CHAPTER 3

THE IMPACTS OF INVASION AND CLEARING ON THE ENVIRONMENT

3.1 Introduction

There have been a number of ecological studies on the impacts of exotic invasions in the savanna and grassland biomes. Some work has also been done to evaluate the ecological and economic impacts of southern Africa's exotic organisms. The most frequently studied impact of invasion by exotic species is the partial to complete replacement of indigenous vegetation by exotics. This is used to explain the reduction in species richness and the alteration of the appearance and character of the landscape (Henderson & Wells 1986). In South Africa as a whole, there has been little study of modifications to the physical and chemical environment by exotic species. The exception being within the fynbos biome, where extensive studies have been conducted (Macdonald & Richardson 1986). Degradation of the riverine habitat by exotic species has also been documented in a number of studies (Wells *et al.* 1980; MacDonald 1983; Henderson & Musil 1984; Macdonald & Jarman 1985).

3.1.1 Environmental changes resulting from exotic plant invasions

It has been observed that where an increased plant biomass exists, through exotic invasion (Vitousek 1990; Midgley *et al*. 1992; Dye & Poulter 1995), an alteration of the infiltration of water into the soil occurs. This is a result of increasing runoff and rainfall interception by vegetation (Henderson & Wells 1986). The hydrology (Bosch & Hewlett 1982; Vitousek 1990; Van Wilgen *et al.* 1992) and potential soil erosion (Young & Weirsma 1973; Henderson & Wells 1986; MacDonald & Richardson 1986) are thus altered by the invasion of the community by exotic species. The alteration of soil hydrology has in turn implications for soil nutrient retention and nutrient cycling (Witkowski 1991a; Musil 1993). For example, the loss of nutrients from an ecosystem has been shown to affect it's productivity (Venter *et al.* 1989; Midgley *et al*. 1992; Dye & Poulter 1995) and hence the vegetation able to survive and compete for resources in that habitat.

Soil nutrient cycling is also affected by the input of nutrients into the soil from the vegetation (Theng 1980; Milton 1981). The input of nutrients can be modified by alterations to litter deposition and decomposition rate. Increased vegetation production generally results in increased litter deposition

(Milton 1981; Milton & Siegfried 1981), and hence increased inputs of nitrogen and phosphorus into the soil (Theng 1980; Milton 1981). This has been shown to have implications for indigenous species in Australian heathlands, where the addition of phosphate fertilizers resulted in the elimination or reduction of some indigenous species and their replacement by a range of herbaceous exotic species (Heddle & Specht 1975).

Exotic species also change the fire regime as a reduction in ground cover occurs (O'Connor 1995), but there is also an increased fuel load, resulting in fewer fires of greater intensity (Henderson & Wells 1986; Scott & Van Wyk 1990; Scott & Schulze 1992; Van Wilgen *et al.* 1992). Although this system, the riverine bush, is not necessarily driven by fire, the inclusion of exotic species that increase the fuel load, may result in extremely intense fires once the vegetation actually burns. Increased fire intensity changes vegetation structure, the litter layer and soil micro-organisms, impacting on nutrient cycling within the community.

Modification of the soil nutrient status can also occur by elevating nutrient levels. For example, the introduction of some species has increased soil nitrogen availability through nitrogen fixation, such as *Acacia cyclops* in the fynbos biome (Roux & Warren 1963). Not only are soil chemical processes interrupted or modified by invasion of exotic plant species, but so are some soil physical attributes. Soil physical attributes such as compaction, may escalate due to increased splash energy of rain drops falling from tall growing individuals (Jacot Guillarmod 1980). This typically occurs in exotic and not in indigenous stands of vegetation, as the increased competition for resources, particularly light in invaded communities, leads to the reduction of under-canopy vegetation which exposes more soil to the effects of erosion and compaction.

3.1.2 Environmental changes resulting from removal of exotic plants

Some forest and range management clearing practices conjure vivid images of ecosystem destruction (Lewis *et al*. 1988). With removal of exotic species, the availability of resources (light, nutrients and water) reaches a peak soon after the disturbance event (Canham & Marks 1985). Consequently, the first plants to establish after a disturbance should encounter greater availability of resources, improving the probability of establishment and survival within the community. The first plant individuals that establish after such a disturbance however, are of a weedy nature or of an exotic origin (Venter *et al.* 1989).

Human intervention, such as clear-felling of exotic plant species, can be disruptive to the ecosystem, in ways other than the physical removal of vegetation. Clearing often results in soil profile disturbances (mixing and/or removal of soil) and soil compaction (Rab 1996). This may cause changes in soil physical and hydrological properties, which could affect site productivity and catchment water quality (Rab 1996). For example, mixing or disturbance to the upper soil layer may result in a decrease in the litter layer, affecting soil organic matter content. This also has implications for compaction of the topsoil, which should increase, resulting in reduced water retention properties and greater resistance to root extension. Hence clearing of exotic species may indirectly influence the maintenance and establishment of individuals, and has implications for erosion (Lückhoff 1951), species recruitment and recovery of the community after clearing.

3.1.3 Aim and objective

The aim of this chapter is to gain an insight into the relationship between the environment and invasion by exotic plant species and their removal. In order to gain this insight into the interactions of the invasion of exotic plant species and the riverine environment, the identification of variables modified by these processes is a priority. This is the objective of the chapter and once this has been determined, the precise effect and magnitude of invasion or clearing of exotic species on the riverine community can be determined. The chapter will also provide a source of baseline information on the environment for comparison with future studies. The examination of soil physical and chemical properties, and the modifications to ground cover under different invasion intensities for both cleared and uncleared management/treatments will be undertaken. With this in mind it was hypothesized that environmental modification would be directly related to the degree of invasion and inversely related to time since clearing.

3.2 Materials and Methods

3.2.1 Sampling methods

Ground cover

Within each Modified-Whittaker nested plot, the ten 1 m^2 quadrats were used to determine ground cover. Each quadrat was marked out using a rigid metal quadrat of 2 x 0.5 m. A visual estimation of aerial cover was determined as a percentage. The percentage cover of exposed soil, litter cover, herbaceous vegetation cover, grass aerial cover and exposed rock were estimated. The depth of litter was also measured, from the centre of the largest litter patch when present.

Soil sampling and laboratory analyses

Soil samples were collected by carefully removing the litter layer and sampling the surface or A horizon (0-10 cm), and B horizon (10-20 cm), using a soil auger (12.5 cm diameter). Four samples of each soil horizon were collected from corner markers from each plot, and bulked. The samples were air-dried for 3 weeks and then oven-dried for 72 hours at 45 °C. Samples were sieved through a 2 mm sieve, and gravel determined as a percentage of the total sieved mass. Sieved soil was analyzed for pH, texture, organic carbon content and mineral nutrient composition using X-ray fluorescence spectrometry (XRF). Elements were all converted to oxides by XRF (although not all the elements analyzed are in oxide form in the soil) (Jones 1982).

Soil pH was determined using 20 g of soil in a 50 ml volume of 1 % KCl solution at 24 °C after a two hour standing interval (Anderson and Ingram 1993). Organic matter content of soil was determined using loss-on-ignition of 20 g soil at 450 °C for 4 hours in a muffle furnace. Soil texture was determined using the hydrometer method (Anderson and Ingram 1993).

Study site heterogeneity

The slope of each plot was determined using a clinometer and trigonometric calculation. Aspect was determined using a compass. Altitude was determined using GPS readings and 1:50 000 orthophotos. Rainfall data for each plot was obtained from the nearest weather station (no further than 5 km distant). Data for mean rainfall overlaps for some plots due to weather station proximity.

3.2.2 Statistical analyses

Analyses for ground cover

Each variable collected for ground cover (including litter depth) was compared between altitudinal ranges, invasion intensity and clearing using a three way ANOVA and Ryan's Q post hoc tests (Ryan-Einot-Gabriel-Welsch Multiple Range Test). Regression analyses of litter cover and litter depth (cm) with invasion intensity (%) were also undertaken.

All regression relationships were checked for outliers. If outliers were detected, a new relationship was determined by excluding those outlying points, and this then compared with the original relationship for slope and elevation (Zar 1984). For ease of understanding, all new relationships were found to be not significantly different from those containing outliers unless otherwise stated in the figure caption. Regression relationships for cleared and uncleared treatments were also tested for significant differences in both slope and elevation (Zar 1984).

Soil

Three-way ANOVA's with repeated measures (the two soil depths) were used to analyze soils data for altitude, invasion intensity and clearing differences. Data were transformed prior to statistical analyses using either logarithmic, arcsine or square root transformations. Repeated measures were used as the A (0 - 10 cm) and B (10- 20 cm) horizons were essentially not independent. Ryans Q post hoc test was used in all ANOVA's using SAS (SAS Institute 1985). The Ryans Q post hoc test was selected due to the robust nature of the test, even with populations approaching non-normal distributions (Day & Quinn, 1989).

3.2.3 Multivariate statistics for site heterogeneity

Variable selection

Two approaches to determine non-essential environmental variation were utilized. This allowed a reduction of co-variables, commonly found in large environmental data sets. Isolation of environmental variables best representing the overall environmental variation was accomplished using bi-plots from an initial standardized principal components analyses (PCA), and a co-variance table of environmental variables.

A bi-plot of environmental data and sites displayed variables with close associations to each other. The strongest (i.e. explains a greater part of the variation) and most biologically informative of these variables were utilized for further analyses. These were placed into a co-variable table generated in Quattro-pro Version 7 and tested for significant correlations between the variables (Zar 1984). Those found to be significant were considered co-variables and the least biologically important variables and were then discarded from the analysis.

Analysis approach

The analysis of variables for both univariate and multivariate analysis was repeated for both high and low altitude divisions with each being treated as a separate data set. The reasons for the altitudinal separation/divisions of data was that different biological processes, and different rates of these processes, occur at different altitudes, as also these altitudinal ranges occur on two different biomes. It was reasoned that altitudinal differences were not the main focus of the study and hence they were largely ignored for the sake of simplicity of explanation (T.G. O'Connor, *pers. comm.* 1997). In addition, the high altitude sites occur within the grassland biome, and the low in the savanna biome.

