

**Invasion Success of
Chromolaena odorata in
the Terai of Nepal**

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Invasion Success of *Chromolaena odorata* in the Terai of Nepal

by

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I certify that although I have conferred with others in preparing for this assignment, and drawn upon a range of sources cited in this work, the content of this thesis report is my original work.

Nawang Norbu

to my parents
with love

ABSTRACT

Globally, invasion of an ecosystem by alien species is acknowledged as one of the major threats to biodiversity. Disturbances that modify ecosystem structure and dynamics have been shown to facilitate invasion success. Increasing population and related changes in land cover determine the amount of disturbances to which an ecosystem is subjected. The aim of this thesis is: (1) to examine changes in population and land cover following malaria eradication in the Terai of Nepal; (2) to investigate factors influencing the presence, abundance and age composition of the invasive species *Chromolaena odorata* (L.) R. King & H. Robinson in the *Shorea* forests of the Terai in Nepal; and (3) to provide evidence for the hypothesis that the success of *Chromolaena* is dependant on the degradation status of the *Shorea* forests.

Land cover and census data were used to estimate changes in population growth and subsequent changes in land cover and population pressure on forest and arable land. Gaussian regression models were employed to examine relationships of *Chromolaena* cover, biomass and biometric properties to independent variables comprised of understorey light intensity ($\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), understorey biomass and grazing. Relationships of *Chromolaena* presence and age composition to independent variables were examined using logistic regression.

Human population in the Terai has increased substantially after the initiation of malaria eradication programmes in the early 1950s. Forest cover has declined while arable land area has increased. Human population pressure on forest resources have risen considerably since 1958. Understorey light intensity and understorey biomass differed significantly in grazed and ungrazed areas. Grazing is taken as an indicator of human presence. This suggests that increased human utilization together with grazing has degraded the *Shorea* forests in terms of forest canopy openness and understorey biomass levels. *Chromolaena* presence, cover, biomass and biometric traits were significantly related to understorey light intensity and understorey biomass. Grazing exhibited an indirect effect on *Chromolaena* cover and biomass. Higher values for *Chromolaena* cover; biomass and biometric properties (height, diameter, number of stems and number of branches) were found in areas with medium understorey light intensity ($1.5 - 3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and low understorey biomass. The age composition of *Chromolaena* populations was also significantly related to understorey light intensity and understorey biomass, where the probability to find *Chromolaena* populations with potential to reproduce was low in environments with low light intensity. Populations that existed in environments characterised by low light intensity ($<1.3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and high understorey biomass appeared to be small plants that had not matured beyond seedling stage. That these plants would set flower and produce seeds is highly unlikely.

Human utilisation of forests in the Terai intensified after the initiation of malaria eradication programmes made the Terai suitable for settlement to people from the Hill and Mountain regions. Human use together with grazing has contributed to bringing about changes in the forest overstorey and understorey by making forest canopies more open and reducing understorey biomass levels. This has helped the successful establishment of *Chromolaena*, where success is measured in terms of presence, cover, biomass, biometric traits, and age composition.

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ACRONYMS

ABPSD	Agri-Business Promotion and Statistics Division, Ministry of Agriculture and Cooperatives. His Majesty's Government of Nepal
CBI	<i>Chromolaena</i> Biomass Index
CBS	Central Bureau of Statistics, Nepal
DDT	A chlorinated organic insecticide [1,1,1-Trichloro-2,2-bis-(4'-chlorophenyl)ethane]
GIS	Geographic Information Systems
IUCN	The World Conservation Union
PPA	Number of people per hectare of arable land
PPF	Number of people per hectare of forest
RS	Remote Sensing
SPD	Simple population density
UBI	Understorey Biomass Index
WWF	World Wildlife Fund

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1. Introduction

1.1. General Introduction

Globally, invasion of an ecosystem by alien species is acknowledged as one of the major threats to biodiversity. Undesired effects range from changing species composition and community structure^{83, 95, 102, 103}, increasing frequency of fires¹⁸, to lowering the water table⁷. These effects have resulted in some cases to the displacement of native species¹⁰³. Mooney and Drake⁷⁰ argue that this may cause a net loss of species and thereby a possible homogenisation of the earth's biota.

The question what makes invaders successful has been approached using two broad explanations: (1) the biological traits of the invading species^{3, 77, 82}, and (2) the characteristics of the recipient ecosystem. Rejmánek^{80, 82} and other authors^{58, 107} claim that species traits such as phenotypic plasticity, genetic polymorphism, ecotypic differentiation, eurytophy and polyphagy increase the chance of invasion success. Small seed mass, prolific production, rapid growth, low nuclear DNA also promote invasion success^{50, 80, 82, 102}. Recently, evidence has been provided that some invasive species reduce the ability of surrounding plants to take up nutrients⁹ thereby reducing the ability of native species to resist invasion.

Despite advances in the species-centered approach^{80, 82}, the need to consider characteristics of the recipient ecosystem in studies of invasion biology have been raised^{99, 77}. Elton²⁵ proposed a negative relationship between species diversity of a recipient community and its susceptibility to invasion. This hypothesis has been supported by results from field observations²⁹ and experimental studies⁹⁸ at local as well as continental scale⁸¹. However, contradictory results from other experimental⁹⁶ and observational studies⁵⁹ have hampered the generalization of this hypothesis. For example, Robinson and Quinn⁸⁴ and Robinson *et al*⁸⁵ found that species-rich areas were more easily invaded than species poor areas. It has also been suggested⁵⁰ that productivity of an ecosystem determines its invasibility. Lonsdale⁵⁹ in a comparison of invasibility amongst biomes noted that more productive biomes (multiple biome regions and temperate agricultural or urban sites) were invaded to a greater extent than deserts and savannas.

It is generally agreed that disturbance facilitates invasion success^{22, 44, 75} by increasing resource availability and decreasing competition from native species. It has been observed⁵⁰ that disturbance facilitates invasion more in productive environments⁴² than in unproductive ones⁴³. The idea that disturbance plays an important role in invasions is not new²⁵. Changes in land-use or the continuation of inappropriate levels of use often provide the necessary conditions for an invading species to become established⁴⁴. For instance, colonisers are successful only in disturbed environments^{5, 79}. However, situations where invasions occur in the absence of disturbance have also been reported^{8, 57, 61}. Thus, there has been little progress in generalisations about what makes an ecosystem susceptible to invasion⁵⁰.

Human domination of ecosystems¹⁰¹ and resultant modification of landscapes is pervasive all around the world. This trend has led in many instances to the degradation of ecosystems⁴⁴. In developing

countries, these changes nowadays occur at an accelerated pace as a result of increasing population and subsequent increase in demand for natural resources. Other causes include but are not limited to aspects related to socio-economics and politics. To date, few studies¹⁰⁰ have tried to link changes in human population and related changes in land use to plant invasions.

In Nepal, it has been generally accepted^{32, 36, 37, 89} that increased changes in land cover in the Terai have occurred after the initiation of malaria eradication programmes in the 1950s and 60s^{12, 37, 38, 54, 94}. Prior to the 1950s, except for the malaria-immune indigenous ethnic groups such as the *Tharu*, *Dhimal*, *Kumhal* and *Rajbansi* who occupied pocket settlements in dense jungles, the Terai remained a forbidden frontier for the Hill and Mountain population⁷⁴. Following the initiation of malaria eradication programmes⁹⁰, the Terai has been a destination for migrants from the Hill and Mountain regions. Apart from increased changes in land cover, the remaining forest areas would also have been subjected to greater human use. These changes can be seen as disturbances that might facilitate the establishment of opportunistic invaders such as *Chromolaena*.

In the present study, it is first examined how human population changed in the Terai of Nepal as a result of malaria eradication programme and subsequent increases in human migration. Following that, changes in forest and arable land resources in relation to human and cattle population are assessed. Second, factors influencing the presence, abundance and age composition of the invasive species *Chromolaena odorata* (L.) R. King & H. Robinson in the *Shorea* forests of the Terai are examined. Finally, evidence is provided for the hypothesis that the success of *Chromolaena* hinges upon the degradation status of the recipient ecosystem (*Shorea* forests in the Terai of Nepal). Forest degradation status in this thesis is considered in terms of forest canopy cover and understorey biomass, where a forest is considered degraded when characterized by more canopy openness and less understorey biomass.

The innovative aspect of this thesis is the effort to establish links between demographic processes at a macro scale to ecological patterns exhibited by an invasive species at a local scale. Also, the response of an invasive species to gradients in an invaded ecosystem is examined. The need for such studies in invasion biology has been proposed⁹⁶.

1.2. Research Hypotheses

1. Malaria eradication in the Terai of Nepal brought about demographic changes. Increase in population and related pressure on ecosystems have led to land use changes and ecosystem degradation. This has helped the successful establishment of the invasive species *Chromolaena odorata* in the Terai of Nepal.
2. In the case of *Chromolaena*, success of invasion hinges upon the degradation status of the recipient ecosystem.

1.3. Research Objectives

The objective of this study is to contribute towards understanding relationships between human population growth, related changes in land cover and invasion success of an alien invasive species.

1.4. General Research Questions

1. How has demography and land cover responded to malaria eradication programmes in the Terai of Nepal?
2. Is the invasion success of *Chromolaena* dependant on the state of ecosystem degradation?

1.5. Outline of the Thesis

This thesis is designed to answer the two main research questions outlined in Section 1.4. For reasons of clarity, the research questions are addressed in different parts of this thesis. Question 1 is addressed in Chapter 3, while question 2 is addressed in Chapter 4. Since the data types and the approach needed to answer these research questions differed, it was deemed appropriate to structure the thesis with different Chapters having a more specific and separate *Introduction*, *Methods and Materials*, *Results* and *Discussion* section. A short summary of the remaining Chapters is as follows.

Chapter 2 provides a general description of *Chromolaena odorata*.

Chapter 3 examines how resource dynamics in terms of human population, cattle number, forest area and arable land area have changed in the Terai of Nepal as a result of malaria eradication programme and subsequent increase in human migration. The aim is to document these changes in order to provide insights into the dynamics that may have led to an increase in pressure on remaining forest resources in the Terai of Nepal.

Chapter 4 explores the response of *Chromolaena odorata* to ecological gradients and investigates whether *Chromolaena odorata* presence, abundance, biometry and age composition are related to differences in understorey light intensity, understorey biomass and human disturbance (indicated by grazing) in the *Shorea* forests of the Terai in Nepal.

In Chapter 5, the main conclusions are presented following a synthesis aimed at linking the findings in Chapter 3 and Chapter 4.

2. *Chromolaena odorata*

2.1. Introduction

Chromolaena odorata (L.) R. King & H. Robinson henceforth called *Chromolaena* in this thesis has been studied by many authors^{2, 6, 19, 30, 31, 33, 48, 51, 65, 66, 68, 73, 92, 106, 108}. This Chapter provides a brief description of it.

Chromolaena is a perennial shrub species native to neotropical America stretching from southern Florida to the upper drainage basin of the Amazon in Southern Bolivia⁶⁵. The *Invasive Species Specialist Group* (<http://www.issg.org/>) of the IUCN has identified *Chromolaena* as one of the hundred worst invaders. It is known by different common names in different parts of the world: such as Banmara in Nepal⁵³, Siam weed in Thailand⁶⁵, herbe Indépendance in Côte d' Ivoire¹⁹, Christmas Bush in West Indies⁶⁶, Traffic weed and King's weed in different parts of Africa³³. Till recently, it was taxonomically classified as *Eupatorium*^{30, 66}. The genus *Chromolaena* belongs to the family Asteraceae, one of the largest and most evolved of plant families^{30, 66}.

In its native habitat, *Chromolaena* is always found in close association and competition with closely related species which are absent from Asia and Africa⁶⁶. Further, invasiveness in its native habitat is restricted by a host of predatory insects and diseases⁶⁶.

2.2. Distribution

Chromolaena is widely distributed^{19, 68} in Asia and parts of Africa (Figure 2.1). Some authors¹⁹ suggest that *Chromolaena* was introduced in Asia for its ability to suppress *Imperata* sp. and other coarse grasses, while others note that it was first introduced in Calcutta, India prior to 1870 as an ornamental⁶⁸ from where it spread to other parts of Asia³⁰. It was probably introduced to West Africa in the 1930s^{46, 68}. *Chromolaena* introduction in Nepal has been suggested to have occurred a few years before 1940⁵².

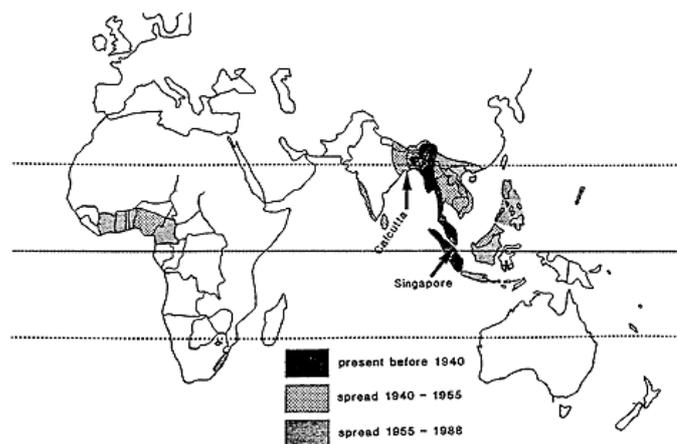


Figure 2.1 Extent of *Chromolaena* distribution as of 1988⁶⁴.

In Nepal, *Chromolaena* is not found beyond 83°15' East longitude to the west as it requires a minimum rainfall of about 1200 mm, and does not extend beyond 28°11' North latitude to the North⁵³. However, along riversides *Chromolaena* can be found beyond the specified limit towards the North. It

has been suggested that *Chromolaena* has reached its climatic potential in Asia limited by cold to the north and dry conditions to the west⁶⁷.

