvaded	8/5/2007	21° 15.721′	032° 22.113′
12	Heavily Invaded	8/5/2007	21° 15.658′	032° 22.094′
13	Moderately Invaded	10/5/2007	21° 15.675′	032° 22.125′
14	Uninvaded	10/5/2007	21° 15.598′	032° 22.024′
15	Moderately Invaded	11/5/2007	21° 15.595′	031° 53.664′
16	Uninvaded	11/5/2007	21° 15.606′	031° 53.712′
17	Heavily Invaded	11/5/2007	21° 16.104′	031° 54.280′
18	Moderately Invaded	12/5/2007	21° 16.095′	031° 54.266′
19	Uninvaded	12/5/2007	21° 16.105′	031° 54.277′
20	Moderately Invaded	14/5/2007	21° 16.046′	031° 54.230′

APPENDIX 3: List of all the species identified during the study in Northern GNP, their occurrence in the different categories and the abbreviations used on the ordination diagrams.

Abbreviation	Full Species name	Uninvaded	Moderately Invaded	Heavily Invaded
	Woody Species			
A. atax	*Acacia ataxacantha*	+		
A. karoo	*Acacia karroo*	+	+	+
A. xanth	*Acacia xanthophloea*			+
B. cath	*Bridelia cathartica*	+	+	+
B. disc	*Berchemia discolor*		+	
B. mollis	*Bridelia mollis*	+	+	

C. afric	*Cordyla africana*	+	+	
C. imber	*Combretum imberbe*	+		
C. mop	*Colophospermum mopane*	+	+	
Maer. sp	*Maerua sp*	+		
D. ciner	*Dichrostachys cinerea*	+	+	+
D. condyl	*Diplorhynchus condylocarpon*	+		
D. lourei	*Diospyros loureiriana subsp loureiriana*	+	+	
D. melan	*Dalbergia melanoxylon*	+	+	+
D. mesip	*Diospyros mespiliformis*	+	+	+
D. rotun	*Dombeya rotundifolia*		+	
E. natal	*Euclea natalensis*	+	+	
F. albida	*Faidherbia albida*	+		+
F. obov	*Friesodielsia obovata*	+	+	+
F.capen	*Ficus capensis*		+	+
G. americ	*Gyrocarpus americanus*	+		+
G. mont	*Grewia monticola*	+	+	+
G. volken	*Gardenia volkensii*	+	+	+
K. afric	*Kigelia africana*	+		
K. curat	*Kalahari curatit*	+		
L. capas	*Lonchocarpus capassa*	+	+	+
L. frax	*Lecaniodiscus fraxinifolius*	+	+	+
L. seric	*Leucosidea sericea*		+	
P. retic	*Phyllanthus reticulatus*	+	+	+
R. lancea	*Rhus lancea*		+	
S. afric	*Spirostachys africana*	+	+	
S. virosa	*Securinega virosa*		+	+
T. afric	*Thilachium africanum*	+		
T. elegens	*Tabernaemontana elegans*	+	+	
T. emetica	*Trichilia emetica*	+		+
T. pavett	*Tarenna pavettoides*	+	+	+
V. infaus	*Vangueria infausta*		+	
V. momb	*Vitex mombassae*	+		
V. payos	*Vitex payos*	+	+	+
X. stuhlm	*Xeroderris stuhlmannii*			+
Z. mucron	*Ziziphus mucronata*		+	+
	Herbaceous Species			
A. angul	*Abutilon angulatum*	+		+
A. asper	*Achyranthes aspera var. sicula*	+	+	+
A. malv	*Astripomoea malvacea*	+	+	+
B. elegan	*Barleria elegans*		+	
B. pilosa	*Bidens pilosa*	+	+	
C. obtus	*Cassia obtusifolia*	+	+	+