Further divisions in the analysis of environmental data were made. Soil variables were divided into chemical (soil elements: XRF) and physical components (% gravel, % sand, % silt, % clay, including altitude, rainfall per annum, slope, aspect and soil depth). All other environmental variables were grouped together as they were considered "biological" or "transient", and hence derivatives of the clearing operations or invasion of exotic species. These "biological" or "transient" variables included % soil surface exposed, % litter cover, litter depth, % herbaceous vegetation cover, woody plant biomass, grass biomass and invasion intensity (% exotic species aerial cover).

The reason for the division of variables into "soil" and "biological" or "transient" for analysis was because soils tend to have a "lag-phase" before changing after any disturbance event. With sampling taking place approximately 1 - 2 years after clearing operations, it was assumed that the soils had either not changed to any significant extent or were in the process of changing, and that these soils were still moderately indicative of the "original" soil conditions. The soil physical and chemical attributes were separated to simplify the PCA and better explain which, if any, variables would isolate sites based on soil heterogeneity.

In addition to determining the environmental variables best explaining changes in habitat, it was also important for uni-variate statistical analyses and for the experimental design, that the sites were inherently the same. The analyses of data were conducted using centred and standardized PCA's for all environmental variable groups ("soils" [physical and chemical] and "transient").

3.3 Results

3.3.1 Multivariate analysis of soils data

Soil chemical parameters

Low altitude sites from different experimental categories were found to have no apparent pattern based on invasion intensity (Red and Blue groupings) (Figure 3.1). One axis of separation was, however visible for cleared and uncleared sites (Figure 3.1). This separation can be distinguished, not due to one variable, but a range of interacting soil elements acting along the 1st axis. This separation is corroborated by the uni-variate analyses of the same data even though only a few soil elements illustrated significant differences (several tendencies to be different occurred in other elements).

The multivariate results viewed on the 1st and 2nd axes explained only 41.1% of the cumulative percentage variance for low altitude sites. Further analyses on the 1st and 3rd axes, 1st and 4th axes and 2nd and 3rd axes (explaining part of the remaining 58.9% of the cumulative percentage variance of data) also yielded the cleared/uncleared division. This separation of groupings was weaker than in the first two axes and resulted in three groupings (Red, Blue and Green) (Figure 3.2 A-C). From these data it was observed that a cleared/uncleared division of sites occurs based on soil chemical variables at low altitude sites. Clearing of sites leads to an overall shift in soil chemistry towards a higher nutrient status (Figure 3.1).

Centred and standardised PCA's of high altitude sites mimic the trends seen at low altitude (Figure 3.3). The observed split of cleared and uncleared sites at high altitude was observed to have a greater variance in the association of sites on the 1st and 2nd axes (Figure 3.3). Thus clearing of sites appears to lead to an overall shift in soil chemistry at both altitudes.

No evidence of spatial auto-correlation was observed for either high or low altitude sites. This was determined by the lack of any sites grouped together by the analysis, which correlated to the study design in the field (Figures 3.1 & 3.2). This means that sites were not associated by their soil chemical composition. This is essential in order to remove any underlying variable that may have complicated the associations between sites in later analyses.

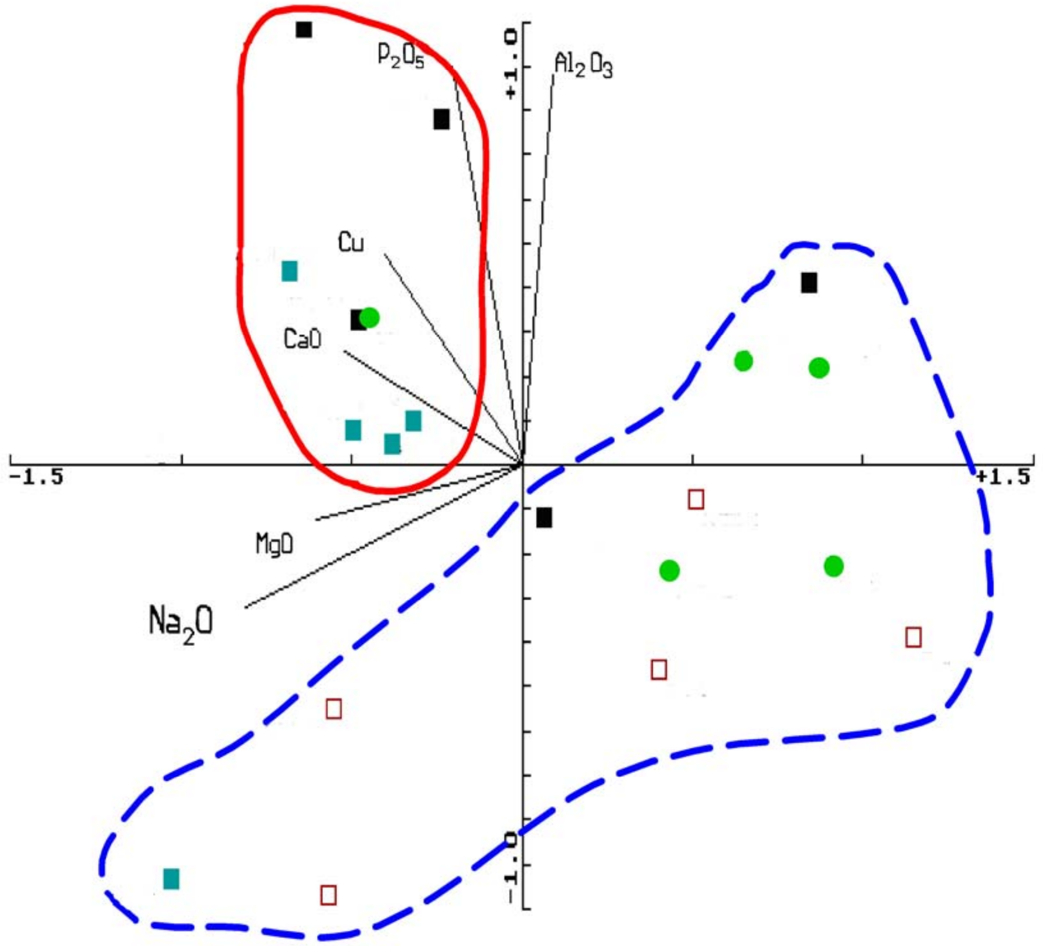
Soil physical analyses

Centred and standardised PCA analyses of soil physical attributes illustrated an identifiable pattern between sites under different experimental categories based on clearing treatments (Red and Green groupings) (Figure 3.4). For different altitude sites there were no discernible groupings. The variance in plot distribution with soil physical attributes was found to be small (Standard Deviation (S.D.) < 2.5 for both 1st and 2nd axis) and the S.D. for high altitude sites on the 2nd axis was less than that for the low altitude sites as the sites had a lower scatter across the first two axes (Figure 3.4 & 3.5). This indicates that high altitude sites were more closely associated than low altitude sites with similar soil physical characteristics. Although the PCA bi-plot for the high altitude sites explains less of the variation in the data (sum of cumulative percentage variance = 55.7) than does the PCA for the low altitude sites, the majority of the variation was nevertheless explained. Hence the interpretation of the bi-plot for high altitude sites based on only the 1st and 2nd axes alone has merit, and no further interpretations were done on the 3rd and 4th axes.

Centred and standardised PCA analyses of the high altitude sites illustrated a more grouped distribution than observed for the low altitude sites with a very low variance in the PCA 1st and 2nd axis (Figure 3.5). This centralization of sites without separation of the different experimental categories indicates that sites did not group by experimental categories/treatments, but by spatial auto-correlation. This means that based on the soil physical characteristics, no underlying soil physical properties exist which may complicate the interpretation of the analysis of clearing effects and invasion between sites.

Biological heterogeneity

The PCA analysis of the low altitude sites shows a separation of treatments by the environmental variables directly modified by clearing/invasion. Using the 1st and 2nd axes, which account for 54.5 % of the cumulative variance, woody species biomass, litter cover, herbaceous vegetation cover, bare soil cover and invasion intensity appear to be key variables in creating three distinctive groupings (Figure 3.6). These three distinct groups were as follows: 1) high invasion cleared sites (Black); 2) low invasion uncleared sites (Red); and 3) low invasion cleared sites (Blue). High invasion uncleared sites separated out on the basis of the invasion variable (% exotic species aerial cover) (Figure 3.6). Low invasion uncleared sites also related to the invasion intensity on the 1st axis, but had a strong positive association with woody biomass on the 2nd axis. Low invasion cleared sites had an overall lower woody biomass on the 1st axis, but were separated out from the low invasion uncleared sites on the 2nd axis by invasion intensity. High invasion uncleared sites spanned the high invasion uncleared and low invasion uncleared plot groupings. The reason for this is that low invasion uncleared sites also retain their woody biomass, but to a lesser degree than those of high invasion uncleared sites due to the contribution of large woody exotic species such as *E. grandis*.



Key:

High Invasion Cleared Sites ■

High Invasion Uncleared Sites ●

Low Invasion Cleared Sites ■

Low Invasion Uncleared Sites □

Figure 3.1 Centered and standardized PCA of soil chemical attributes for low altitude study sites using Euclidian distance measure showing two groupings of cleared (Red) and uncleared (Blue) sites. Soil chemical attributes included Na_2O, MgO, CaO, Cu, P_2O_5 and Al_2O_3. Eigen values for the 1st and 2nd axes were 0.388 and 0.221 respectively, explaining 60.9% cumulative variance of species data.