2.3. Plant Traits

Chromolaena possesses many of the traits that are attributed to successful plant invaders. Seed production is prolific⁶⁵ with up to 87000 seeds per mature plant or 400000 per m². Long distance dispersal is ensured by human activity. *Chromolaena* seeds bear minute hooks which enable clinging on humans, animals and vehicles⁶⁷. However, dispersal by wind is limited to short ranges (a maximum of up to 80 metres)⁶.

Chromolaena is a short day length plant flowering in late November and February in the northern hemisphere⁵³. The flowers are white or pale bluish-lilac and are borne on terminal corymbs of about 20 to 60 heads on stems and branches. The root system is fibrous and does not penetrate beyond 20-30cm. *Chromolaena* grows on most soil types, though it is restricted in sandy and waterlogged soils. The ability of *Chromolaena* to establish itself under a wide range of environmental conditions has been noted by many authors^{30, 66, 68, 106}. It has also been suggested to exhibit allelopathic properties².

Height of mature *Chromolaena* plants range from 1.5-2.0 metres⁶⁶. Growth is optimal under open or in partial shade, and *Chromolaena* plants in such environments can have as many as 20 or more stems per plant⁶⁶.

2.4. *Chromolaena* and Forest Ecosystems

Chromolaena has been generally considered as a typical species of secondary succession rapidly colonising forest clearings⁶⁶. It is usually found in disturbed environments and due to its heliophilous nature persistence in forests with dense canopies is doubtful⁵³. There is vigorous resprouting of *Chromolaena* after mild fires¹⁹. In South Africa, *Chromolaena* is considered a fire hazard due to its inflammability and is considered a potential threat to the persistence of coastal forests which are not resistant to fires¹⁰⁸.

2.5. Conclusions

Chromolaena is considered a nuisance and a threat to native biodiversity in many parts of the world^{52, 65, 108}. However, despite its prolific seed production, effective dispersal and establishment, literature suggests that once trees start to regenerate and form canopy, *Chromolaena* is not able to persist⁶⁶. These reports and field observations in Nepal seem to suggest that the survival of *Chromolaena* in forest ecosystems may be a function of how degraded the forest is.

3. Demographic and Land Cover Changes following Malaria Eradication in the Terai of Nepal

3.1. Introduction

3.1.1. General Introduction

Understanding the history of land cover and demographic changes is critical for proper understanding of contemporary landscapes and ecosystems³⁹. Humans have been the dominant force in bringing about changes in land cover and ecosystems¹⁰¹, and human land use have been shown to be critical in determining which species of plants and animals are dominant at a particular place⁷². This reflects the inextricable link between changes in ecological conditions and demographic variables. Amongst other concerns, human population growth is considered a key threat to the sustenance of the earth's biodiversity⁶². Therefore, the need to explore human-environment relationships has been identified as a key research theme for demographers^{17, 27}.

The existence of a relation between abundance of an invasive species to land-use and socio-economic variables have been noted and research in the context of relating rates of invasion to changes in land-use has been identified as important¹⁰⁰. However, studies testing this hypothesis are lacking.

Only a limited number of studies have been carried out to assess population pressure on natural resources for the whole of Nepal^{37, 89, 90}. Most of these studies have only considered population density per district and arable land⁹¹. No studies have considered population pressure on forest resource. Shrestha⁹⁰ has argued that models which utilise only simple population density (See Section 3.2.4) does not fully capture the pressure on natural resources due to variability of resource endowments across regions. In 2001, Nepal recorded a total population of approximately 23 million of which more than 60 % rely on agriculture to earn a living¹⁵. Given this, many authors have described Nepal's economy as predominantly agrarian where "...peasants, land (including forest/plant resources) and domestic animals are tightly interlocked"⁹⁰. This nexus between peasants, land and natural resources therefore are more pronounced and each component within this nexus influences each other profoundly.

It has been generally accepted^{32, 36, 37, 89} that increased changes in land cover in the Terai of Nepal have been facilitated by: (a) increased population due to increased migration; and (b) initiation of development programmes such as establishment of roads and infrastructure. Both of these are believed to have been possible to a greater extent after the initiation of malaria eradication programmes in the 1950s and 60s^{12, 37, 38, 54, 94}. Except for the malaria-immune indigenous ethnic groups such as the *Tharu*, *Dhimmal*, *Kumhal* and *Rajbansi* who occupied pocket settlements in dense jungles, the Terai remained a forbidden frontier for the Hill and Mountain population prior to malaria eradication⁷⁴. Since the Terai

has the largest portion of arable land, the region is considered the ‘granary of Nepal’ and has been a destination for migrants from the Hill and Mountain regions following the initiation of malaria eradication programmes⁹⁰. Malaria eradication was started in the Terai in phases. Eradication activities⁵⁴ employed spraying of DDT and pyrethrum in addition to prophylactic treatment with paludrine tablets. Protective nets were also supplied. Eradication activities were first started in central Terai in 1959, followed by different parts of Eastern Terai in 1959 to 1962 and western Terai in 1964^{37, 54}. See Figure 3.1. By the early 1970s, it was realized that complete eradication was not possible. The Government of Nepal then adopted a strategy focusing on control rather than total eradication of malaria⁵⁴.

In this Chapter, we examine how resource dynamics in terms of human population, cattle number, forest area and arable land area have changed in the Terai of Nepal as a result of the malaria eradication programme and subsequent increase in migration. Where data allowed, comparison across the whole of Nepal is made. The aim is to document these changes and examine them in order to provide insights into the dynamics that may have led to an increase in pressure on the remaining forests in the Terai of Nepal. Emphasis is on the demonstration of the patterns of change and not on the accurate determination of absolute figures.

Unavailability of a dataset on *Chromolaena* for the whole of Terai made it impossible to test part of the hypothesis put forward in Chapter 1 for the whole of the Terai. The relation of *Chromolaena* to ecological factors is therefore examined at a smaller scale in Chapter 4. It is assumed that the processes that have been taking place over the whole of the Terai are similar in nature though it may differ in magnitude. It is further assumed that the changes these processes would have had on the environment would have manifested similar patterns on smaller scales.

3.1.2. Research Hypothesis

It is hypothesised that land cover and demographic changes increased after the successful eradication of malaria. This has led to a decrease in forest area and associated increase in number of people per unit forest area. This increase in pressure on the remaining forest areas might have led to possible changes such as increased forest canopy gaps and reduced understorey biomass.

3.1.3. Research Questions

The following research questions have been formulated to guide the research.

1. How have population and population growth rates changed for the Terai of Nepal after the eradication of malaria in the 1950s?
2. What has been the change in number of migrants coming into the Terai after the 1950s?
3. Do in-migrants account for population growth in the Terai after the 1950s?
4. What has been the change in land cover since the late 1950s in the Terai?
5. How has the density of people per unit of forest and arable land changed since the late 1950s in the Terai?
6. How has cattle population changed in the Terai?

3.2. Methods and Materials

3.2.1. The Study Area

Nepal lies in the southern slopes of the Central Himalayas sandwiched between China to the North and India to the south. It covers an area of approximately 147 181 km² and lies between latitudes 26° 20' and 30° 10' N and longitudes 80° 15' and 88° 15' E. Almost rectangular in shape, it extends over 850 km in length from east to west and 180 km in width from north to south. Due to the rise in altitude from the lowlands in the South to the mountains in the North, Nepal is physiographically divided into three regions: the Mountains, the Hills and the Terai (Figure 3.1).

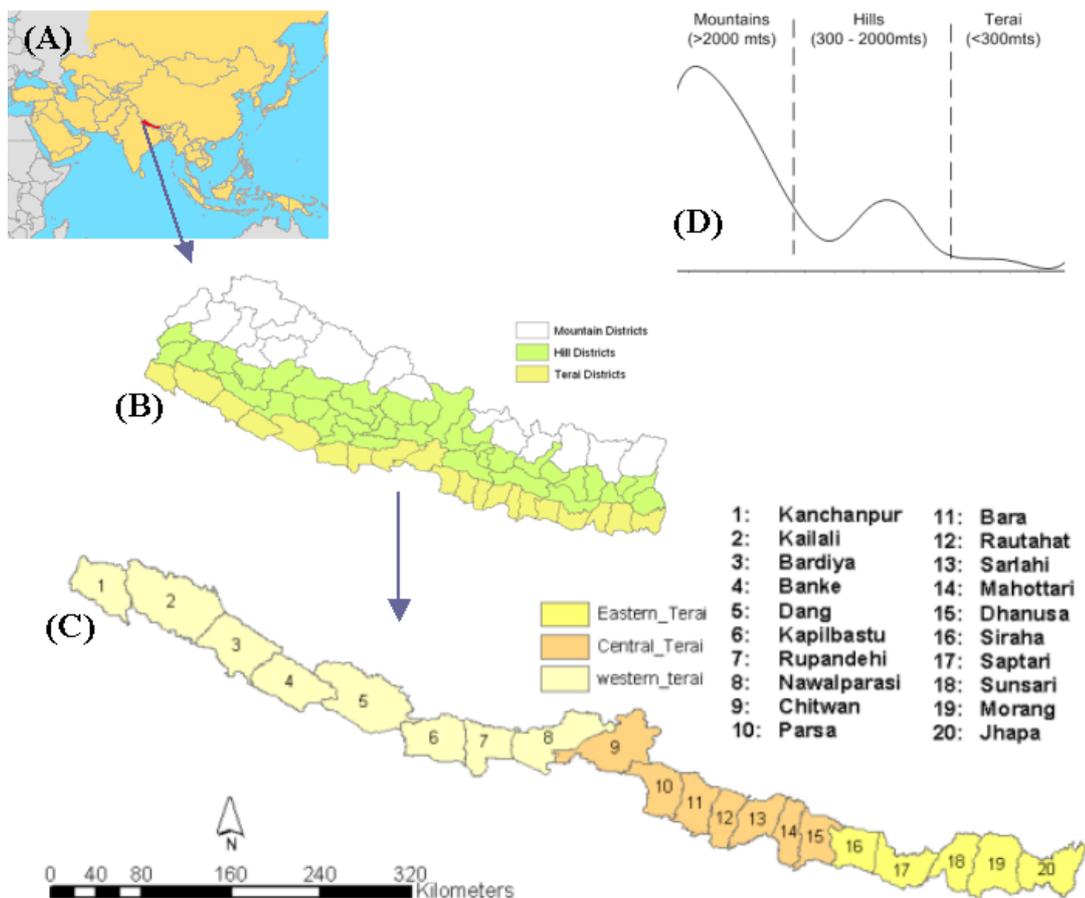


Figure 3.1 Details of the study area. Location map of Nepal (red spot) in Asia (A). Map showing allocation of districts in the Mountain, Hill and Terai Region (B). Map showing division of Terai regions into western, central and eastern zone with district names (C). Simplified elevation profile on which division of districts into Mountain, Hill and Terai are based (D). Note: Scale pertains to Map C only.

The Terai region covers 23% of the total area. It is organised into 20 districts and accommodates approximately 48 % of the total population¹⁵. The Terai experiences humid tropical climate and is characterised by tropical deciduous vegetation¹².

3.2.2. Data Set

Landcover maps for the Terai for three years: 1958, 1978 and 1996 were obtained from the World Wildlife Fund, Nepal. Human and cattle population figures were obtained from the Central Bureau of Statistics (CBS) of Nepal, Agri-Business Promotion and Statistics Division (ABPSD), Ministry of Ag-

riculture and Cooperatives, Nepal and literature^{37, 38, 89, 90}. The details for the data used and their sources are shown in Table 3.1.

Table 3.1 Data types, year and source

Data	Year						Source
	1958	1978	1996				
Land cover maps for the Terai	1958	1978	1996				WWF, Nepal
Population figures	1952-54	1961	1971	1981	1991	2001	CBS and others ^{11, 12, 14-16, 90}
Migration data	1971	1981	1991				CBS and others ^{15, 37}
Cattle figures	1996						ABPSD ¹

3.2.3. Calculation of Net-migrants

Only data for internal migration has been considered in this study. Internal migration refers to the mobility of population within a country between clearly defined geographical units resulting in a change of residence. Further, migration statistics pertaining only to *life-time* migrants have been used; where *life-time* migrants have been defined as those whose area of birth is different from the area of residence during the time of enumeration, irrespective of the number of moves the migrant has made¹². In-migrants are people entering a migration defining area from some point outside the area, while out-migrants are people who have left to some other point outside a migration defining area. All the definitions are based on those provided by the CBS¹², Nepal.

Total net migrants have been calculated as the difference between total in-migrants and total out-migrants. The number of total net-migrants was subtracted from total population growth to provide figures for population growth attributable to other factors. This has been referred to as autonomous growth in this thesis.

3.2.4. Derivation of Population Pressure Indices

Forest and arable land area per district was obtained from the land cover maps for 1958, 1978 and 1996. All GIS operations were carried out with ARCGIS8.3^{©26}. Indices for population pressure on forests (PPF), arable land (PPA) and simple population density (SPD) were calculated for individual districts of the Terai based on land cover data and interpolated population figures:

- PPF = Number of People/Forest Area (ha)
- PPA = Number of People /Arable Land Area (ha)
- SPD = Number of People /District Area (ha)

Census data had to be interpolated to date of the land cover since the year of the census data did not match that of the land cover data. Census data from the year closest to the land cover year was used for interpolation. Population figures from 198¹⁰ were interpolated back to 1978, and figures from 2001¹³ to 1996. However, in the case of the 1958, population figures from 1971 were used. This was to enable comparison with latter years since the Terai was organized into less than 20 districts prior to the 1971 census. Growth rates are based on CBS^{11, 12, 16}, where growth rates are average annual exponential rates of growth. Population figures were interpolated using the following equation as suggested in Ehrlich and Ehrlich²⁴: $N_t = N_0 e^{rt}$; where N_t is population at time t , N_0 is population at time 0, r is the growth rate per year and t is time in years.