C. obtus	*Cryptolepis obtusa*	+		
C. plumb	*Commicarpus plumbaginens*		+	
C. roger	*Crotalaria rogersii*	+	+	+
C.sphaer	*Commerina sphaerosperma*	+	+	+
D. gigan	*Dactyloctenium giganteum*	+		
D.zangue	*Dicerocaryum zanguebarium*	+		
H. kirkii	*Hermannia kirkii*	+		
I. pleba	*Ipomoea pleba*	+		+
I. sp	*Indigofera sp*	+		
M. aspar	*Myrsiphyllum asparagoides*		+	+
P. max	*Panicum maximum*	+	+	+
S. alba	*Sida alba*		+	
S. incra	*Setaria incrassata*	+	+	+
S. nigrum	*Solanum nigrum*		+	
S. pum	*Setaria pumila*		+	
T. vill	*Tephrosia villosa subsp ehrenbergiana var. ehrenbergiana*	+	+	+
U. mos	*Urochloa mosambicensis*		+	
V. nuda	*Vigna nuda*	+	+	+
V. poske	*Vernonia poskeana subsp poskeana*		+	
V. vex	*Vigna vexillata var. angustifolia*	+		
W. indica	*Waltheria indica*	+		

APPENDIX 4: CHI-SQUARE TESTS ON HEIGHT AND BASAL AREA SIZE CLASS DISTRIBUTIONS IN NORTHERN GNP.

a) Chi-Square Test: Uninvaded, Moderately Invaded, Heavily Invaded (Height classes)

Expected counts are printed below observed counts

	Uninvaded	Moderately Invaded	Heavily Invaded	Total
1	57	32	5	94
	48.00	25.71	20.29	
2	101	47	53	201
	102.65	54.97	43.38	
3	52	32	23	107
	54.64	29.26	23.09	
4	20	9	17	46
	23.49	12.58	9.93	
5	9	8	3	20
	10.21	5.47	4.32	
Total	239	128	101	468

Chi-Sq = 1.686 + 1.539 + 11.519 +

```
        0.026 +  1.157 +  2.134 +
        0.128 +  0.256 +  0.000 +
        0.519 +  1.019 +  5.039 +
        0.144 +  1.170 +  0.401 = 26.738
Df = 8, P-Value = 0.001
1 cell with expected counts less than 5.0
```

b) Chi-Square Test: Univaded, Moderately Invaded, Heavily Invaded (Basal area size classes)

```
Expected counts are printed below observed counts

          Uninvaded       Moderately Invaded      Heavily Invaded       Total
   1         167               110                      75               352
             159.73            115.36                   76.91
   2          19                13                      5                 37
              16.79             12.13                   8.08
   3          11               19                      18                 48
              21.78            15.73                   10.49
   4          19               14                       6                 39
              17.70            12.78                    8.52
Total        216              156                      104               476

Chi Sq =  0.331 +  0.249 +  0.047 +
        0.291 +  0.063 +  1.177 +
        5.337 +  0.679 +  5.382 +
        0.096 +  0.116 +  0.746 = 14.513
Df = 6, p-value = 0.025
```

APPENDIX 5: One-Way ANOVA Summary results on the vegetation attributes

NB: *-P<0.05, **-P<0.001, ***-P<0.0001, NS-P>0.05

a) ANOVA: Diversity Index (H')

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	51.57264	51.57264	1050.581	0.000000***
Level	2	0.94412	0.47206	9.616	0.001609*
Error	17	0.83452	0.04909		
Total	19	1.77864			

b) ANOVA: Species Richness (S)

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	2307.580	2307.580	673.3193	0.000000***
Level	2	151.538	75.769	22.1083	0.000019***
Error	17	58.262	3.427		
Total	19	209.800			

c) ANOVA: Species Evenness (E)

Factor	Df	SS	MS	F	P
Intercept	1	9.432495	9.432495	1075.863	0.000000***
Level	2	0.027293	0.013646	1.556	0.239478^{NS}
Error	17	0.149045	0.008767		
Total	19	0.176338			

d) ANOVA: Tree Density/ha

Factor	Df	SS	MS	F	P
Intercept	1	8262456	8262456	247.4578	0.000000***
Level	2	462381	231190	6.9241	0.006315*
Error	17	567619	33389		
Total	19	1030000			

e) ANOVA: Shrub density/ha

Factor	Df	SS	MS	F	P
Intercept	1	251649142	251649142	636.2024	0.000000***
Level	2	8021763	4010882	10.1400	0.001263*
Error	17	6724330	395549		
Total	19	14746094			

f) ANOVA: Percentage herbaceous layer cover

Factor	Df	SS	MS	F	P
Intercept	1	52760.94	52760.94	1104.876	0.000000***
Level	2	3902.39	1951.19	40.860	0.000000***
Error	17	811.80	47.75		
Total	19	4714.19			