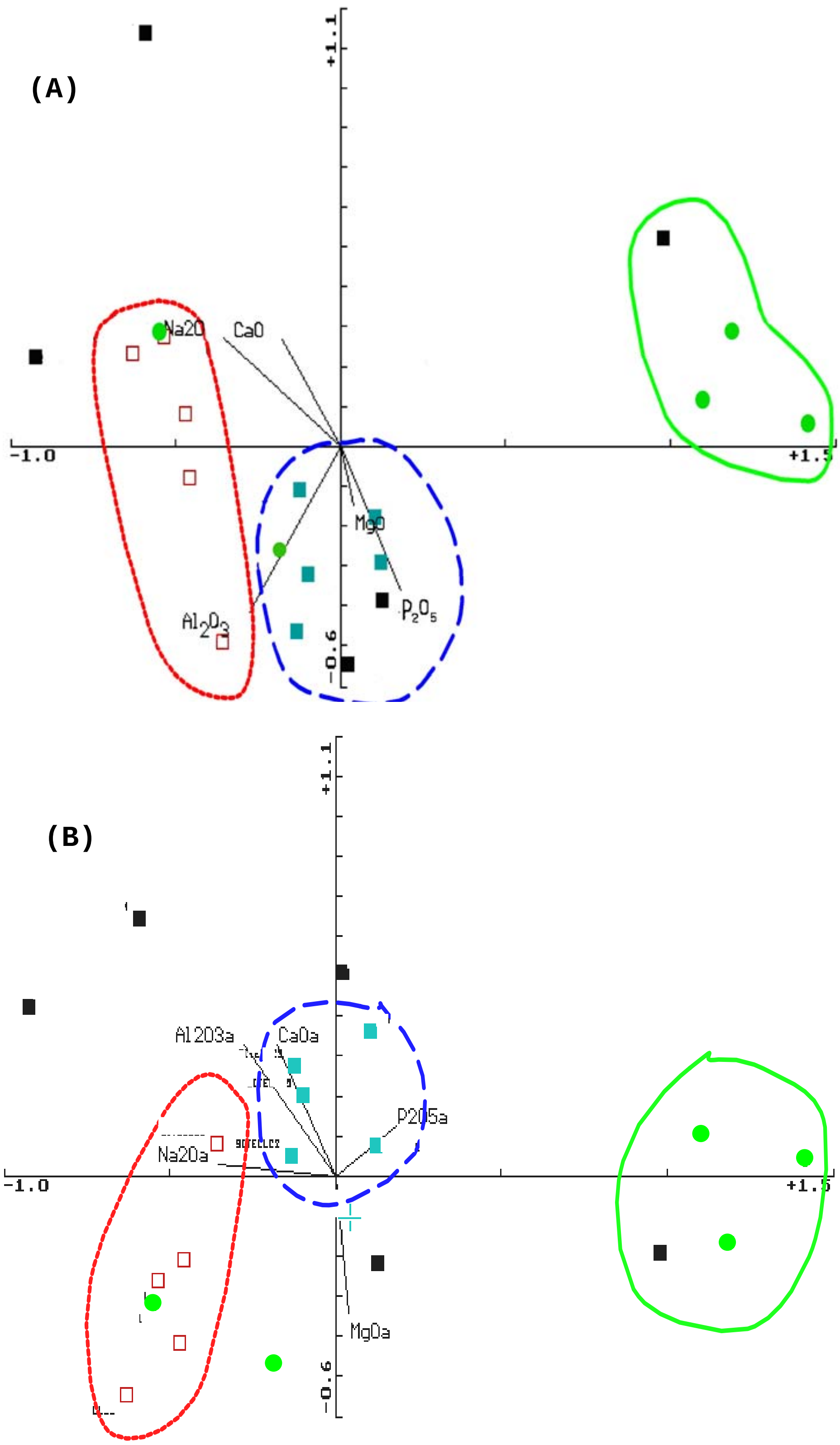
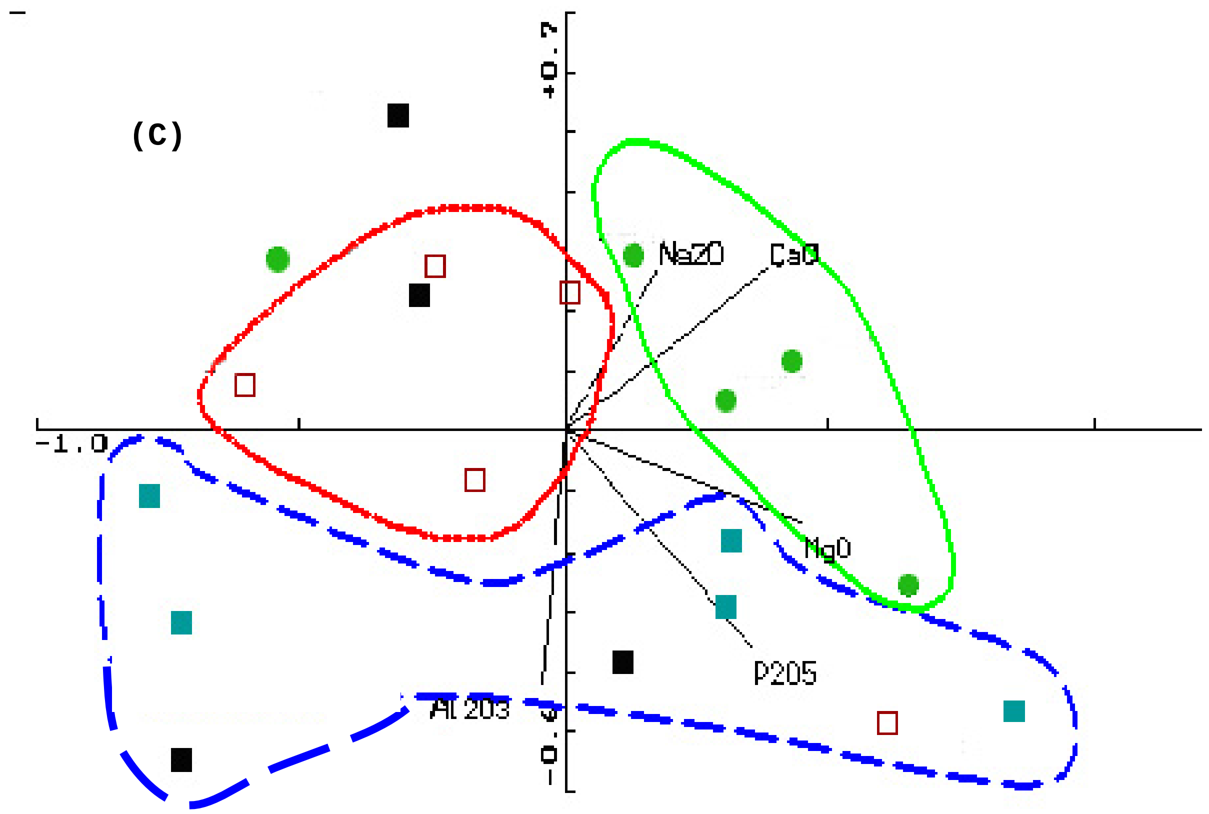


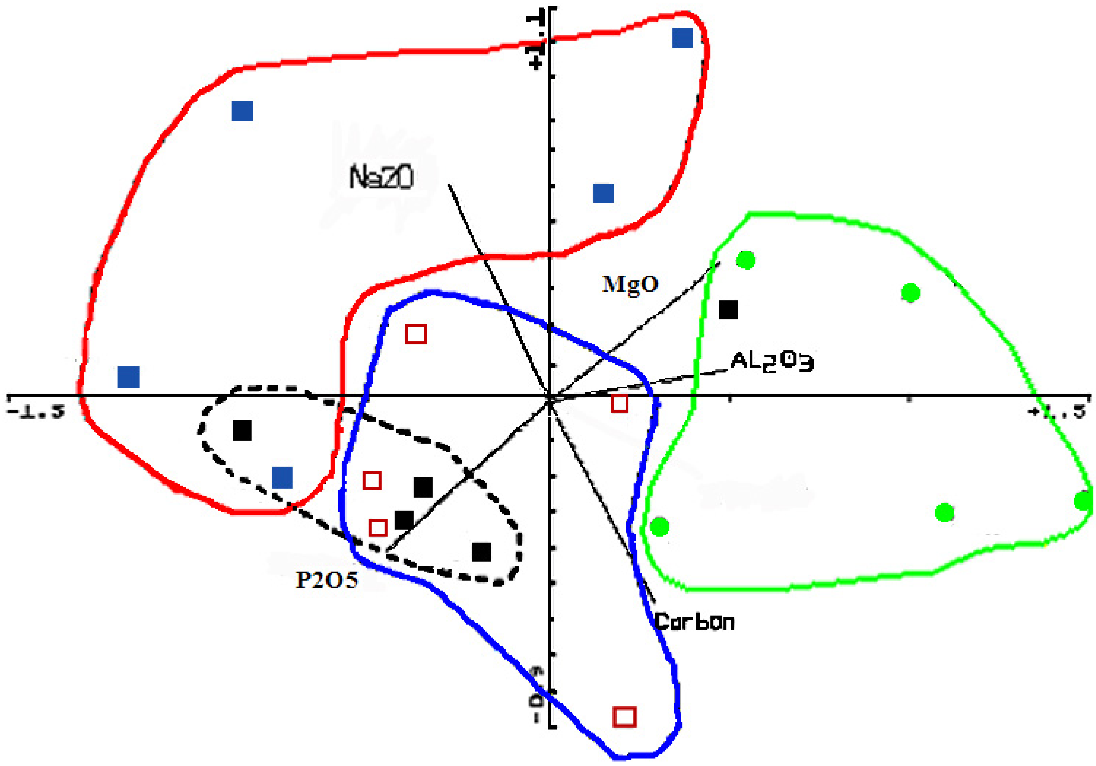
Figure 3.2 Cont....