3.3. Results

3.3.1. Migration and Population Growth

The Terai region had a population of about 2.9 million in 1952. By 2001, it reached 11.2 million. Growth rates for Terai has been consistently higher compared to the average national growth rate, as well as the average growth rates for the Hill and Mountain regions (Figure 3.2). Growth rates for the Mountain and Hill region have been on a constant decrease. Note the jump in growth rate between 1971 to 1981 for the Terai.

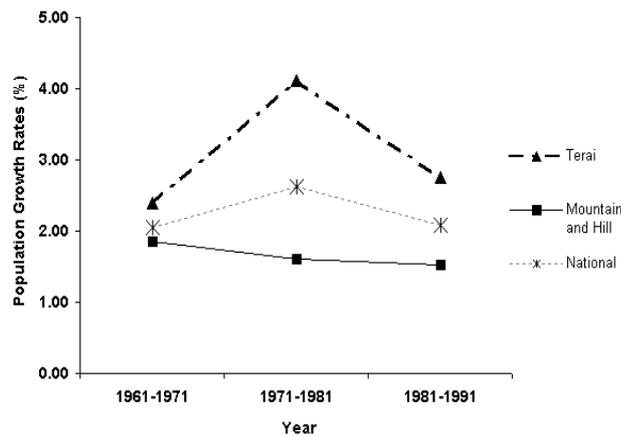


Figure 3.2 Population growth rates over ten year periods for the Terai, Mountains and Hills and the whole of Nepal (National).

Internal migration¹² data revealed that migration to the Terai was chiefly from the Hill and Mountain regions (Figure 3.3). While the Terai region experienced consistent increase in in-migrants, the Hill and the Mountain regions showed increased number of out-migrants. Figure 3.4 revealed that immigration accounted for a significant proportion of population growth in the Terai.

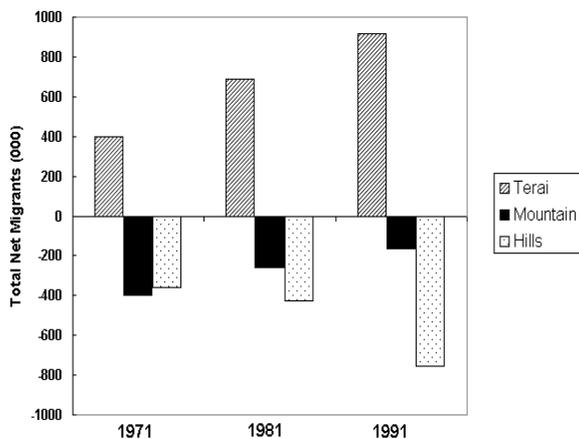


Figure 3.3 Net Migrants for the different regions of Nepal. Positive values represent a net gain (immigration) while negative values indicate a net loss (emigration).

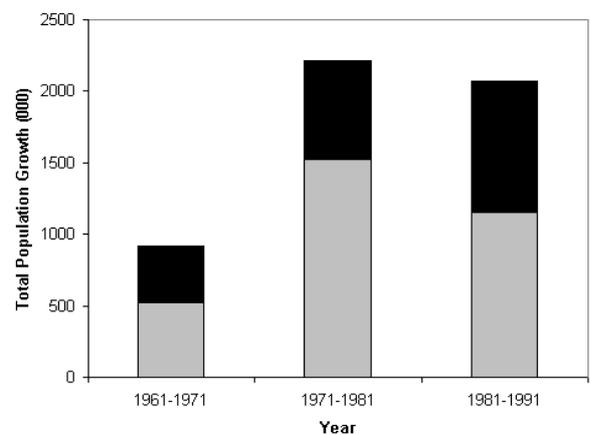
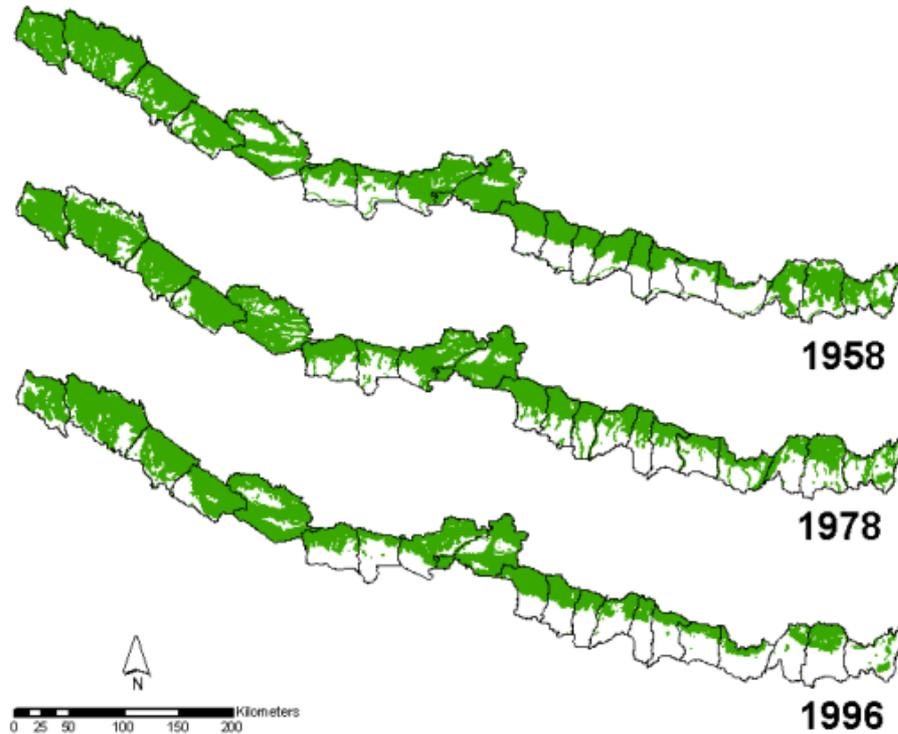


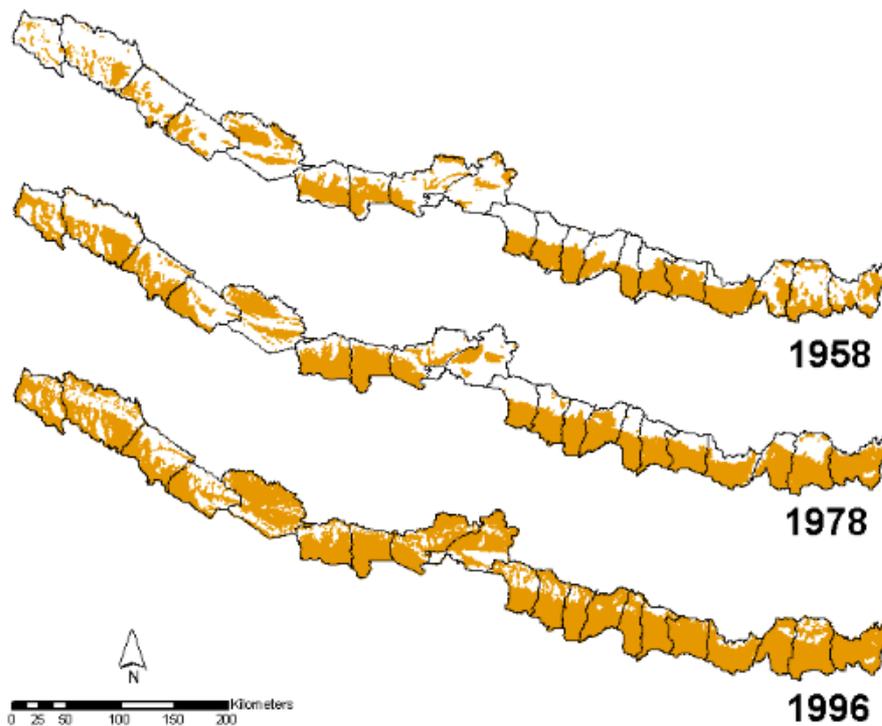
Figure 3.4 Total population growth in the Terai over ten year periods where population growth as a result of migration is represented by black bars, and growth due to autonomous growth is shown in grey

3.3.2. Land Cover Change

Given the significant increase in population in the Terai, changes in land cover were examined. Map 3.1 and 3.2 and Figure 3.5 showed that the proportion of land under forest cover in the Terai has declined steadily, while arable land has increased.



Map 3.1 Forest cover in the Terai of Nepal (1958, 1978 and 1996)



Map 3.2 Arable land cover in the Terai of Nepal (1958, 1978 and 1996)

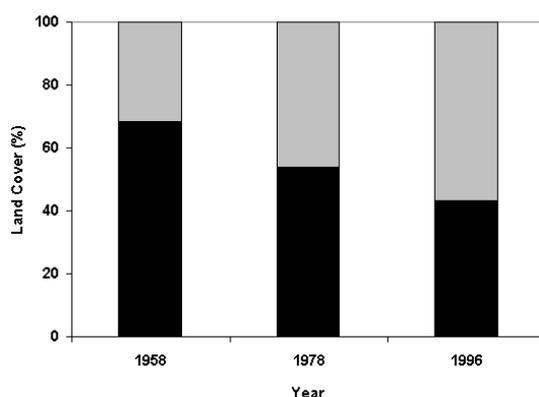
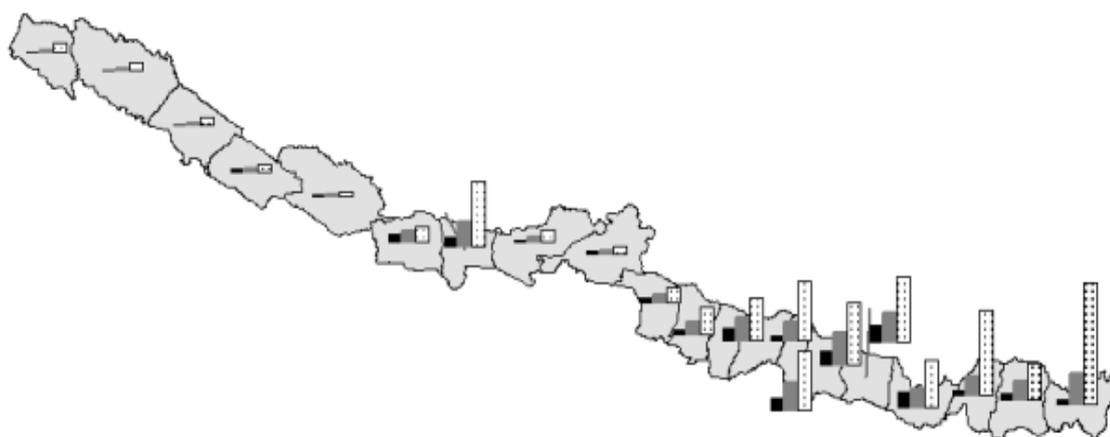


Figure 3.5 Proportion of forest cover (black) and arable land (grey) in the Terai

3.3.3. Population Pressure on Forests

So far, the results have demonstrated that population and land cover have changed significantly in the Terai of Nepal. Given a rising population and a decreasing forest cover, it was worth examining how the number of people per unit forest area had changed. As expected, the number of people per hectare of forest had increased substantially since 1958 (Map 3.3 and Table 3.2).



Map 3.3 Changes in number of people per hectare of forest (1958, 1978 and 1996). Black bars indicate population density in 1958, medium-grey bars in 1978, and dotted bars in 1996.

The average increase in number of persons per hectare of forest has been almost seven fold since 1958 while population itself has increased only by about three times (Table 3.2). Changes in number of people per unit arable land showed a slight increase.

Table 3.2 Simple population density (SPD), number of people per hectare of forest (PPF), number of people per hectare of arable land (PPA) and estimated population for the Terai. SPD, PPF and PPA are averages for the whole of the Terai

Year	SPD	PPF	PPA	Estimated Population
1958	0.95	2.34	3.40	3252000
1978	1.63	5.58	4.11	5558000
1996	2.94	14.63	5.59	10029000

3.3.4. Cattle Population

Examination of changes in cattle density per unit forest area and arable land area over time was not possible due to unavailability of data. The density of cattle per forest area and arable land area for 1996 are shown in Figures 3.6 and 3.7.

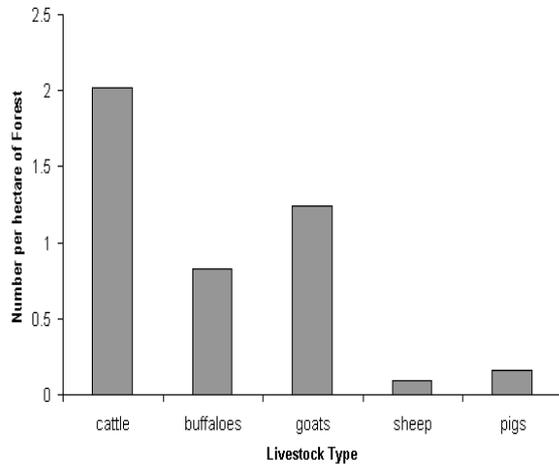


Figure 3.6 Number of different livestock per hectare of forest in the Terai in 1996

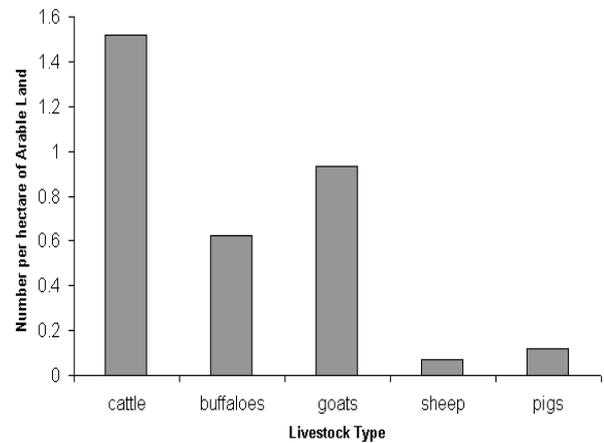


Figure 3.7 Number of different livestock per hectare of arable land in the Terai in 1996.