g) ANOVA: Mean Tree height

Factor	Df	SS	MS	F	P
Intercept	1	1837.717	1837.717	186.1053	0.000000***
Level	2	1.722	0.861	0.0872	0.916911^{NS}
Error	17	167.868	9.875		
Total	19	169.590			

h) ANOVA: Basal area

Factor	Df	SS	MS	F	P
Intercept	1	14.92477	14.92477	70.08520	0.000000***
Level	2	3.62129	1.81064	8.50260	0.002759*
Error	17	3.62018	0.21295		
Total	19	7.24147			

i) ANOVA: Mean shrub height

Factor	Df	SS	MS	F	P
Intercept	1	101.9858	101.9858	1516.287	0.000000***
Level	2	0.2074	0.1037	1.542	0.242495 NS
Error	17	1.1434	0.0673		
Total	19	1.3508			

j) ANOVA: Canopy cover

Factor	Df	SS	MS	F	P
Intercept	1	419637.8	419637.8	86.97088	0.000000***
Level	2	122829.9	61415.0	12.72839	0.000418**
Error	17	82025.6	4825.0		
Total	19	204855.6			

APPENDIX 6: One-Way ANOVA Summary results on the explanatory variables

NB: *-P<0.05, **-P<0.001, ***-P<0.0001, NS-P>0.05

a) ANOVA: Soil depth

Factor	Df	SS	MS	F	P
Intercept	1	46461.05	46461.05	206.5643	0.000000***
Level	2	1308.11	654.05	2.9079	0.081999NS
Error	17	3823.69	224.92		
Total	19	5131.80			

b) ANOVA: Soil pH

Factor	Df	SS	MS	F	P
Intercept	1	928.5422	928.5422	6556.360	0.000000***
Level	2	0.2979	0.1489	1.052	0.371015 NS
Error	17	2.4076	0.1416		
Total	19	2.7055			

c) ANOVA: Phosphorus

Factor	Df	SS	MS	F	P
Intercept	1	3250.263	3250.263	698.5164	0.000000***
Level of	2	1360.565	680.283	146.2000	0.000000***
Error	17	79.103	4.653		
Total	19	1439.668			

d) ANOVA: Nitrogen

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	26836.60	26836.60	4213.921	0.000000***
Level	2	2341.40	1170.70	183.825	0.000000***
Error	17	108.27	6.37		
Total	19	2449.67			

e) ANOVA: Potassium

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	18.35318	18.35318	161.6913	0.000000***
Level	2	1.23003	0.61501	5.4183	0.015121*
Error	17	1.92963	0.11351		
Total	19	3.15965			

f) ANOVA: Clay

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	3180.011	3180.011	122.9239	0.000000***
Level	2	28.764	14.382	0.5559	0.583612 ^{NS}
Error	17	439.786	25.870		
Total	19	468.550			

g) ANOVA: Silt

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	7176.001	7176.001	105.8980	0.000000***
Level	2	37.824	18.912	0.2791	0.759873 ^{NS}
Error	17	1151.976	67.763		
Total	19	1189.800			

h) ANOVA: Sand

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	92854.22	92854.22	673.1299	0.000000***
Level	2	81.75	40.88	0.2963	0.747309 ^{NS}
Error	17	2345.05	137.94		
Total	19	2426.80			

i) ANOVA: Moisture

Factor	**Df**	**SS**	**MS**	**F**	**P**
Intercept	1	1677.099	1677.099	246.8011	0.000000***
Level	2	235.862	117.931	17.3547	0.000078***
Error	17	115.521	6.795		
Total	19	351.383			

j) ANOVA: Altitude

Factor	Df	SS	MS	F	P
Intercept	1	871120.8	871120.8	233.2589	0.000000***
Level	2	3162.5	1581.3	0.4234	0.661525 NS
Error	17	63487.6	3734.6		
Total	19	66650.2			

Appendix 7: Regression model used for mapping *L. camara* cover in Northern GNP

Regression Summary for Dependent Variable: Lantana, R= 0.61507497, R²= 0.37831722
Adjusted R²= 0.34377929, F (1,18)=10.954