Key:

High Invasion Cleared Sites	■	Low Invasion Cleared Sites	■
High Invasion Uncleared Sites	●	Low Invasion Uncleared Sites	□

Figure 3.2 Centered and standardized PCA's of soil chemical attributes for low altitude study sites using Euclidian distance measure illustrating three groupings (Red – low invasion uncleared sites, Blue – cleared sites & Green – high invasion uncleared sites) based on site categories. High Invasion Cleared Plots illustrated no discernable grouping. Soil chemical attributes included Na_2O, MgO, CaO, Cu, P_2O_5 and Al_2O_3 Eigen values for the (A.) 1st and 3rd axes were 0.388 and 0.172 respectively explaining 56% cumulative variance of species data, (B.) 1st and 4th axes were 0.338 and 0.132 respectively, explaining 51% cumulative variance of species data, (C.) 2nd and 3rd axes were 0.221 and 0.172 respectively, explaining 39.3% cumulative variance of species data.

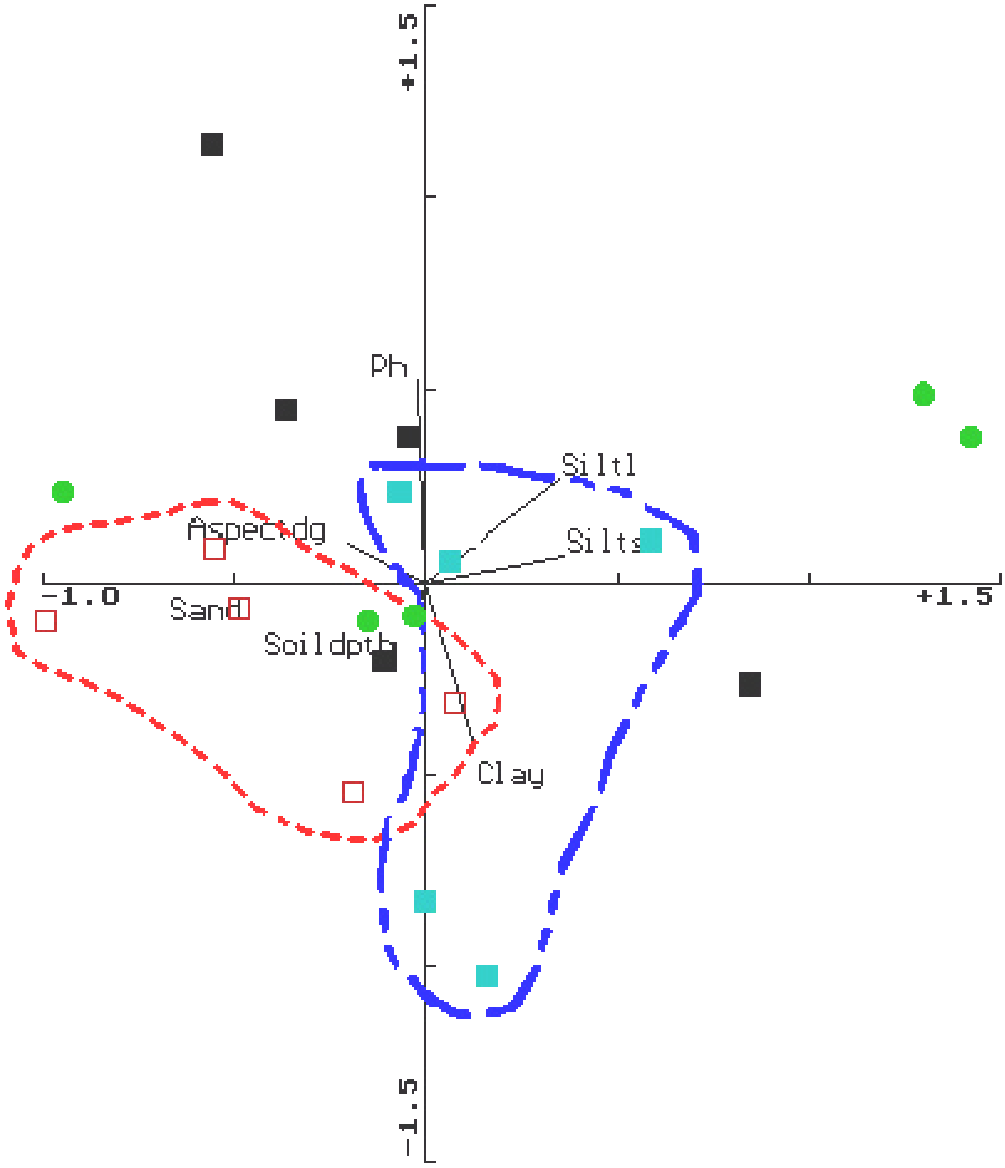


Key:

High Invasion Cleared Sites ■ Low Invasion Cleared Sites ■

High Invasion Uncleared Sites ● Low Invasion Uncleared Sites □

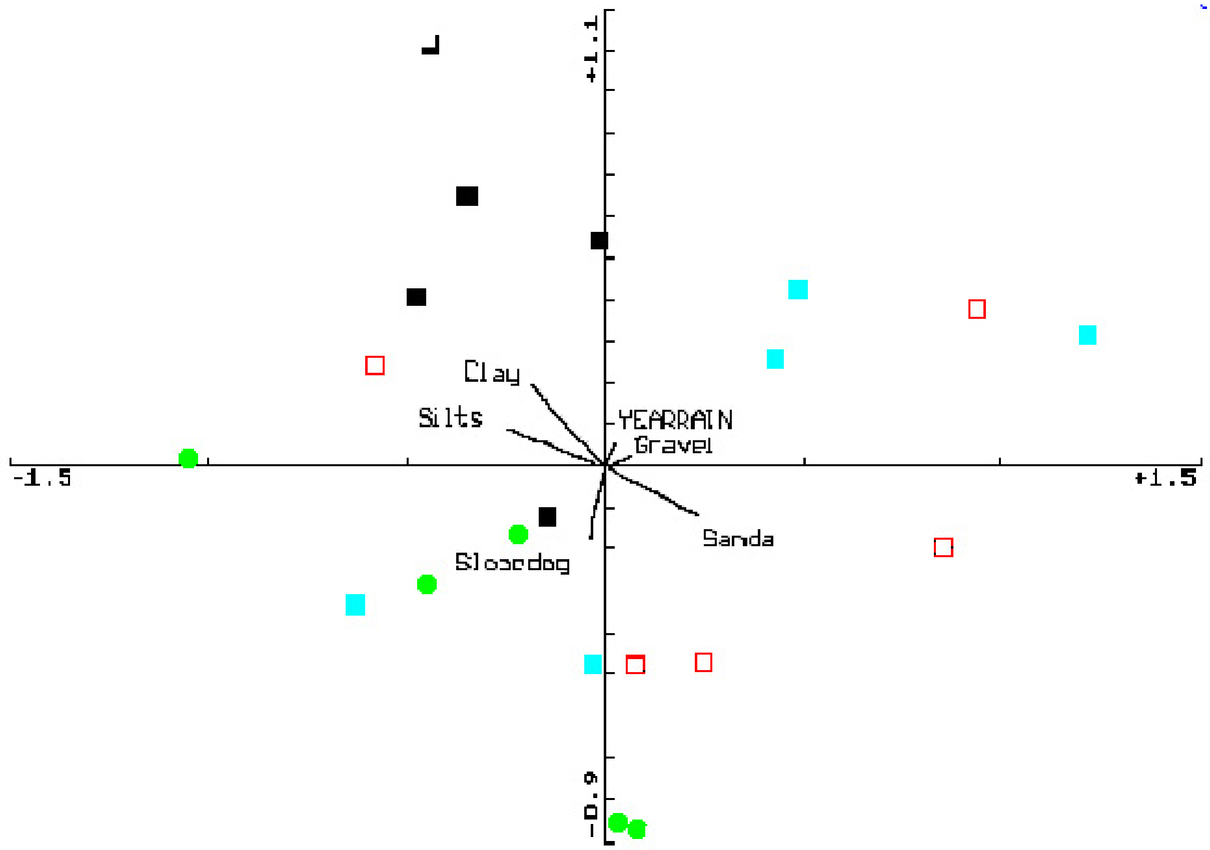
Figure 3.3 Centred and standardized PCA of soil chemical attributes for high altitude study sites using Euclidian distance measure illustrating the clear grouping of sites based on soil physical attributes (Groupings of Green, Red, Black and Blue based on site categories of invasion and clearing treatments are identified). Soil chemical attributes include Na_2O, CaO, P_2O_5 and Al_2O_3. Eigen values for the 1st and 2nd axes were 0.411 and 0.244 respectively, explaining 65.6% cumulative variance of species data.



Key:

High Invasion Cleared Sites	■	Low invasion Cleared Sites	■
High Invasion Uncleared Sites	●	Low Invasion Uncleared Sites	□

Figure 3.4 Centered and standardized PCA of soil physical attributes for low altitude study sites using Euclidian distance measure with two identified groupings of Low invasion cleared sites (Blue) and low invasion uncleared sites (Red). Soil physical attributes include sand, gravel, silt (2 - 20 µm), silt (20 - 50 µm), clay, aspect and soil pH. Eigen values for the 1st and 2nd axes were 0.388 and 0.221 respectively, representing 60.9% cumulative variance of species data.