3.4. Discussion

3.4.1. Malaria Eradication and Population Growth

Malaria eradication programme made the Terai a more secure environment for human settlement from an epidemiological point of view. This resulted in increased number of migrants coming into the Terai from the Hill and Mountain regions^{36-38, 74, 89, 90}. Increase in number of migrants coming into the Terai partly accounted for the higher population growth.

3.4.2. Implications on Forest Ecosystems

Results have showed a significant decrease in forest cover in the Terai since 1958. The remaining forest areas in the Terai were subject to fulfilling a variety of socio-economic needs ranging from fuelwood to fodder. Results have also showed that the number of people per unit forest area has increased significantly since the 1950s. Given estimates which suggest that almost 95% of fuelwood requirements in rural Nepal are met from forests³⁶, the increase in number of people per unit forest area would have effected significant changes in the forest canopy density and understorey biomass. The amount of forest canopy determines the understorey light availability. The relationship between forest canopy density and understorey light intensity is shown in *Appendix 2*.

Time series analyses on cattle data have not been possible. Field observations have revealed that most cattle are grazed in the forests. Further, it is tenable to assume that the number of cattle in the Terai would have been lower prior to the 1950s given less number of people. Cattle population may have increased considerably in the Terai since then due to an increasing population. This may have resulted in an increase in the number of cattle per unit forest area. However, this assertion needs to be confirmed.

Though not shown in the results, the conversion of forests to other landuses implies increasing fragmentation of forest patches. Fragmentation has been shown to have profound impact on species and community dynamics^{20, 87} and may facilitate the success of invasive species⁴⁵. Quantification of the extent of fragmentation could be explored in future studies.

3.4.3. Limitations of the Dataset

The interpretation of the results must be moderated due to limitations in the data. First and foremost, the land cover types that were used for the analyses were classified using different criteria. The land cover data for 1958 had three classes: (1) Forest; (2) Arable land; and (3) others, while the land cover data of 1978 had many more classes such as grazing land, stones and gravels, and others. The 1996 data had only three classes: (1) Forest, (2) Arable land and others and (3) water bodies. In 1996, arable land and other classes had been merged together. This has resulted in most areas being shown to be under arable land in 1996 (Map 3.2).

Since land cover change and comparison of population pressure on forests was based on these maps, the actual figures shown in Tables 3.2 may not be very accurate. However, as mentioned earlier (Section 3.1.1), the emphasis is on the demonstration of the pattern of change. And this pattern would not have been grossly misrepresented with the present dataset, since a misclassification of a few forest and arable land areas into other classes would not have significantly changed the overall average figures.

Comparison of population data for Nepal with dates prior to 1971 has always presented a problem due to changing district and census boundaries^{11, 12}. In 1958, Nepal had a lesser number of districts than it did in 1971. For this purpose, population data for 1958 was extrapolated using average growth rates for the Terai for 1961 to 1971. This means that the population data for 1958, 1978 and 1996 are not realistic. However, it provides a reasonable estimate.

3.5. Conclusions

Despite limitations in the dataset, what emerges from the results and the discussion is a clear indication that human population in the Terai increased substantially after the successful eradication of malaria. Though crude, estimations using land cover and census data provided evidence that the index of human population pressure on forest resources have risen considerably since 1958. Forests are also subjected to grazing. Increase in human utilization and grazing could have left the *Shorea* forests degraded in terms of forest canopy openness and amount of understorey biomass.

4. *Chromolaena*: Its Relation to Understorey Light, Understorey Biomass and Grazing

4.1. Introduction

4.1.1. General Introduction

The negative side of human domination of earth's ecosystems are manifold¹⁰¹. One of the effects associated with human population growth and related changes in land cover is the growing threat to biodiversity⁶⁹ from an increasing number of invasive species often favoured by these changes⁴⁴. It has been generally agreed that degradation of an ecosystem favours the success of invasive species⁴⁵. Degradation is usually a result of disturbances to an ecosystem most often related to human activities when natural causes are not considered.

A clear definition of 'what constitutes disturbance?' and 'what does not?' is not offered by literature⁸⁶. Disturbance may be understood as: (1) the removal or damage of biomass from a system³⁴; (2) "...processes that alter birth and death rates of individuals present in a patch; and (3) '...any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment'⁴⁵.

It has been suggested that *Chromolaena* and shrub species similar to it (e.g. *Lantana camara*) respond positively to understorey light availability and negatively to disturbance intensity²³. Examination of species response to ecological gradients is considered important⁴. Such examinations prove useful in providing valuable insights into how species respond to various ecological gradients and indicate the ability of a species to persist along such gradients. Studies relating the response of an invasive species to such gradients appear limited and the need to study whether invasion might be limited in stressful environment have been raised^{45, 96}. Recently, improved techniques to model the response of an species to ecological gradients employing Generalised Linear Models⁶³, Generalised Additive Models⁴⁰ and other curve fitting procedures (e.g. Huisman–Olf–Fresco Models⁴⁹) show promise and have been used in favour of the classical Gaussian models.

The need to differentiate between the fundamental and realised niche of a species in statistical models have been highlighted^{4, 21, 35}. Regional variation in source and sink patterns have been described in animals^{28, 56, 105} and in a few plant species^{41, 55, 104}. Except in a few cases^{41, 55, 104}, statistical models have not considered niche and source-sink concepts together. Literature reveals that ideas on source-sink have been primarily explored and assessed by means of birth and death ratios in both animals and plants^{55, 76, 104}. In the case of plants, a short cut may be to look at populations which flower and populations that do not. The ability of a plant to flower may also be related to its attributes such as height, diameter, number of branches and the age attained by plant populations across ecological gradients.

Most studies applying statistical modeling techniques to map species distribution have been limited in robustness due to the inconsideration of ecological knowledge during model formulation⁴. Incorporation of ecological knowledge such as whether a given local population function as a source⁷⁶, or as a sink without the capacity to maintain a population on its own would yield useful additional information from the models. Consideration of such ideas may prove particularly valuable in the case of invasive species where you want to implement control measures under circumstances of limited capital and manpower.

Field observations⁵³ in the *Shorea* forests of the Nepalese Terai suggest that *Chromolaena* displays variation in sexually reproductive and non-reproductive population. Reproductive populations tend to be predominant in disturbed environments, while populations that prevail in non-disturbed environments seem non-reproductive. Given these observations it is postulated that *Chromolaena* populations are locally segregated into source and sink populations. It is further hypothesised that the nature of this segregation is determined by the degradation status of the forest.

The aim of this Chapter is to examine the relationship of *Chromolaena* presence, abundance, biometry and age composition to differences in understorey light intensity, understorey biomass and grazing. The presence of grazing is taken as an indicator for the presence of human associated disturbance.

4.1.2. Research Hypotheses

1. Understorey light intensity and understorey biomass are different in grazed and un-grazed areas.
2. The success of *Chromolaena* invasion in the Terai of Nepal hinges on these differences, where *Chromolaena* success is measured in terms of presence, cover, biomass, height, diameter, number of branches and number of stems.
3. Reproductive *Chromolaena* populations are only found in areas with higher light intensity and low understorey biomass.

4.1.3. Research Questions

1. Does understorey biomass differ significantly in grazed and non-grazed areas?
2. Does understorey light intensity differ significantly in grazed and non-grazed areas?
3. Is *Chromolaena* presence and absence related to understorey light intensity, understorey biomass and grazing?
4. Is *Chromolaena* Biomass related to understorey light intensity, understorey biomass and grazing?
5. Are biometric traits of *Chromolaena* (diameter, height, number of stems and branches) related to understorey light intensity, understorey biomass and grazing?
6. What are the strengths of the effects of understorey light intensity, understorey biomass and grazing on *Chromolaena* cover and biomass?
7. Is *Chromolaena* age composition related to understorey light intensity, understorey biomass and grazing?
8. Do *Chromolaena* populations exhibit source-sink patterns?

4.2. Methods and Materials

4.2.1. Study Area

The study area covers an area of approximately 120 sq km and is located between 87°24' – 87°29' East longitude and 27°33' – 27°43' North latitude. It falls within the buffer zone of the Royal Chitwan National Park in the Chitwan district of Nepal (Figure 4.1).

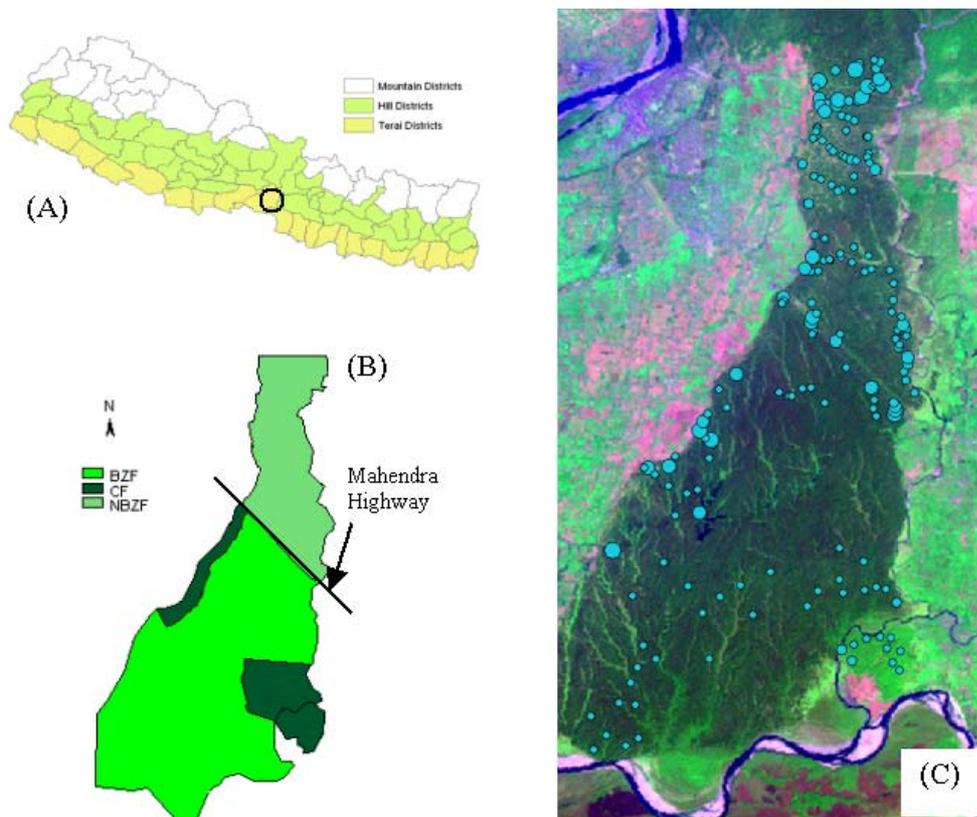


Figure 4.1 Study area in Chitwan. Map of Location of the Study Area (A). Map showing three different forest management regimes within the study area (B): 1) BZF: Buffer Zone for the Chitwan National Park; 2) CF: Community Managed Forest and 3) NBZF: Non Buffer Zone Forest – Government Managed. Landsat TM image (March 2003) of the study area (C) with sample point distribution shown as blue circular dots. Size of dots is proportional to Chromolaena cover. Maps not to scale.

Forest is the dominant land cover with Sal (*Shorea robusta*) as the dominant species. Other associates such as Asna (*Terminalia alata*), Bahera (*Terminalia bellerica*), Banjhi (*Anogeissus latifolius*) are also found. Grassland also account for a substantial portion of the study area. The soils are Eutric Fluorsols with mostly sandy loam texture. The average rainfall is about 2263 mm per year of which more than 80 % fall during the months of June to September. The months of April and May experience the highest temperatures with maximum temperatures exceeding 40°C. Elevation ranges from 100 to 300 metres above sea level. A mild fire occurs once a year through most part of the study area.

Major portion of the forest in the study area (south of the Mahendra highway – see Figure 4.1) is managed as part of the buffer zone of the Royal Chitwan National Park. The forest area to the north of the Mahendra highway is managed by the State (Figure 4.1). Forests at the fringes to the south of the Highway have mostly been handed over to nearby communities. This process of giving the *right to manage* to the communities has been initiated some 7 years ago and continues. In essence, there are

three different forest management regimes within the area: 1) State Owned; 2) Buffer Zone for Protected Area Network; and 3) Community Owned. All three regimes are subjected to different degrees of protection: from the state owned being the most utilised without any clear sense of management; to the community owned where use is regulated by the communities; to the buffer zone where any kind of use is prohibited. This protection determines the kind of disturbances to which the forest is subjected. For instance, grazing is only found in the forest north to the Mahendra highway. In areas to the south of the Mahendra highway, grazing has not been allowed for over 7 years in the community forests, and since the gazetting of the National Park in 1996 in the buffer zone.

4.2.2. Field Data Collection

A random sampling scheme was adopted to measure the variables listed in Table 4.1 and 4.2. A sample plot size of 30m by 30m was selected to: (1) match with the pixel size of the Landsat TM image that was used for forest canopy density classification⁵³; and (2) capture – to some extent – the variability within *Chromolaena* populations. Field data was collected during the months of September and October 2003. Centre of the sample plots was located with the help of a GPS. A total of 175 plots were sampled (Figure 4.1). Data collection sheets (*Appendix 1*) were used for collecting information from the sample location.