	Beta	Std. Error.	B	Std. Error.	t(18)	P-level
Intercept			110.262	24.2080	4.55475	0.000246**
SAVI	-0.615075	0.185844	-336.910	101.7968	-3.30963	0.003898*

Appendix 8: Canonical Correspondence Analysis and Permutation Tests

```
*** Unrestricted permutation ***
 Seeds:  23239   945

 **** Summary of Monte Carlo test ****
 Test of significance of first canonical axis: eigenvalue =     .930
                                        F-ratio    =    1.151
                                        P-value    =     .01150

 Test of significance of all canonical axes  : Trace      =    4.555
                                        F-ratio    =    1.125
                                        P-value    =    0.0185

(  199 permutations under reduced model)
 No species-weights specified
 No  sample-weights specified
 No downweighting of rare species

 No. of active  samples:     20
 No. of passive samples:      0
 No. of active  species:     41

 Total inertia in species data=
 Sum of all eigenvalues of CA =    8.20037
 ****** Check on influence in covariable/environment data ******
 The following sample(s) have extreme values
 Sample Environmental        Covariable  + Environment space
       variable Influence   influence     influence
     9      8      10.1x
    11      2      9.0x
    12      6      7.5x
    13      5      5.9x
 ****** End of check ******

 **** Start of forward selection of variables ****
 *** Unrestricted permutation ***
```

```
 Seeds:  23239   945

   N     Name Extra fit
   9 . moistu      .22
   4 ppm N          .30
  10 . lantan      .35
   3 ppm P          .38
   1 soil dep      .58
   5    K           .60
   7     Silt      .65
   8   Sand        .68
   6    Clay        .71
   2 Ph            .75

P-value  .0400 (variable   2; F-ratio=  1.80; number of permutations=   199)
P-value  .0350 (variable   8; F-ratio=  1.65; number of permutations=   199)
P-value  .01200 (variable   6; F-ratio=  1.63; number of permutations=   199)
P-value  .0500 (variable   5; F-ratio=  1. 76; number of permutations=   199)
P-value  .2600 (variable  10; F-ratio=  1.16; number of permutations=   199)
P-value  .3600 (variable   3; F-ratio=  1.10; number of permutations=   199)
P-value  .5700 (variable   1; F-ratio=   .90; number of permutations=   199)
P-value  .6050 (variable   4; F-ratio=   .85; number of permutations=   199)
P-value  .5050 (variable   9; F-ratio=  1.00; number of permutations=   199)
P-value  .8950 (variable   7; F-ratio=   .24; number of permutations=   199)
*** End of selection ***

   N      name       (weighted) mean            stand. dev.       inflation factor

   1      SPEC AX1               .0000               1.0206
   2      SPEC AX2               .0000               1.0120
   3      SPEC AX3               .0000               1.0301
   4      SPEC AX4               .0000               1.0453
   5      ENVI AX1               .0000               1.0000
   6      ENVI AX2               .0000               1.0000
   7      ENVI AX3               .0000               1.0000
   8      ENVI AX4               .0000               1.0000
   1      soil dep      41.9446           15.5130             2.2160
   2      Ph             6.8480             .4193             2.9155
   3      ppm P          8.2695            6.4848            23.9597
   4      ppm N         30.9082            7.9627            18.6536
   5      ppm K          1.1322             .3920             2.3751
   6      . Clay        11.6726            5.0241          4158.4406
   7      . Silt        17.7723            7.4125          8868.7689
   8      . Sand        70.5480           10.7899         18911.0603
   9      . moistu      11.0135            3.9018             5.1905
  10      . lantan      17.8637           22.9766            32.6829

 **** Summary ****
----------------------------------------------------------------------------
 Axes                                1        2         3        4    Total inertia

----------------------------------------------------------------------------
 Eigenvalues                     :  .930     .834      .750     .609        8.200
 Species-environment correlations  :  .980     .988      .971     .957
 Cumulative percentage
variance  of species data          :  11.3     21.5      30.7     38.1
   of species-environment relation  :  20.4     38.8      55.3     68.7

 Sum of all unconstrained eigenvalues                                    8.200
 Sum of all canonical     eigenvalues                                    4.553
----------------------------------------------------------------------------

[Tue Jul 10 01:34:13 2007] CANOCO call succeeded
```