Key:

High Invasion Cleared Sites ■ Low invasion Cleared Sites ■

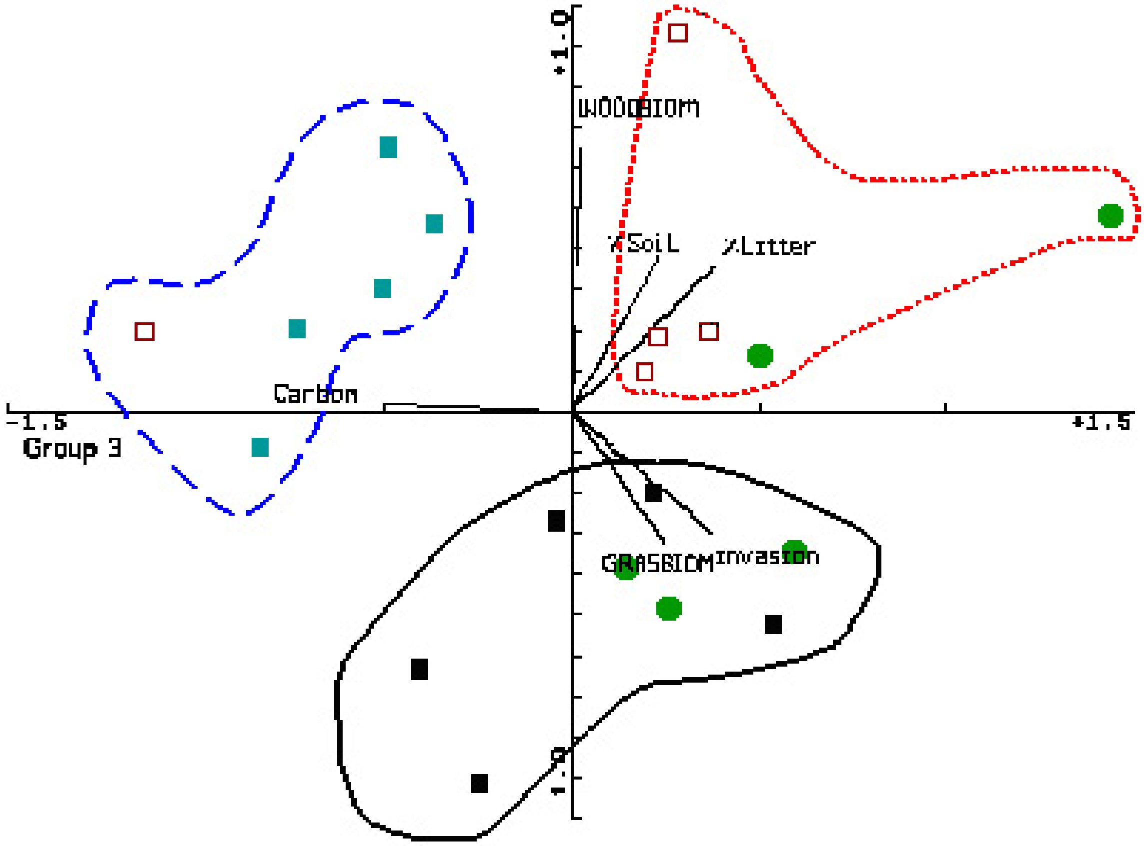
High Invasion Uncleared Sites ● Low Invasion Uncleared Sites □

Figure 3.5 Centred and standardized PCA of soil physical attributes for high altitude study sites using Euclidian distance measure illustrating no clear groupings or separation of sites. Soil physical attributes including sand, gravel, silt (2 - 20 µm), clay, yearly rainfall and slope had no discernable groupings. Eigen values for the 1st and 2nd axes were 0.312 and 0.245 respectively, representing 55.7% cumulative variance of species data.

A similar relationship occurs for cleared sites where a positive association with grass cover is observed (Figure 3.6). High invasion sites that are uncleared of exotic plant species have a great variation in woody biomass but are generally high in biomass. The reason for the association of these sites with high grass biomass once cleared, may be due to the orientation of the invasion variable that appears to correlate with grass biomass on the 2nd axis. In low altitude sites, where plant biomass is not more closely linked to exotic vegetation due to higher rainfall and larger indigenous growth forms, a closer relationship was observed.

The PCA of high altitude sites showed a distinguishable grouping of high invasion sites into cleared (Red) and uncleared (Blue) groups using the 1st and 2nd axes (Figure 3.7). High altitude cleared sites (part of the red group in Figure 3.7) grouped together based on herbaceous cover and woody biomass. This grouping (Red) overlapped with the grouping of low invasion cleared sites. Cleared sites were distinguished from uncleared sites by the increased exposure of soil and increased herbaceous cover based on the 2nd axis of the multivariate analysis (Figure 3.7). The high invasion uncleared plot grouping (Red) correlated with high invasion intensity (INVASION) and high woody biomass (Figure 3.7). The grouping of low invasion uncleared sites (Blue) was based on lower biomass and invasion intensity.

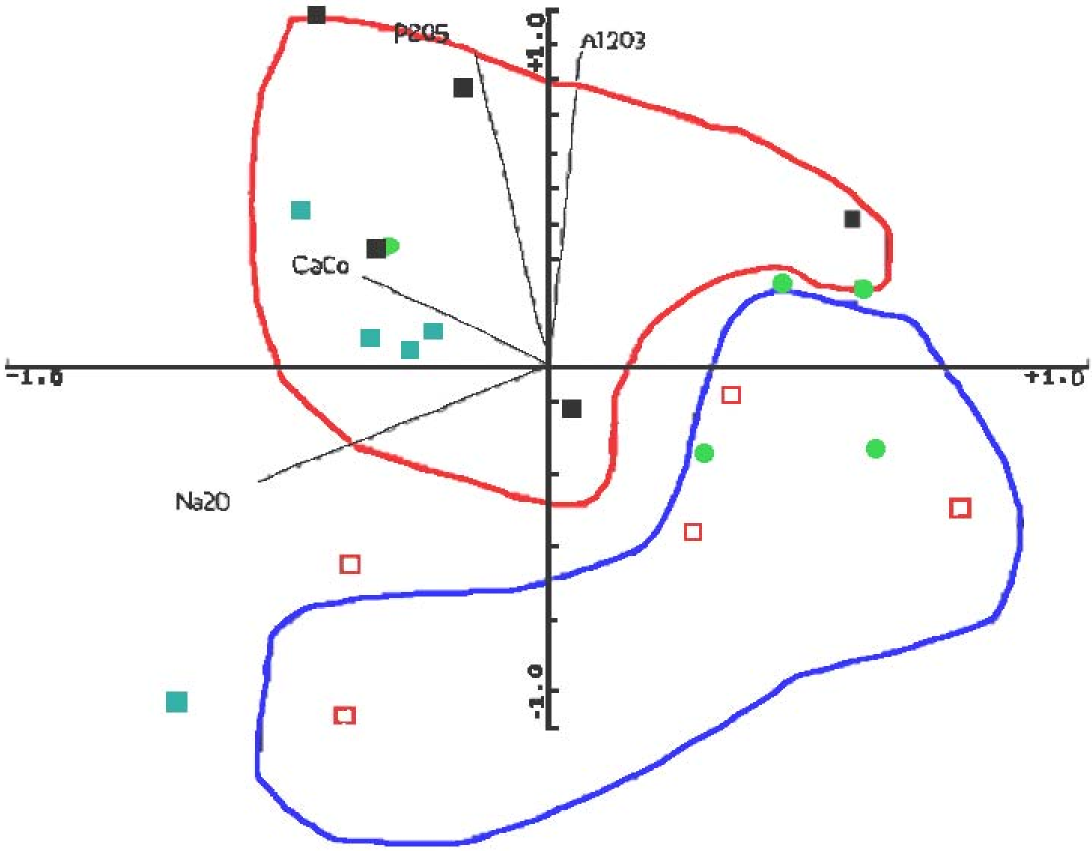
The disturbance caused by clearing would also allow the introduction of primary successional species, typically herbaceous and/or exotic species. This was reflected in the PCA of low altitude sites with separation of the cleared and uncleared sites. These correlations between invasion intensity, woody biomass and herbaceous cover were not as strong as that seen in the high invasion intensity sites of the cleared (Red) and uncleared (Blue) groupings in Figure 3.7.



Key:

High Invasion Cleared Sites	■	Low Invasion Cleared Sites	■
High Invasion Uncleared Sites	●	Low Invasion Uncleared Sites	□

Figure 3.6 Centered and standardized PCA representation of low altitude study site relationships in ordinal space based on "biological" transient variables illustrating three mixed groupings based generally on site invasion category (Uncleared – Red; High Invasion Cleared – Black; Low Invasion Cleared – Blue). Eigen values for 1st and 2nd axes are 0.338 and 0.207 respectively, representing 54.5% of the cumulative variance of species data.



Key:

High Invasion Cleared Sites	■ (black)	Low Invasion Cleared Sites	■ (cyan)
High Invasion Uncleared Sites	● (green)	Low Invasion Uncleared Sites	□ (red)

Figure 3.7 Centered and standardized PCA representation of high altitude plot relationships in ordinal space based on "biological" transient variables illustrating two groupings based on clearing status (Cleared – Red grouping & Uncleared – Blue grouping). Eigen values for 1st and 2nd axes are 0.481 and 0.197 respectively, representing 67.8% of the cumulative variance of species data.

3.3.2 Ground cover in relation to invasion intensity and clearing

The percentage exposed rock did not differ significantly for any of the experimental categories (Table 3.1; Appendix 3), thus illustrating ground and overall vegetation cover was not influenced by high rock cover in any site or treatment. Percentage bare soil also did not differ significantly between experimental treatments/management categories (cleared versus uncleared) (Table 3.1). A significant increase in percentage litter cover in the high invasion categories (high and low altitudes) was noted, however (Table 3.1). Litter overlays soil and it can be said that increases in litter cover under high invasion intensity signifies an increase in exposed soil through decreased herbaceous vegetation cover. Regression analyses of percentage litter cover against invasion intensity corroborated this observation (Figure 3.8). Hence, litter deposition masks the effect of shading out of vegetation ground cover caused by tall growing vegetation in high invasion categories. The increased deposition of litter by exotic vegetation is evident in Figure 3.8. The regressions of litter with invasion intensity also indicate that as the invasion intensity increased, the percentage litter cover (or deposition) increased. This relationship of increasing litter with invasion had a steeper slope in invaded communities than in indigenous stands or cleared sites (Figure 3.8). Cleared sites had a greater litter depth in relation to invasion intensity (as calculated in section 4.4.2 of the Vegetation Chapter) than did uncleared sites (Figure 3.9).

The percentage herbaceous vegetation cover showed a significant interaction between invasion, altitude and clearing treatment/management categories (INV*CLR*ALT) (Appendix 3). For high invasion sites, cleared treatments tended to have a greater herbaceous cover than did uncleared sites (Table 3.1).