Table 4.1 Independent variables measured in the field

Independent Variable	Description	Instrument
Coordinates	In X and Y bearings	GPS
Altitude	In metres above sea level	Altimeter
Forest Canopy Density	In percentages	Visual estimation
Hemispherical photographs of forest canopy	Digital images. Photographs taken with camera at 0° zenith angle	Nikkor Fish eye lens fixed on digital camera (Nikon Coolpix 995)
Vegetation Cover	In percentages	Visual estimation
Disturbance Indicators	Presence and absence	Visual estimation

Table 4.2 Dependent variables measured in the field

Dependant Variable	Description	Instrument
<i>Chromolaena</i> Cover	In percentages	Visual estimation
<i>Chromolaena</i> Height	Height of tallest plant in the plot was recorded in centimetres	Measurement with measuring tape
<i>Chromolaena</i> Diameter	Diameter of thickest plant in the plot was recorded in millimeters. Measured 10cms above the ground.	Measurement with callipers
Number of <i>Chromolaena</i> Stems	Number counted on the plant showing maximum number of stems	Manual counting
Number of <i>Chromolaena</i> Branches	Number counted on the plant showing maximum number of branches	Manual counting
Age composition of <i>Chromolaena</i> populations	Two classes recorded as: (1) Mixed populations – with all age classes from 1 to 4; and (2) Population with only first year recruitments (≤ 1 year) which have not grown beyond seedling stage (very small plants). A plot was recorded as either Class 1 or Class 2.	Visual Assessment based on height and diameter measurement

4.2.3. Data Processing

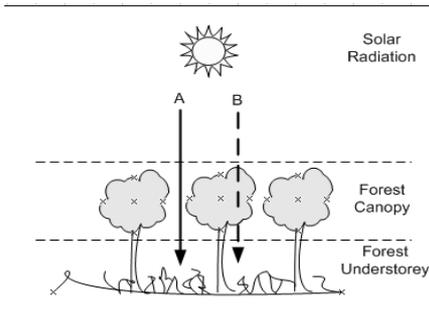


Figure 4.2 Total Transmitted Light (Total Understorey Light) = A (Total Direct Transmission) + B (Total Indirect Transmission).

Processing of the digital hemispherical photographs to calculate total understorey light intensity was carried out by Joshi⁵³ with the help of the *GAP Light Analyser* software. Total understorey light is to be understood as the total amount of light transmitted to the forest understorey (Figure 4.2). It is estimated in *micro joules per square meter per day* ($\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$). In the preceding sections and henceforth in the thesis, it is referred to as understorey light intensity.

Two indices have been developed during the course of data analyses to facilitate analyses and interpretation of results:

1. *Chromolaena* Biomass Index (CBI) = (*Chromolaena* cover/maximum *Chromolaena* cover) X (*Chromolaena* height/maximum *Chromolaena* height) X (*Chromolaena* diameter/maximum *Chromolaena* diameter) X (Number of *Chromolaena* branches/maximum *Chromolaena* branches) X (Number of *Chromolaena* stems/maximum *Chromolaena* height)
2. *Understorey* Biomass Index (UBI) = [(Shrub Cover * Shrub Height) + (Herb Cover * Herb Height)]/100

This *CBI* was derived to obtain a variable that would describe and reflect the abundance and vigour of *Chromolaena* populations together in one parameter. The *UBI* provides a measure for the understorey biomass excluding *Chromolaena*.

4.2.4. Statistical Analyses

Linear regression and variants of the linear regression in the form of polynomial and factorial regression were tested to determine functional relationships between dependant variables and the criterion variables. For reasons such as the possibility to come up with unrealistic values (e.g. negative values for cover), subsequent model building effort was restricted to the use of a Gaussian logit model⁴⁹ with the following specifications.

$$Y = M / (1 + \exp(a + b \cdot x + c \cdot x^2))$$

where *M* is a constant which equals the maximum value that can be obtained by the dependant variable. For the sake of simplicity and to make interpretation of results easier, only understorey biomass, understorey light intensity and grazing were used as independent variables in the above model. The model was built stepwise and the *F* statistic with tabulated critical values was used to assess significance of added parameters as proposed by Huisman, Olff and Fresco⁴⁹.

A Gaussian logistic regression using backward elimination was employed to assess relationships between independent variables and (1) *Chromolaena* presence and absence, and (2) age composition of *Chromolaena* populations. To enable the execution of a logistic regression, age composition was recoded to 0 and 1, where mixed populations (see Table 4.2) were coded 1, and populations with only first year recruitments were coded 0.

Chromolaena cover and *Chromolaena Biomass Index (CBI)* were chosen for a path analyses⁹³ to evaluate the strengths of direct and indirect effects of independent variables on dependent ones. Plots where *Chromolaena* was absent were not included in the analysis, since some of these plots fell within grasslands. Stepwise forward regression was carried out to derive partial standard correlation coefficients. Cover was chosen since it is the dominant variable measured in many ecological studies; and CBI since it is a composite of both abundance and vigour of *Chromolaena* plants.

All statistical analyses were carried out with SYSTAT 7.0, STATISTICA 6 and SPSS 11. As part of preliminary analyses, all the variables were subjected to normality tests and tests for homogeneity of variances. Appropriate statistical tests were employed to check for significant differences.

4.3. Results

4.3.1. Presence and Absence

A Gaussian logistic regression in the form of $y = e^z / (1 + e^z)$ was employed to reveal the best fitting combination of variables (understorey light intensity, understorey biomass and presence of grazing) to describe the presence of *Chromolaena*. The presence of *Chromolaena* was significantly related to understorey biomass and light intensity as follows:

$$Z = -1.81 + 3.70 * X_1 - 0.84 * X_1^2 - 0.001 * X_2;$$

where X_1 and X_2 are light intensity and understorey biomass respectively. The model gave a McFadden's Rho^2 of 0.13, which was highly significant ($2 * [LL(N) - LL(0)] = 29.16$, $df = 3, 172$, $p = 0.0001$). Grazing and the interaction factors between independent variables did not significantly contribute to the model.

The response of *Chromolaena* to light followed a bell shaped curve, the level of which was influenced by the amount of understorey biomass (Figure 4.3). As expected, the probability of *Chromolaena* presence was low under low light intensities and increased to intermediate light intensities. However, the probability to find *Chromolaena* declined when light intensities increased further towards irradiance of open areas. It is noted that some of these open areas were grasslands, which differed from the forest environment.

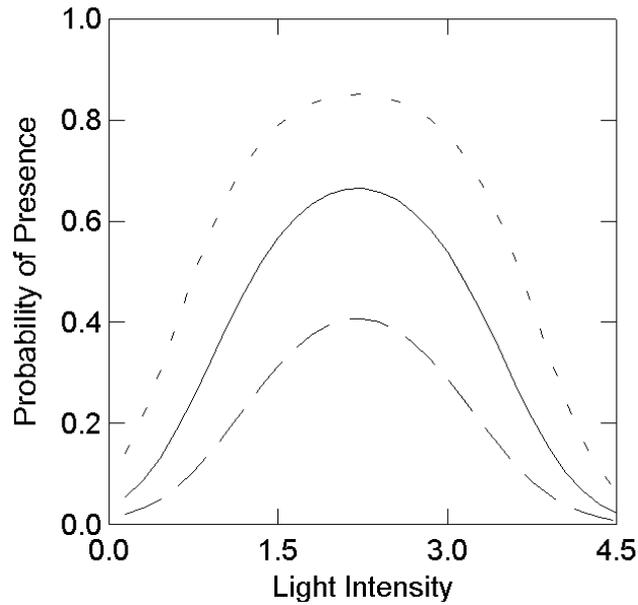


Figure 4.3 Probability of *Chromolaena* presence in relation to light intensity ($\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) at three levels of understorey biomass index: --- = 50; — = 150; - · - = 250

4.3.2. Cover

The relationship of *Chromolaena* cover to understorey light, understorey biomass and grazing was explored with the use of a Gaussian logit model⁴⁹ (See Section 4.2.4): where $Y = M / (1 + e^Z)$. Understorey light intensity and understorey biomass explained 28% of the variation in *Chromolaena* cover:

$$Z = 4.85165 - 3.60416 * X_1 + 0.74825 * X_1^2 - 0.00548 * X_2 + 0.00025 * X_2^2$$

with $F_{(5,169)} = 30.08$ ($n = 174$, $p < 0.05$) and where X_1 and X_2 are understorey light intensity and understorey biomass respectively. Again, grazing and interaction factors between independent variables did not significantly contribute to the model.

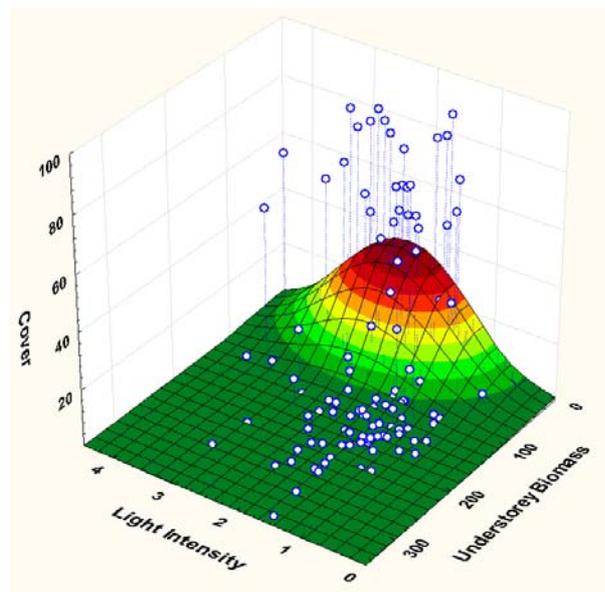


Figure 4.4 *Chromolaena* cover (%) in relation to light intensity ($\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and understorey biomass

The model predicted higher values at medium light intensity and low understory biomass (Figure 4.4). Similar to the response exhibited by presence, *Chromolaena* cover increased with increase in light intensity to intermediate levels, beyond which it decreased. Understorey biomass also showed significant influence on *Chromolaena* cover, where cover declined with an increase in understory biomass.

4.3.3. Biomass

Chromolaena cover was shown to differ along gradients of understory light and biomass. To further examine which combination of variables would explain *Chromolaena* biomass, a model similar to the one used for *Chromolaena* cover was tested. *Chromolaena* biomass was significantly related to understory light intensity and understory biomass:

$$Z = 1.64396 - 1.32358 * X_1 + 0.19565 * X_1^2 + 0.00581 * X_2 + 0.000001 * X_2^2;$$

with a R^2 of 0.37 ($F_{(5,11)}=141.89$, $p < 0.05$) and where X_1 and X_2 are understory light intensity and understory biomass respectively. Grazing and interaction factors did not contribute significantly to the model.

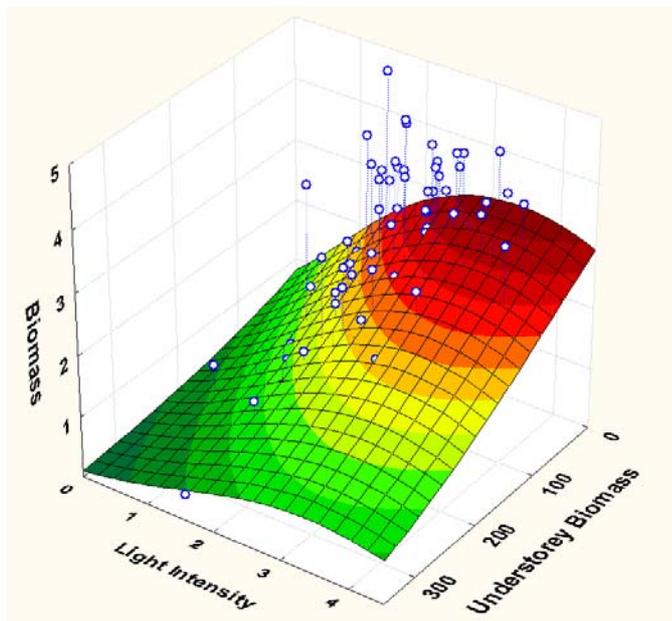


Figure 4.5 *Chromolaena* Biomass in relation to light intensity ($\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and understory biomass

A pattern similar to that exhibited by *Chromolaena* cover was observed. Higher biomass of *Chromolaena* concentrated along regions of intermediate light intensity and decreased with a decrease in light intensity and increase in understory biomass (Figure 4.5).

4.3.4. Path Analysis

Light intensity and understory biomass significantly influenced *Chromolaena* cover and biomass. Unexpectedly, grazing did not emerge as a significant variable in the models. However, understory biomass differed significantly between grazed and ungrazed areas (Kruskall-Wallis test, $H=21.66$,

df=1,174, $p < 0.001$). Understorey light intensity also differed significantly between grazed and ungrazed areas (Kruskall-Wallis test, $H=13.51$, df=1,174, $p < 0.001$). Grazing could therefore influence the abundance of *Chromolaena* through its impact on the abundance of competing plant species in the understorey. A path analysis was carried out to further investigate whether grazing indirectly influenced *Chromolaena* abundance.

Path analysis is based on correlation coefficients and assumes a linear relationship between the variables. In the analyses so far, we used Gaussian models, which do not conform to this central assumption of path analysis. However, it was indicated (section 4.4.1) that the Gaussian response surface might be due to the inclusion of a number of grassland sites in the analysis. In the path analyses, these sites – which were not representing the forest environment proper and where *Chromolaena* was absent – were excluded from the analyses.

Figure 4.6 shows the hypothesised model with the path coefficients reported alongside. Only significant effects are shown in the path diagram where solid arrows indicate direct effects with standardised partial regression coefficients reported above them. The width of the line is proportional to the size of the path coefficients.

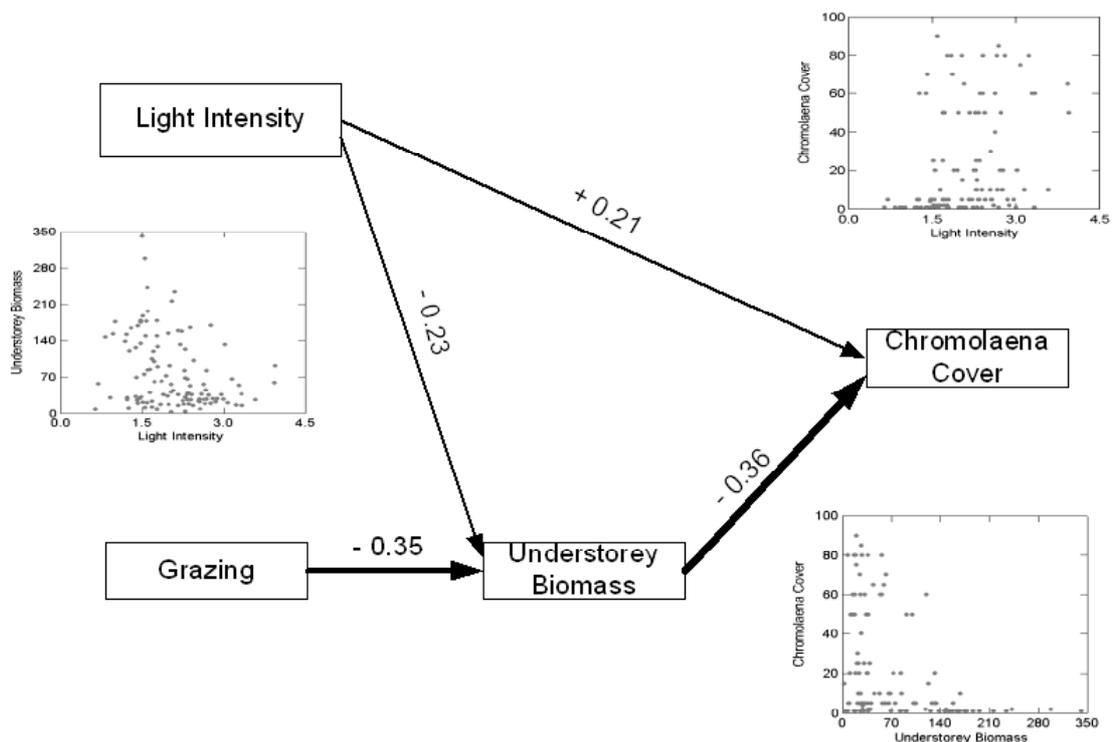


Figure 4.6 Path diagram for the effect of three independent variables on *Chromolaena* cover. Standardised partial regression coefficients are reported above the arrows, where width of the line is proportional to the size of path coefficients. Scatter plots for the variables connected by the arrows are shown alongside to illustrate the relationship between a single independent variable to the dependant variable.

Table 4.3 shows the direct, indirect and total effect of predictor variables on *Chromolaena* cover. Higher values for the path coefficients denote higher influence on dependant variable.

Table 4.3 Path Coefficients for *Chromolaena* cover (%). Signs indicate negative and positive relationships accordingly.

Predictor Variables	Effect on <i>Chromolaena</i> Cover (%)		
	Direct	Indirect	Total
Light intensity ($\text{mj}^{-1} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)	0.21	0.08	0.29
Understorey Biomass	-0.36	—	-0.36
Grazing (Presence/Absence)	—	0.12	0.12

Path analyses showed that understorey biomass had a stronger effect on *Chromolaena* cover than understorey light intensity. In consistence with results from the Gaussian models for *Chromolaena* cover and biomass, path analysis confirmed that grazing did not affect *Chromolaena* abundance directly. However, it showed considerable indirect effect. Unfortunately, the significance of this indirect effect cannot be estimated⁹³. Predictor variables exhibited similar effects on *Chromolaena* biomass with slightly different magnitudes.

4.3.5. Biometric Properties

Results so far have suggested a reduction in *Chromolaena* biomass and cover in environments characterised by low light intensities and high understorey biomass. This implies that physical attributes of *Chromolaena* plants such as diameter, height, number of stems and number of branches differ across gradients in understorey light intensity and biomass. To confirm whether this was so, it was examined whether the same combination of variables, which explained differences in *Chromolaena* cover and biomass, could also explain variation in the biometric properties of *Chromolaena*.

All the biometric properties of *Chromolaena* were significantly related to understorey light intensity and understorey biomass (Figure 4.7, Table 4.4). Grazing and interaction factors did not contribute significantly to model improvement.

Table 4.4 R^2 and best models for *Chromolaena* biometric properties; where X_1 =Understorey biomass, and X_2 = Understorey light Intensity ($\text{mj}^{-1} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$). All R^2 s are significant at $\alpha = 0.05$

Property	Model	R^2
Diameter	$12/(1+\text{Exp}(0.41690+0.00576* X_1-0.48721* X_2))$	0.32
Height	$250/(1+\text{Exp}(1.68403+0.00208* X_1+0.00001* X_1^2-1.86138* X_2+0.32340* X_2^2))$	0.29
Number of Stems	$20/(1+\text{exp}(1.39463+0.00829* X_1-0.43474* X_2))$	0.27
Number of Branches	$25/(1+\text{exp}(3.02292-0.00340* X_1+0.00006* X_1^2-2.40638* X_2+0.43764* X_2^2))$	0.39

Similar to the models for *Chromolaena* cover and biomass, biometric traits of *Chromolaena* showed higher values in regions with higher understorey light intensities and lower understorey cover (Figure 4.7). Number of stems and diameter showed an almost linear positive relationship with light intensity levels; while height and number of branches appeared to decrease after a threshold light intensity of about $3 \text{mj}^{-1} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Understorey biomass showed a negative relationship with all the plant traits.

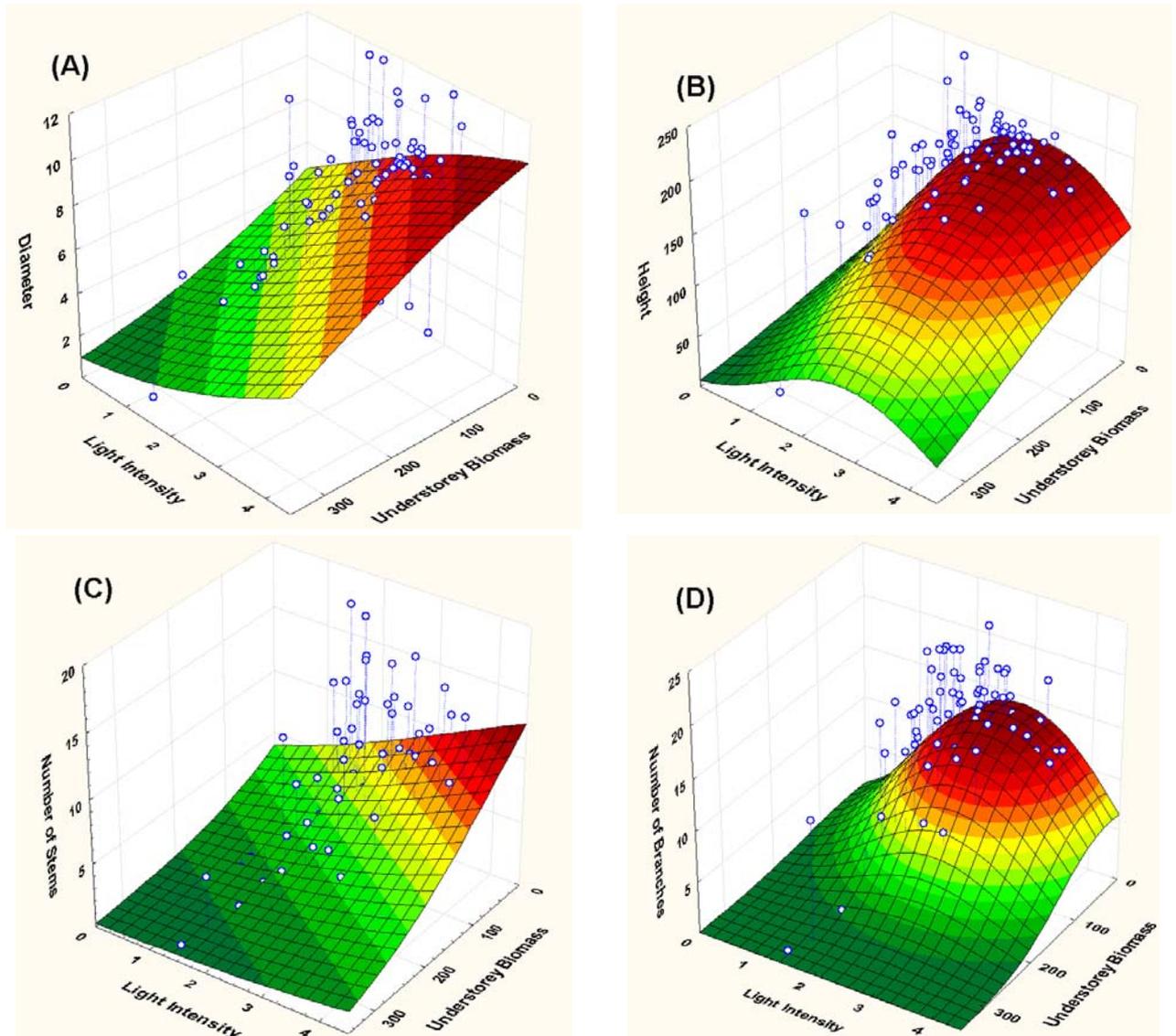


Figure 4.7 Understorey light intensity ($\text{mj}^1 \cdot \text{m}^2 \cdot \text{day}^{-1}$) and understorey biomass in relation to *Chromolaena* biometric properties: (A) diameter (mm) of *Chromolaena* stems; (B) height (cm) of *Chromolaena* plants; (C) number of *Chromolaena* stems per plant; and (D) number of branches per stem

4.3.6. Age Composition

In addition to plant size, the ability of a plant to mature and attain reproductive status has important implications for the sustenance of a population. A Gaussian logistic regression in the form of $y = \frac{e^z}{1 + e^z}$ was carried out to examine the combination of variables (understorey light intensity, understorey biomass and grazing) that best described age composition (see Table 4.2) of *Chromolaena* populations. Age composition was significantly related to understorey biomass and light intensity as follows:

$$Z = -4.25116 + 5.03808 * X_1 - 0.89921 * X_1^2 - 0.00933 * X_2;$$

where X_1 and X_2 are light intensity and understorey biomass respectively. The model gave a McFadden's Rho^2 of 0.21, which was highly significant ($2 * [LL(N) - LL(0)] = 29.39$, $n = 116$, $p < 0.0001$). Grazing and the interaction factors between independent variables did not significantly contribute to the model.

The probability of finding mixed *Chromolaena* populations (having plants with age > 1) was highest at intermediate light intensity levels of about 1.5 – 3 $\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and below an understorey biomass index of about 150. Note the presence of grazing at these sites. Further, there is a very low probability (<0.3) of finding mixed *Chromolaena* populations in areas with a light intensity level below 1.3 $\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$.

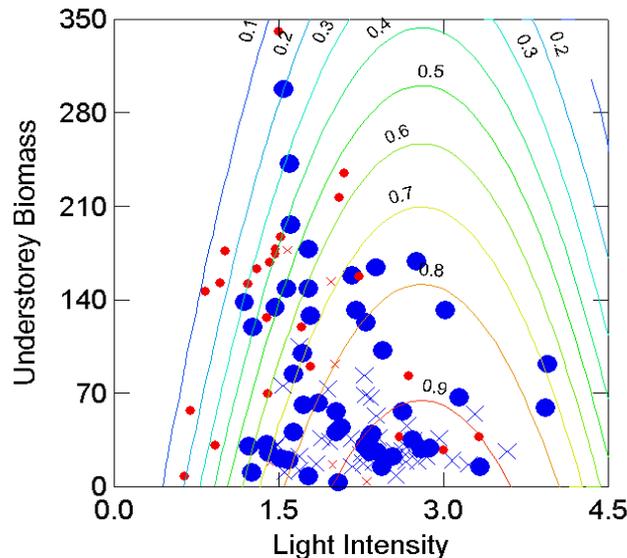


Figure 4.8 Age composition of *Chromolaena* populations in relation to light intensity $\text{mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and understorey biomass. Age of *Chromolaena* populations classified as Mixed populations consisting of a mixture of younger and older plants (big blue dots and crosses) and young populations with only first year recruitment (small red dots and crosses). Fitted lines represent the best fitting logistic model. The cross symbols represent areas where grazing is present, and the circle symbols indicate grazing absence.

4.4. Discussion

4.4.1. *Chromolaena* and Ecological Gradients

The results presented in this study revealed that the probability of *Chromolaena* presence together with its abundance and other plants traits differed considerably along gradients of understorey light intensity and understorey biomass. More importantly, for all the different *Chromolaena* parameters measured, higher values were registered in regions with intermediate understorey light intensity and lower understorey biomass. In consistence with ecological theories in plant community dynamics⁹⁷ the results highlight the importance of resource availability and competition.

The model chosen to evaluate the response of *Chromolaena* to ecological gradients was selected on the basis of the necessity to obtain realistic estimates. Comparison of different models was not possible within the framework of this thesis. The maximum R^2 obtained was 0.39 (model for *Chromolaena* branches – Figure 4.7). This implies that the models have not captured a major portion of the variation exhibited by *Chromolaena* populations. This could be “...due to sampling error or stochasticity in the studied phenomenon...”⁴⁹. Also, *Chromolaena* distribution pattern is highly discontinuous even within a very micro scale. Microclimate may have a significant role in determining distribution pattern. Con-

sequently, efforts to sample local variability of other environmental variables such as pH, temperature and soil moisture may have helped obtain better results. These factors were initially not considered important since many studies^{30, 51} have highlighted the eurytopic property of *Chromolaena*.