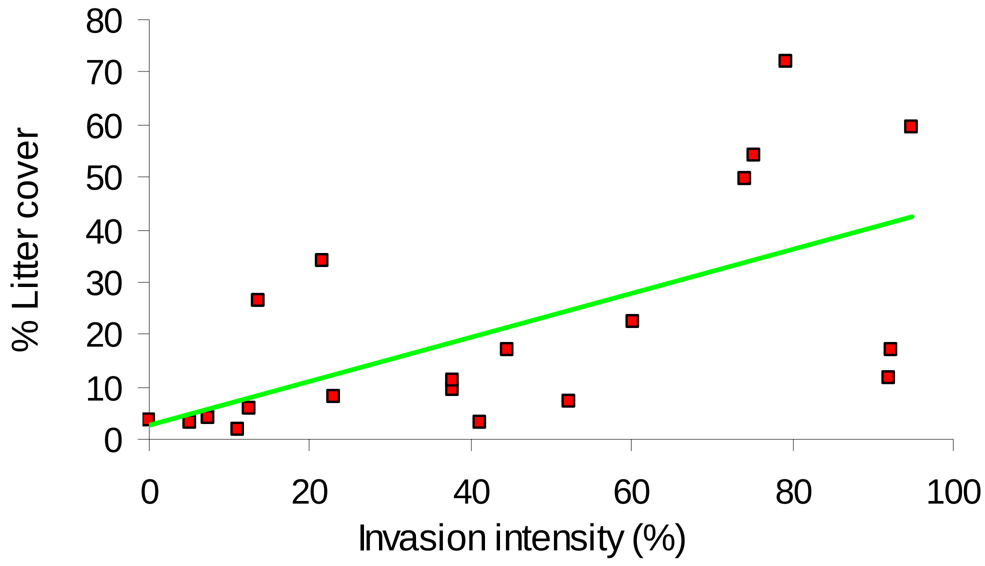
Treatment/management of low invasion sites showed little change in herbaceous vegetation cover, but high invasion treatments/management categories tended to have a greater herbaceous cover in cleared sites (Table 3.1).

Percentage grass cover was only significantly different for the interaction between the experimental categories of management and altitude (Appendix 3). Altitudinal differences in grass cover that did occur were minor, with increased grass cover at lower altitudes (Table 3.1). There were no clear trends with regards to the effects of weed control and invasion intensity on grass cover (Table 3.1).

Table 3.1 Mean and standard error for percentage ground cover estimates of soil, litter, grass, herbaceous vegetation, rock and depth of litter. Values with the same superscript letter within rows are not significantly different using Ryan's Q post-hoc test ($p < 0.05$).

Treatment / Variable	High Altitude				Low Altitude			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Exposed Soil (%)	0.9 ± 0.5^{a}	0 ± 0^{a}	3.5 ± 1.3^{a}	0.2 ± 0.2^{a}	1.5 ± 1.3^{a}	4.3 ± 2.8^{a}	4.2 ± 2.6^{a}	2.2 ± 0.9^{a}
Litter (%)	19.9 ± 4.3^{ab}	42.1 ± 12^{a}	5.1 ± 1.9^{b}	8.8 ± 4.5^{b}	11.3 ± 4.7^{b}	20.5 ± 8.8^{ab}	10.4 ± 2.8^{b}	12.7 ± 5.5^{b}
Herbaceous (%)	59.3 ± 5.9^{ab}	30.9 ± 5.8^{b}	48.4 ± 8.8^{ab}	49.8 ± 6.7^{ab}	38.6 ± 5.3^{b}	34.5 ± 6.1^{b}	68.6 ± 6.2^{a}	51.7 ± 6.3^{ab}
Rock (%)	0.3 ± 0.3^{a}	0 ± 0^{a}	2 ± 1.2^{a}	0.4 ± 0.4^{a}	1.2 ± 1.2^{a}	1.8 ± 1.2^{a}	0.1 ± 0.1^{a}	1.2 ± 1.2^{a}
Grass (%)	19.6 ± 4^{ab}	26.9 ± 9.1^{ab}	41.2 ± 9.1^{ab}	38.7 ± 4.9^{ab}	46.4 ± 4^{a}	39.7 ± 8.1^{ab}	16.9 ± 2.3^{b}	31.9 ± 5.2^{ab}
Depth of litter (cm)	4.4 ± 2^{a}	8.6 ± 1.5^{a}	4.2 ± 2.8^{a}	1.8 ± 0.8^{a}	2.8 ± 1.4^{a}	2.8 ± 1.3^{a}	1.3 ± 0.5^{a}	1.9 ± 0.8^{a}

(A)



(B)

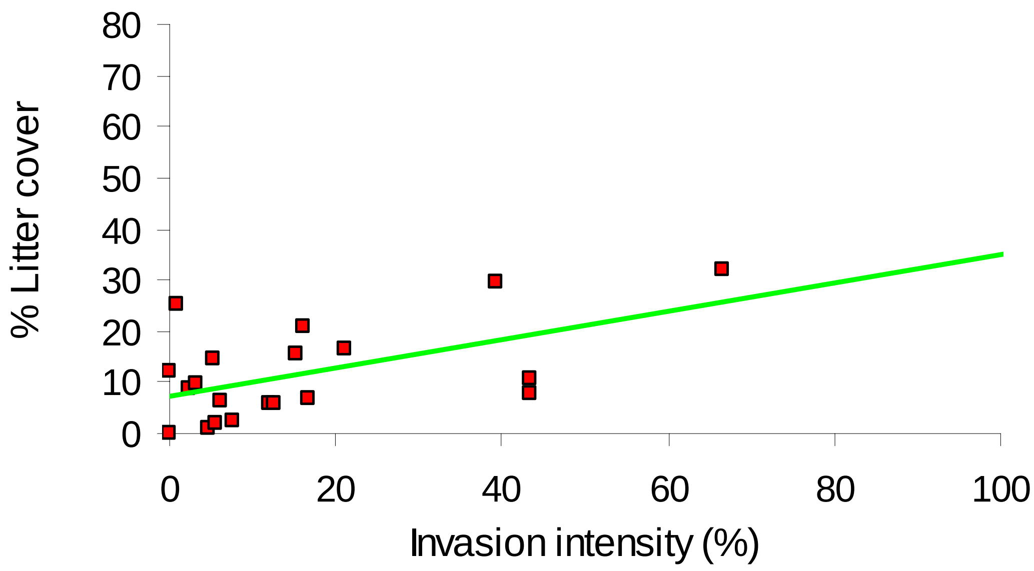
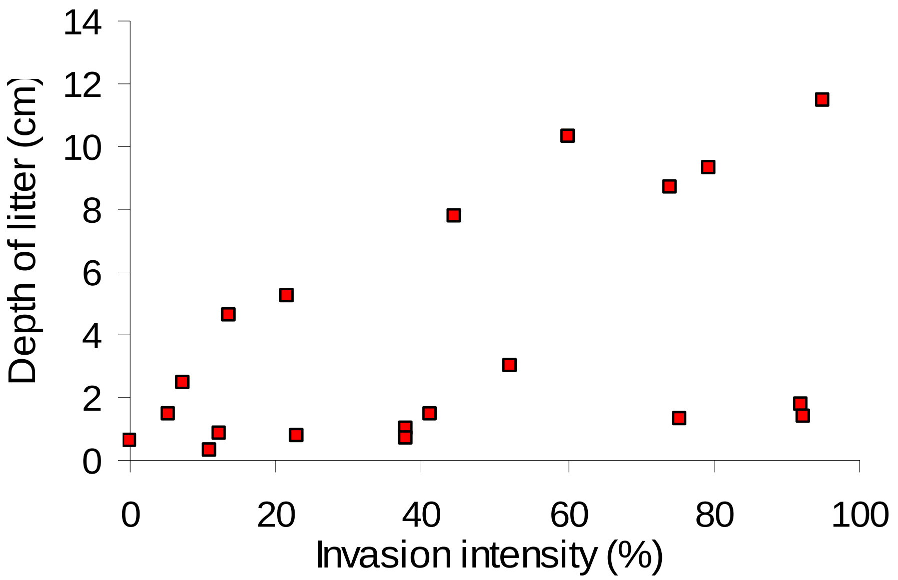


Figure 3.8 The relationship of percentage litter cover on the soil surface with increasing invasion intensity (% exotic cover of alien plants as calculated in section 4.4.2 of the Vegetation Chapter) on sites; (A) uncleared and (B) cleared of exotic plant species along the Sabie River, South Africa. The two regression slopes were not significantly different between cleared and uncleared plots ($P > 0.05$). The regression relationship (A) is $Y = 2.853003 + (0.4147964 * X)$ ($r^2=0.39$; $P<0.05$) and for (B) $Y = 4.205003 + (0.2004332 * X)$ ($r^2=0.30$; $P<0.05$).