Factors such as the extent of fragmentation from increase in agricultural landscapes and road networks, which have been shown to facilitate invasion¹⁰⁹ have also not been considered. Other indirect factors⁴ such as the edge effects, distance to roads and settlements which have been shown to change micro-environment factors^{60, 78} such as light, wind speed and relative humidity leading to a shift in species composition at forest edges have also not been considered. This was done under the assumption that effects of these factors could be accounted for by the more proximate causes³⁵, which have been considered in this study.

Despite the low R^2 s of the models, the finding that higher values for the different *Chromolaena* parameters are more likely to be found in areas of medium understorey light intensity and low understorey biomass are valid. Examination of Scatter plots for response of different *Chromolaena* parameters (*Appendix 3*) show that variation is mainly in areas of high light availability and low understorey cover. This implies that in areas of with more understorey light and low understorey cover, there are *Chromolaena* plants which exhibit both higher as well as lower values for different parameters. In contrast, in areas with low light intensity and high understorey biomass, only small *Chromolaena* plants with lower cover and abundance are found. In this case there is not much variation observed (*Appendix 3*). Similar results have been reported by Witkowski¹⁰⁸ who noted higher density of *Chromolaena* plants in semi-shade compared to lower densities in full sun and shade. The competitive edge of *Chromolaena* over other species proves doubtful since understorey biomass exhibits a stronger effect on *Chromolaena* cover and biomass compared to light availability.

Apart from the model for *Chromolaena* stems (Figure 4.7), all the other models showed a decrease in *Chromolaena* parameters when understorey light intensities increased beyond $3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. The reason for this is not clear. It could be that grasses of *Imperata* sp. covers most of these areas. Field observations have shown that *Chormolaena* is rarely present where *Imperata* is found.

Closer examination of the data revealed that there are relatively fewer samples plots in areas having understorey light intensities beyond $3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ (very open canopy forests with a mean canopy cover of less than 20% or grasslands – see *Appendix 2*). Similarly, only a few sample plots have been measured in regions having understorey light intensity below $1.3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ (very closed canopy forests with a mean canopy cover of greater than 50% – see *Appendix 2*). This may have biased the results to some extent. Consequently, collection of more data from these regions may have helped obtain better fitting models.

4.4.2. Evidence for Source-Sink Patterns

The hypothesis that Source and Sink populations of *Chromolaena* exists is difficult to prove with the present dataset. More detailed analyses would have been possible if data had been available on number of flowering *Chromolaena* plants. Unfortunately, *Chromolaena* plants were not in flower during the period of field data collection. So far, the results and discussion showed that probability of presence, biometry and abundance of *Chromolaena* populations differ along a resource gradient (understorey light intensity) and that the nature of this response is moderated by the amount of competition (sug-

gested by the amount of understorey biomass). This suggests that suitable habitats for *Chromolaena* are restricted to areas with intermediate light levels and lower competition.

Results from the logistic regression analyses showed that the probability to find *Chromolaena* populations with a mixed age composition is very low in areas with low light intensities and high understorey biomass. In these areas of low light and high understorey biomass there appear to be only small *Chromolaena* plants which have not matured beyond seedling stage. That these plants would set flower and produce seeds is highly unlikely. Results from studies on similar invasive shrub species (*Lantana camara*) indicate that even plants which have grown beyond seedling stage do not set flower when found under low light intensity levels in dense canopy forests²³. Witkowski¹⁰⁸ noted that *Chromolaena* plants growing in shade did not produce seeds, but this was dependant on the stage of invasion. The physical presence of these small plants at a given point in space and time suggests that there is immigration of seeds from nearby populations that are in a less stressful environment. Thus, their presence without these nearby reproductive populations would not be possible. This pattern of segregation of populations into two with one being admittedly sterile and relying on another more reproductive group for propagules is suggestive of a source-sink mechanism⁷⁶. However, data from long-term observational plots including demographic variables are required to prove this for certain. Also, the scale of study will have implications on the interpretation of results.

4.4.3. Grazing and Fire

Results showed that grazing significantly reduced understorey biomass and indirectly affected *Chromolaena* cover and biomass. This suggests that the removal of understorey biomass is favouring the establishment and propagation of *Chromolaena* plants. This finding is in consistence with suggestions that amount of biomass can serve as an index of community resistance to invasion in some situation⁷⁹ and that open space created by biomass destruction is a vital factor for ensuring invasion success. The effect of grazing on facilitating invasion success have been mentioned^{23, 47} in different ecosystems.

Among other things, physical presence of cattle in the forest means deposition of dung. In all the plots where grazing was present, the presence of dung was also noted. *Chromolaena*⁵³ and other invasives⁴⁵ have been shown to respond opportunistically to increased levels of nutrient availability. Grazing has also been associated with opening of soil which facilitates seedling recruitment^{45, 67}.

A low intensity fire occurs once a year throughout the study area. *Chromolaena* has been shown to be resistant to fire^{19, 108} and it has been claimed to proliferate after fire. Fire results in removal of understorey plant canopy and release of nutrients⁴⁵. Studies have shown that *Chromolaena* takes advantage of the soil nitrogen which becomes available after fire⁸⁸. Further, both young and old plants of *Chromolaena* have been shown to be capable of coppicing with rapid regrowth after mild fires. In the absence of mild fires for more than 15 years¹⁰⁸ *Chromolaena* populations have been shown to become senescent. However, intense fires can kill *Chromolaena*¹⁰⁸. Generally, it has been shown that fire promotes invasion success and that there is interaction between fire and invasive species⁷¹.

The exact process of how grazing, fire, native species and *Chromolaena* interact needs to be investigated further. One reason often cited for invasion success is the escape from natural predators⁵⁹. The fact that *Chromolaena* is not grazed while other competing species are implies that more resources in

terms of light, nutrients and space are available to *Chromolaena*. Grazing may also be contributing to dispersal of *Chromolaena* seeds.

4.4.4. Disturbances and Understorey Light

Grazing can be taken as an indicator for human disturbance. In all the plots where grazing was noted, signs of human presence was also noted. Human use implies illegal logging, lopping of tree leaves for fodder and removal of understorey by grass collection. It would be logical to consider that such activities would disrupt the natural dynamics of forest canopies and alter understorey species composition and biomass levels.

Results showed significant differences in understorey light levels between grazed and un-grazed areas. However, this does not preclude the possibility of open areas being present in undisturbed forests. Examination of such differences therefore should be carried out using spatially explicit methods. Though data has not been collected, there appear to be less regeneration of *Shorea* in grazed areas. The implication of this could be a gradual change in forest age structure resulting in an open canopy forest over time.

Having argued that *Chromolaena* is facilitated by light and given the possibility of areas with high understorey light intensity (open canopy forests) in undisturbed forest patches, it may be that *Chromolaena* may be as easily found in an undisturbed forest as in a disturbed one. However, results have shown that the response of *Chromolaena* to understorey light is moderated by the amount of understorey present. Path analysis showed that understorey biomass had a stronger effect than understorey light intensity. Further, field observations and discussion with locals revealed that there is a renewal of growth of native tree and shrub species and a gradual disappearance of *Chromolaena* from forest stands where grazing has been excluded for more than 5 years. This suggests that in undisturbed forest patches, even if the forest canopy were open, *Chromolaena* presence and abundance would be doubtful.

4.5. Conclusions

Successful invasion depends on effective dispersal strategies, establishment and subsequent persistence by maintenance of a reproductive population of effective size. Seed dispersal does not seem to be a limiting factor for *Chromolaena* establishment within the study site given observations of *Chromolaena* almost everywhere. The many footpaths within the study area, which enable movement of humans, domestic and wild animals may be facilitating this.

However, results suggest that the presence and establishment of *Chromolaena* populations in terms of higher cover, higher biomass levels and plants with higher vigour (suggested by height, diameter, number of stems and branches) are restricted to areas where there is enough light at intermediate levels of transmission. In the study area, the optimum level suggested by the different models appear to be in the range of $1.5 - 3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. The opportunity for *Chromolaena* to exploit the availability of light appears to be moderated by the level of understorey biomass at a given site.

Results hint towards the existence of source-sink populations. Plants that have matured beyond the seedling stage with some potential to flower are only present in areas with more light and less competition. Plants in more stressful environments – low light and high competition – appear sterile. The amount of understorey light and the level of understorey biomass have been found to differ significantly in grazed (disturbed) and ungrazed (undisturbed) areas. This suggests that indirectly disturbances are facilitating the establishment of *Chromolaena* populations as supported by the results from the path analysis. Given these arguments, it can be concluded that the success of *Chromolaena* invasion in the Terai measured in terms of presence, cover, biomass, biometric traits and age composition is dependant on disturbances that change the forest overstorey and understorey environment.

5. Synthesis and Conclusions

5.1. From Patterns to Processes

What emerges from the findings of Chapter 2 and Chapter 3 is an indication towards a process that might have facilitated the invasion success of *Chromolaena* in the Terai of Nepal (Figure 5.1).

Initiation of development programmes was made possible after the successful eradication of malaria. Construction of roads and government infrastructure started concurrently⁵⁴. This facilitated the transportation of the first seeds of *Chromolaena* into Nepal. Locals recall that *Chromolaena* was first observed in the Terai in the late 1950s (1960s) in Chitwan⁵³.

Initiation of malaria eradication programmes turned the Terai into an attractive destination for many Hill and Mountain migrants. Government initiated resettlement programmes together with illegal settlement^{32, 74, 94} resulted in the conversion of a large portion of forestland into arable land (Chapter 3). The continuing influx of migrants into the Terai ensured continuing changes in land cover from forest to arable land. Decreasing forest coupled with a growing population resulted in an increase in number of persons per unit forest area. This consequently resulted in an increased use of forests (Chapter 3).

Results from Chapter 4 showed that *Chromolaena* responds to gradients in the forest understorey in terms of light intensity and biomass. Higher *Chromolaena* cover and biomass are found in areas of medium light intensity levels and low understorey biomass. Further, reproductive populations seem to be present only in these favourable environments.

“Invasion success” can be understood to mean successful establishment and subsequent persistence by maintenance of a reproductive population of effective size. The species traits of *Chromolaena* appear to reflect that of an ideal invader (Chapter 2). However, *Chromolaena* is not able to persist in closed canopy forests with low understorey light intensity levels. This innate requirement of a certain amount of light may prove to be the Achilles heel in this species’ quest to colonise. Further, the ability of *Chromolaena* to persist in the face of competition from other species even under adequate light conditions is doubtful in the absence of disturbances. Though *Chromolaena* populations do exist to a limited extent under environments of low light and high understorey biomass, they seem to display traits of non-reproductive populations.

Grazing and human utilisation of forests for wood and other resources can be considered responsible for bringing about changes in overstorey and understorey components in the *Shorea* forest ecosystems. Without the initiation of the malaria eradication in the Terai during the 1950s, these lowlands would have remained uninhabited except for the few indigenous tribes. Increase in migration, subsequent population increase, land cover changes and increase in demand for resources meant that the remaining forest in the Terai of Nepal was subjected to increasing levels of disturbances. This has left the Terai forests degraded in terms of openness of forest canopy cover and understorey biomass levels resulting

in the creation of suitable environments for the successful establishment of *Chromolaena* populations. To a certain extent, this thesis demonstrates that ecological problems at a local scale can be ascribed to demographic and related changes that have resulted due to Government policy initiatives taken at a macro level.

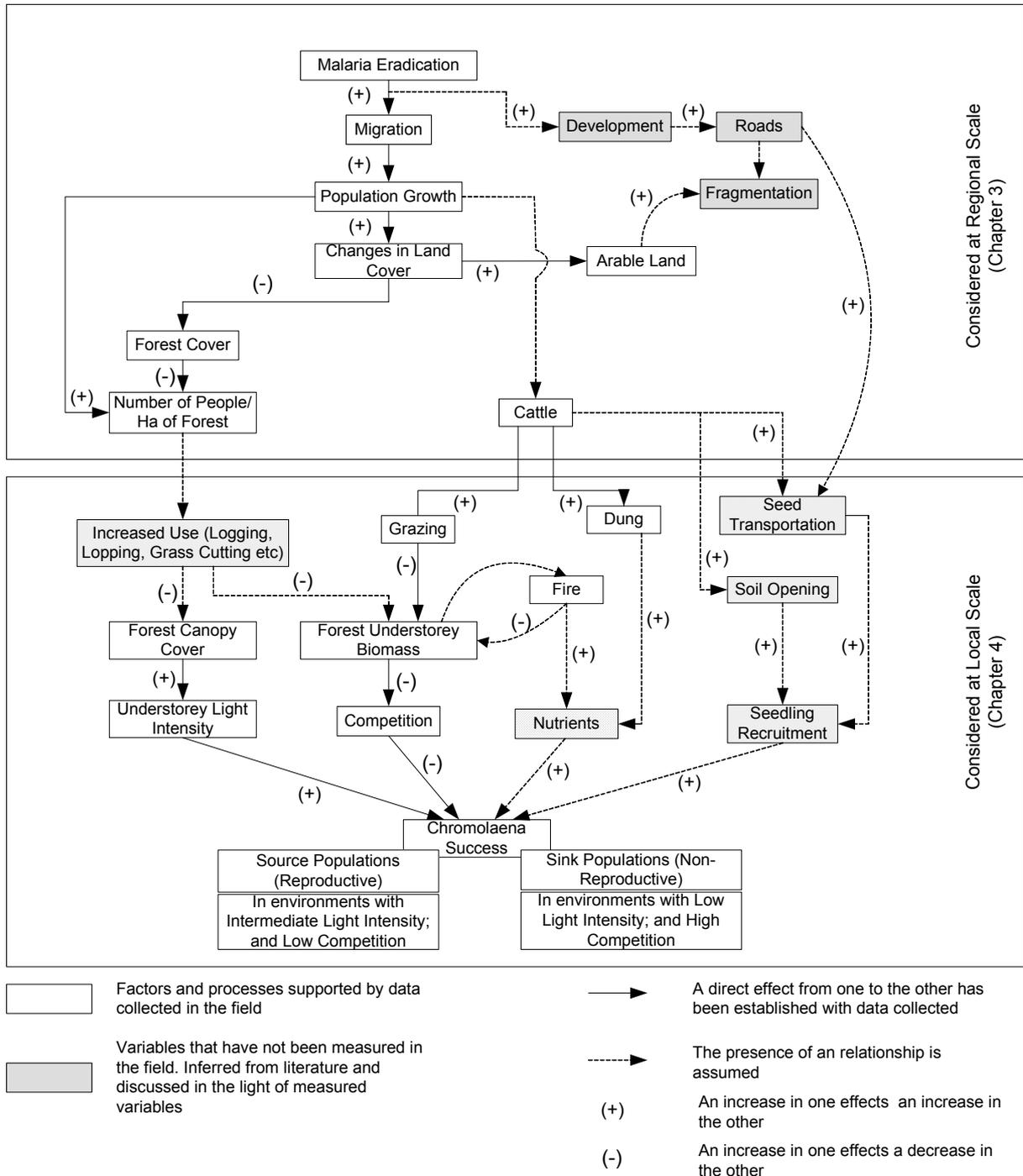


Figure 5.1 Conceptual diagram showing factors and processes that facilitate the success of *Chromolaena* invasion