(A)



(B)

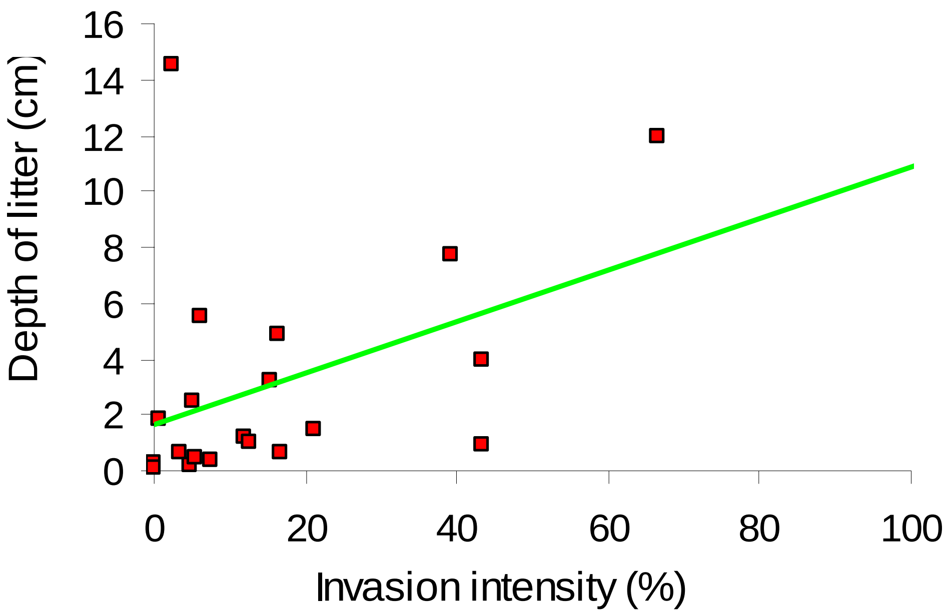


Figure 3.9 The relationship of litter depth (cm) on the soil surface with increasing invasion intensity (% aerial cover of exotic plants as calculated in section 4.4.2 of the Vegetation Chapter) on sites; (A) uncleared and (B) cleared of exotic plant species along the Sabie River, South Africa. ⊡ indicates outliers not included in regression calculation. The regression relationship (A) was not significant (r^2=0.23; P>0.05); and (B) was significant with $Y = 0.701062 + (0.0303288 * X)$ (r^2=0.31; P<0.05).

3.3.3 Changes in soil chemical content with clearing and invasion intensity

Soil pH

The soil pH was relatively acidic in most sites (Table 3.2). However, no significant differences occurred for pH with invasion, clearing, or altitude (Appendix 4). This indicates that the soil is well buffered from any changes in pH by external variables. This is corroborated by the high percentage organic component observed in the soil (Table 3.2), which would inherently lead to a buffering effect. In addition to this, a relatively high percentage of Calcium (Ca) was present in all sites and treatments (Appendix 5). pH did differ significantly with depth (Appendix 4) however, with an observed pH decrease in the deeper soil horizon (Table 3.2).

Soil macro-nutrients

Ca in the B-horizon was significantly different for management categories and depth classes, with higher concentrations of Ca occurring in cleared sites and near the soil surface or A horizon (Table 3.3; Appendix 6). For Potassium (K), a significant difference was observed for percentage invasion, altitude and the interaction of the two (Table 3.3; Appendix 5 & 6). The K concentrations were higher in soils of low invasion sites, and sites that occurred at high altitudes (Appendix 5).

Indicators of leaching and the subsequent loss of elemental and nutrient status of soils such as Aluminium (Al), differed only for altitude and management/treatment experimental categories (Table 3.3). Cleared sites had a higher Al concentration than uncleared sites (Appendix 5). Significant differences in Al with altitude and invasion indicate that high altitude high invasion sites have a higher Al concentration (Table 3.3). Phosphate (P) concentrations were significantly higher in high altitude soils (Table 3.3). There were also significant differences with depth (Appendix 6), with P concentrations being higher in the A horizon (Appendix 5). Sodium (Na) concentrations followed the same trend, except for the higher concentrations found at high altitudes (Table 3.3; Appendix 5).

Soil trace elements

Trace elements found in the soil showed a number of significant differences between the experimental categories. Arsenic (As) was significantly different for invasion categories (Table 3.4), with a higher concentration present in high invasion sites (Appendix 7). Interactions between invasion and altitude also showed significant differences for As (Table 3.4). There was a trend for cleared sites to have greater concentrations of As than uncleared sites (Appendix 7), and high altitude sites had lower As concentrations than low altitude sites (Appendix 7).

The trace element Barium (Ba) was also significantly different for categories of invasion (higher concentrations present at low invasion), and cleared/uncleared categories (higher concentrations present in cleared sites) (Table 3.2). Cobalt (Co) was significantly different between cleared and uncleared sites and interactions of clearing and altitude. Higher Co concentrations occurred in cleared sites than in uncleared sites (Appendix 7). Both Chromium (Cr) and Nickel (Ni) were significantly different for clearing with altitude interactions, with higher concentrations occurring in cleared sites and high altitude (Appendix 7). All other trace elements present in Table 3.3 and Appendix 7 were either not significant for any of the experimental categories, and/or there were no discernible trends evident in the data.

Soil organic matter

Total soil organic matter was significantly different between altitudes (Table 3.2), with higher values at high altitude (Appendix 4). Significantly lower total organic matter occurred with depth (Appendix 8). Interactions of clearing and altitude were significantly different for total soil organic matter (Table 3.2). High altitude high invasion sites were higher in total organic matter than sites of low altitude high invasion (Table 3.2). Regression analyses of total organic matter with invasion intensity, illustrates the clear relationship of increasing organic material with increasing invasion intensity (Figure 3.10). The cleared sites tended to have a greater increase in organic matter per unit invasion intensity than did uncleared sites (Figure 3.10).

3.3.4 Differences observed in soil physical properties

For all soil physical properties, except course silt (20 - 50 *u*m), there were significant altitudinal differences. These significant differences reflected the expected deposition (increase) of finer soil particles at lower altitudes, and the removal of finer particles through erosion leaving course material behind at higher altitudes. Significant differences occurred between cleared and uncleared sites and invasion intensities for clay, fine silt (< 2 - 20 *u*m) and sand (Table 3.2; Appendix 4). Similarly, differences were observed between high and low invasion sites (Table 3.2; Appendix 4). Only gravel differed with depth (Appendix 8), with more gravel in the B horizon (Table 3.2).

Table 3.2 Soil organic matter, pH and physical soil attributes (mean ± S.E.) found under different altitudes, management (cleared versus uncleared) treatments and invasion intensities for A (0 -10 cm) and B (10 - 20 cm) horizons. Values with the same superscript letter within each row are not significantly different (*P* < 0.05, Ryan's Q).

Treatment	Soil horizon	High Altitude				Low Altitude			
		High Invasion		Low Invasion		High Invasion		Low Invasion	
Soil attribute		Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Soil organic matter (%)	A	1.5 ± 0.1^{abc}	1.9 ± 0.3^{abc}	1.2 ± 0.1^{ab}	1.7 ± 0.3^{a}	0.7 ± 0.9^{c}	0.7 ± 0.8^{c}	0.9 ± 0.1^{bc}	0.7 ± 0.1^{c}
	B	1.3 ± 0.1^{ab}	1.4 ± 0.2^{a}	0.9 ± 0.1^{abc}	1.3 ± 0.3^{ab}	0.6 ± 0.1^{c}	0.5 ± 0.1^{c}	0.8 ± 0.0^{bc}	0.6 ± 0.2^{c}
pH	A	4.7 ± 0.2^{a}	4.6 ± 0.4^{a}	4.7 ± 0.2^{a}	4.5 ± 0.1^{a}	5.1 ± 0.3^{a}	4.9 ± 0.2^{a}	4.7 ± 0.2^{a}	4.4 ± 0.1^{a}
	B	4.6 ± 0.1^{a}	4.7 ± 0.2^{a}	4.6 ± 0.1^{a}	4.4 ± 0.1^{a}	4.8 ± 0.3^{a}	4.4 ± 0.2^{a}	4.4 ± 0.2^{a}	4.4 ± 0.1^{a}
% Clay (< 2 um)	A	11.6 ± 1.5^{b}	13.4 ± 1.7^{a}	12.4 ± 1.0^{b}	10.9 ± 1.4^{b}	10.6 ± 1.0^{b}	11.1 ± 0.9^{b}	13.6 ± 1.3^{b}	11.4 ± 0.9^{b}
	B	18.9 ± 2.1^{a}	12.2 ± 0.9^{b}	10.9 ± 1.1^{b}	10.0 ± 1.0^{b}	10.5 ± 1.1^{ab}	10.2 ± 1.1^{b}	14.9 ± 1.8^{b}	12.3 ± 0.9^{b}
% Silt (< 20 um)	A	10.8 ± 1.4^{a}	10.1 ± 2.3^{a}	8.4 ± 2.0^{a}	8.1 ± 2.1^{a}	6.8 ± 0.9^{a}	5.5 ± 1.3^{a}	6.2 ± 0.5^{a}	5.5 ± 0.5^{a}
	B	11.4 ± 0.9^{a}	6.9 ± 2.2^{abc}	9.8 ± 1.7^{ab}	5.2 ± 1.0^{bc}	6.2 ± 0.6^{bc}	5.5 ± 0.9^{bc}	6.4 ± 0.4^{bc}	4.2 ± 0.4^{e}
% Silt (> 20 um)	A	6.5 ± 1.8^{a}	5.1 ± 1.3^{a}	5.1 ± 1.1^{a}	5.2 ± 1.1^{a}	3.9 ± 0.7^{a}	7.9 ± 2.4^{a}	3.7 ± 0.9^{a}	2.5 ± 0.4^{a}
	B	5.0 ± 0.5^{a}	5.0 ± 1.2^{a}	5.8 ± 1.8^{a}	4.3 ± 1.3^{a}	6.5 ± 2.1^{a}	4.3 ± 1.4^{a}	3.7 ± 0.8^{a}	1.1 ± 0.2^{a}
% Sand (> 50 um)	A	63.6 ± 0.9^{b}	71.4 ± 3.3^{ab}	74.1 ± 3.7^{ab}	75.8 ± 4.4^{ab}	78.7 ± 1.9^{a}	75.5 ± 3.6^{ab}	76.5 ± 1.0^{ab}	81.1 ± 1.6^{a}
	B	64.7 ± 2.5^{b}	75.9 ± 3.5^{a}	73.6 ± 4.0^{ab}	80.5 ± 1.9^{a}	76.8 ± 2.3^{a}	80.0 ± 1.3^{a}	75.0 ± 1.1^{a}	83.4 ± 1.2^{a}
% Gravel (>2000 um)	A	56.0 ± 10.2^{bc}	52.6 ± 9.8^{c}	75.1 ± 3.4^{abc}	65.3 ± 16.7^{abc}	78.9 ± 3.7^{abc}	88.6 ± 2.1^{a}	87.7 ± 2.7^{ab}	83.1 ± 4.7^{abc}
	B	71.1 ± 6.4^{a}	80.2 ± 4.9^{a}	81.2 ± 9.7^{a}	90.5 ± 1.9^{a}	82.6 ± 6.1^{a}	$90.7\ 1.5^{a}$	89.1 ± 1.9^{a}	88.5 ± 3.5^{a}