5.2. Conclusions

1. *Chromolaena* presence, cover, biomass and age composition were significantly related to understorey light intensity and understorey biomass.
2. Higher values for *Chromolaena* cover and biomass were found in areas with medium understorey light intensity ($1.5 - 3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and low understorey biomass.
3. Taller *Chromolaena* plants with thicker diameter and having more number of stems and branches were found in areas with medium understorey light intensity ($1.5 - 3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and low understorey biomass.
4. The probability to find *Chromolaena* populations with some potential to reproduce (source populations) was very low in environments with low light intensity ($< 1.3 \text{ mj}^1 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) and high understorey biomass. Populations that exist in environments characterised by low light and high understorey biomass appeared to be small *Chromolaena* plants which have not matured beyond seedling stage. That these plants would set flower and produce seeds is highly unlikely (sink populations).
5. Success of *Chromolaena* can therefore be considered to be dependant upon the degradation status of the *Shorea* forests, where more forest canopy openness and less understorey biomass facilitate the establishment and reproduction of *Chromolaena* populations.
6. Understorey light intensity and understorey biomass are significantly different in grazed and ungrazed areas. Grazing is taken as an indicator for human presence.
7. Human population in the Terai has increased substantially after the initiation of malaria eradication programmes in the early 1950s. Forest cover has declined while arable land area has increased. Human population pressure on forest resources have risen considerably since 1958. The forests in the Terai are also subjected to grazing.
8. Human use together with grazing has contributed to bringing about changes in the forest overstorey and understorey by making forest canopies more open and reducing understorey biomass levels.
9. This has helped the successful establishment of *Chromolaena*, where success is measured in terms of presence, cover, biomass, biometric traits, and age composition.

5.3. Recommendations

1. Possibilities of mapping source and sink areas with the help of GIS and RS should be explored. This could be beneficial for management of invasive species. Targeting source populations in eradication or control programmes might prove to be an effective strategy, and maps showing source-sink locations would help.
2. It may be useful to investigate responses of other invasive species to ecological gradients such as understorey light intensity.

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Appendices

Appendix 1 Field data collection sheet

Date:	<input type="text"/>	Transect No:	<input type="text"/>	Location:	<input type="text"/>
GPS Reading:	<input type="text"/>	Plot No:	<input type="text"/>	Dist from Forest Edge:	<input type="text"/>
	<input type="text"/>	Dist from Road:	<input type="text"/>	Dist from Settlement:	<input type="text"/>
				Altitude:	<input type="text"/>
				Soil Type:	<input type="text"/>

Chromolaena Parameters:

% Cover: <input type="text"/>							Distribution Pattern:	Density:
Type	% Cover	Average No. Stems/Clump	Average Height	Average Diameter	Possible Age	Flowering Potential	Uniform:	<input type="checkbox"/> H <input type="checkbox"/> M <input type="checkbox"/> L
Seedling <50cm	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>		
Weak Stems > 50cm < 1.5mts	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	Patchy:	<input type="checkbox"/> H <input type="checkbox"/> M <input type="checkbox"/> L
Strong Shrubs > 1.5mts	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>	Sporadic:	<input type="checkbox"/>

Stand Parameters:

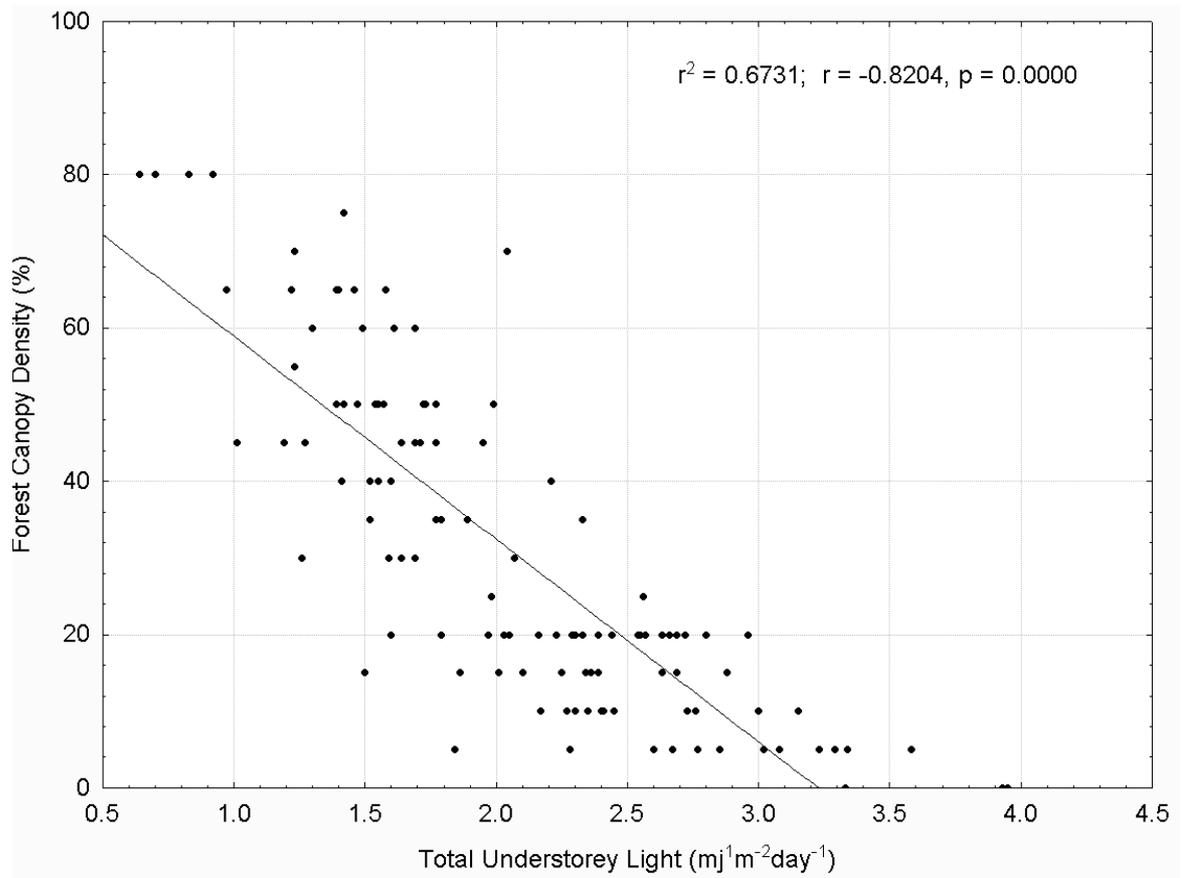
Stratum	Species	As a % of Species	% Aereal Cover of Plot	Remarks
Tree Layer >(5m):	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
Woody Layer (0-5m):	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
Non-Woody Layer:	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
Herb Layer (ground cover):	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>
	<input type="text"/>	<input type="text"/>	<input type="text"/>	<input type="text"/>

Estimated Canopy Cover %:
 Fallen/Dead Trees Cover %:
 Undergrowth Biomass: H M L

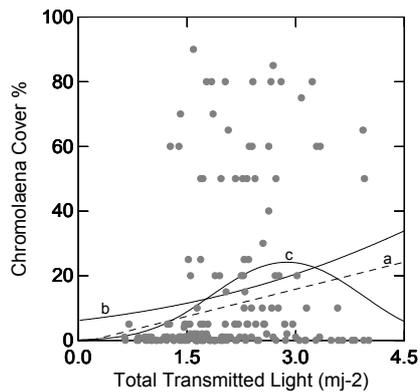
Disturbance Indicators:

Grazing: <input type="checkbox"/>	Fire: <input type="checkbox"/>	Foothpath within the plot: <input type="checkbox"/>	Near foothpath < 50 mts (from plot radius): <input type="checkbox"/>	Far from path > 50 mts (from plot radius): <input type="checkbox"/>
Cows sighting: <input type="checkbox"/>	Lopping: <input type="checkbox"/>	Remarks: <input type="text"/>		
Dung: <input type="checkbox"/>	Thinning: <input type="checkbox"/>			
Footprints: <input type="checkbox"/>	Harvesting: <input type="checkbox"/>			
Cut Grass: <input type="checkbox"/>	Pruning: <input type="checkbox"/>			
Grass collection: <input type="checkbox"/>	Management Regime: <input type="checkbox"/>			

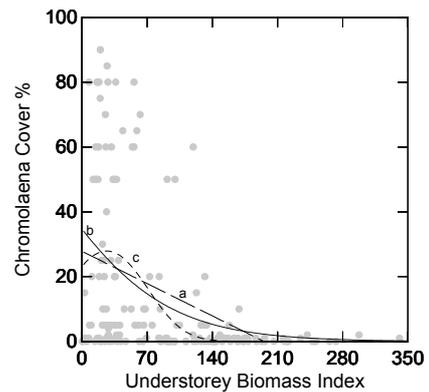
Appendix 2. The relationship of forest canopy density to understorey light intensity



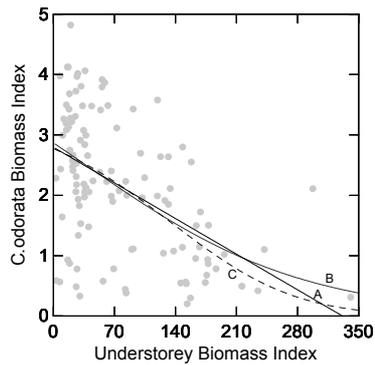
Appendix 3. Response of *Chromolaena* cover and biomass to understorey light intensity and understorey biomass separately.



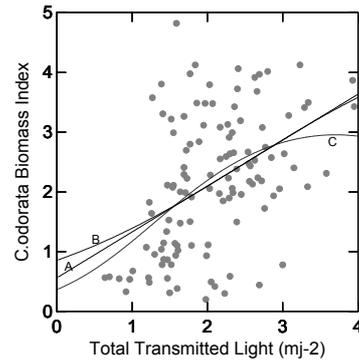
Relationship of *C.odorata* cover % to Total Transmitted Light (mj^{-2}) (TTL). **a:** $y=a+b*\text{TTL}$ ($R^2=0.05307$, $F=37.0661$, $p<0.05$); **b:** $y=m/(1+\exp(a+b*\text{TTL}))$ ($R^2=0.04322$, $F=35.72$, $p<0.05$); **c:** $y=m/(1+\exp(a+b*\text{TTL}+c*\text{TTL}^2))$ ($R^2=0.07705$, $F=26.68$, $p<0.05$)



Relationship of *C.odorata* cover % to Understorey Biomass Index (UBI). **a:** $y=a+b*\text{UBI}$ ($R^2=0.18157$, $F=56.38$, $p<0.05$); **b:** $y=m/(1+\exp(a+b*\text{UBI}))$ ($R^2=0.20162$, $F=59.81$, $p<0.05$); **c:** $y=m/(1+\exp(a+b*\text{UBI}+c*\text{UBI}^2))$ ($R^2=0.22136$, $F=42.02$, $p<0.05$)



Relationship of *C.odorata* Biomass Index to Understorey Biomass Index (UBI). **A:** $y=a+b*\text{UBI}$ ($R^2=0.25$, $F_{(2,114)}=297.24$, $p<0.05$); **B:** $y=m/(1+\exp(a+b*\text{UBI}))$ ($R^2=0.26$, $F_{(2,114)}=301.13$, $p<0.05$); **C:** $y=m/(1+\exp(a+b*\text{UBI}+c*\text{UBI}^2))$ ($R^2=0.26$, $F_{(3,113)}=199.38$, $p<0.05$)



Relationship of *C.odorata* Biomass Index to Total Transmitted Light (TTL). **A:** $y=a+b*\text{TTL}$ ($R^2=0.20$, $F_{(2,114)}=274.06$, $p<0.05$); **B:** $y=m/(1+\exp(a+b*\text{TTL}))$ ($R^2=0.20$, $F_{(2,114)}=271.85$, $p<0.05$); **C:** $y=m/(1+\exp(a+b*\text{TTL}+c*\text{TTL}^2))$ ($R^2=0.21$, $F_{(3,113)}=184.02$, $p<0.05$)