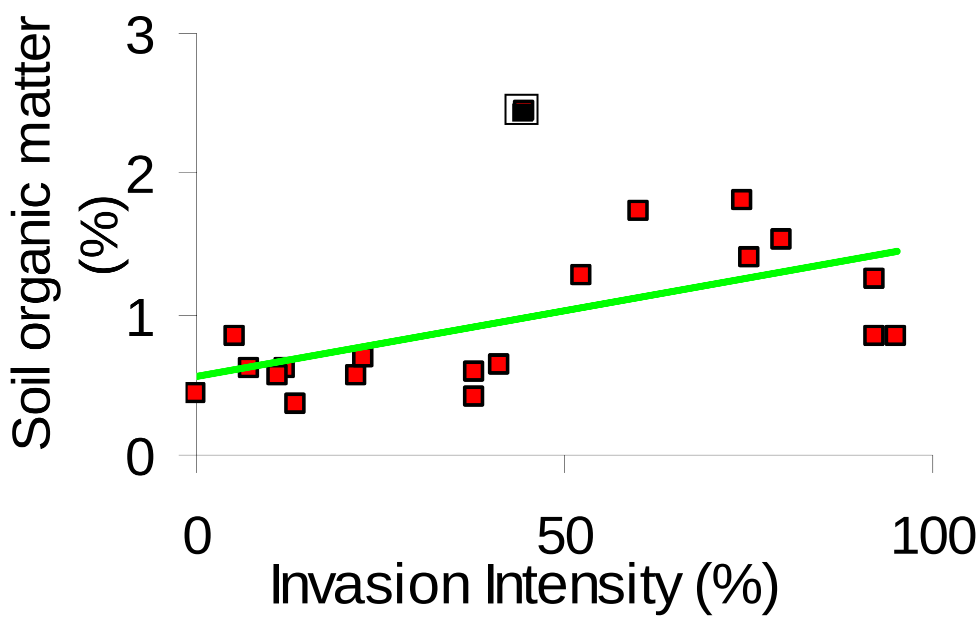
Table 3.3 Soil elements (as oxides, XRF data) significance values for three-way ANOVA's of altitude (ALT), invasion intensity (INV) and management (MAN) for soil depths 0 - 10 cm (A) and 10 - 20 (B). *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Soil Characteristic	Soil horizon	ALT	INV	MAN	ALT*INV	ALT*MAN	INV*MAN	ALT*INV *MAN
Al_2O_3 (%)	A	**0.0004**	0.514	**0.009**	**0.005**	0.776	0.450	0.761
	B	**0.0002**	0.548	**0.002**	**0.002**	0.403	0.331	0.500
CaO (%)	A	0.210	0.782	0.092	0.948	0.295	0.247	0.137
	B	0.190	0.448	**0.005**	0.652	**0.008**	0.909	0.227
Fe_2O_3 (%)	A	**0.004**	**0.030**	0.065	0.328	**0.026**	0.216	0.295
	B	**0.031**	**0.026**	**0.023**	0.174	**0.044**	0.768	0.453
K_2O (%)	A	**0.0003**	**0.004**	0.201	0.766	**0.001**	0.207	0.431
	B	**0.001**	**0.001**	0.145	0.533	**0.002**	0.271	0.845
MgO (%)	A	**0.043**	0.470	0.297	0.232	0.059	0.158	0.456
	B	0.055	0.630	0.215	0.630	0.111	0.289	0.354
MnO (%)	A	0.243	0.861	0.410	0.617	0.253	0.052	0.707
	B	0.533	0.852	0.189	0.551	0.338	0.075	0.791
Na_2O (%)	A	**0.005**	0.139	0.508	0.901	0.436	**0.0089**	0.076
	B	**0.015**	**0.012**	0.964	0.407	0.095	0.199	0.221
P_2O_5 (%)	A	**0.0001**	0.420	0.254	0.254	0.254	0.373	0.330
	B	**0.0001**	0.876	**0.015**	0.365	**0.034**	0.579	0.155
SiO_2 (%)	A	**0.0001**	0.086	**0.007**	**0.028**	0.523	0.323	0.541
	B	**0.0001**	0.810	**0.0001**	0.053	0.165	0.658	0.263
TiO_2 (%)	A	**0.0001**	0.287	**0.006**	0.253	**0.021**	0.508	0.065
	B	**0.0001**	0.216	**0.006**	0.193	0.074	0.968	**0.043**

Table 3.4 Soil element mean ± S.E. under different altitude, invasion intensity and management treatment (cleared versus uncleared) for the A (0 -10 cm) and B (10 - 20 cm) soil horizons. Means with the same superscript letter within row are not significantly different ($P < 0.05$, Ryan's Q).

Elements	Treatment	High Altitude				Low Altitude			
		High invasion		Low invasion		High invasion		Low invasion	
		Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
As (µg.g^{-1})	A	29.6 ± 7.8^{ab}	19.4 ± 4.5^{b}	29.2 ± 4.5^{ab}	16.8 ± 4.8^{b}	403.6 ± 171.7^{ab}	646.0 ± 262.8^{a}	54.8 ± 20.3^{ab}	16.0 ± 4.0^{b}
	B	34.8 ± 5.9^{ab}	23.0 ± 6.8^{ab}	25.0 ± 4.7^{ab}	21.0 ± 3.7^{ab}	739.2 ± 310.8^{a}	547.0 ± 214.1^{a}	26.0 ± 10.8^{ab}	12.0 ± 0.0^{b}
Ba (µg.g^{-1})	A	525 ± 105^{a}	208 ± 112^{b}	670 ± 58^{a}	567 ± 68^{ab}	318 ± 14^{ab}	322 ± 27^{ab}	368 ± 19^{a}	452 ± 30^{a}
	B	530 ± 98^{a}	229 ± 94^{b}	697 ± 111^{a}	336 ± 81^{ab}	294 ± 16^{ab}	322 ± 29^{ab}	405 ± 30^{ab}	419 ± 15^{a}
Co (µg.g^{-1})	A	35.4 ± 6.7^{a}	21.8 ± 8.4^{a}	41.6 ± 7.1^{a}	16.0 ± 2.2^{a}	19.0 ± 3.9^{a}	22.8 ± 1.5^{a}	20.8 ± 2.4^{a}	15.4 ± 1.0^{a}
	B	34.4 ± 8.5^{a}	21.2 ± 7.8^{a}	40.5 ± 9.1^{a}	15.1 ± 2.3^{a}	19.4 ± 3.3^{a}	23.6 ± 1.2^{a}	21.4 ± 3.1^{a}	14.6 ± 1.5^{a}
Cr (µg.g^{-1})	A	281 ± 48^{a}	239 ± 106^{ab}	275 ± 51^{a}	114 ± 24^{ab}	75 ± 24^{b}	141 ± 15^{ab}	81 ± 15^{b}	70 ± 10^{b}
	B	302 ± 50^{a}	225 ± 93^{abc}	277 ± 65^{ab}	115 ± 29^{abc}	94 ± 25^{c}	135 ± 19^{abc}	91 ± 15^{bc}	66 ± 5^{c}
Cu (µg.g^{-1})	A	63.6 ± 15.4^{a}	43.2 ± 19.2^{a}	78.0 ± 13.5^{a}	36.6 ± 12.3^{a}	56.4 ± 24.5^{a}	135.8 ± 45.9^{a}	39.6 ± 9.5^{a}	22.8 ± 2.4^{a}
	B	72.8 ± 14.1^{a}	43.4 ± 17.7^{a}	80.0 ± 17.8^{a}	37.0 ± 13.9^{a}	91.6 ± 35.7^{a}	107.2 ± 33.2^{a}	34.2 ± 6.0^{a}	22.0 ± 2.2^{a}
Mo (µg.g^{-1})	A	5.2 ± 1.1^{a}	6.6 ± 0.3^{a}	5.4 ± 0.7^{a}	5.4 ± 0.8^{a}	5.4 ± 0.9^{a}	5.8 ± 0.7^{a}	4.4 ± 0.3^{a}	4.4 ± 0.8^{a}
	B	5.6 ± 0.5^{ab}	6.8 ± 0.4^{a}	4.3 ± 0.6^{ab}	6.0 ± 0.8^{ab}	5.6 ± 0.8^{ab}	5.2 ± 0.9^{ab}	3.8 ± 0.4^{b}	3.4 ± 0.7^{b}
Ni (µg.g^{-1})	A	83.8 ± 16.8^{a}	63.0 ± 25.6^{a}	96.8 ± 15.5^{a}	45.8 ± 10.8^{a}	38.0 ± 8.1^{a}	64.8 ± 6.2^{a}	45.6 ± 7.8^{a}	32.0 ± 2.5^{a}
	B	93.0 ± 17.3^{a}	67.4 ± 26.4^{a}	97.5 ± 19.9^{a}	47.8 ± 14.0^{a}	48.6 ± 10.4^{a}	65.6 ± 6.2^{a}	45.6 ± 6.7^{a}	32.6 ± 2.3^{a}
Pb (µg.g^{-1})	A	25.4 ± 6.0^{a}	25.4 ± 1.8^{a}	20.8 ± 4.1^{a}	19.4 ± 2.3^{a}	23.2 ± 1.4^{a}	26.0 ± 2.8^{a}	21.4 ± 3.0^{a}	20.4 ± 1.2^{a}
	B	28.0 ± 2.2^{a}	20.4 ± 1.4^{ab}	19.5 ± 4.9^{ab}	19.4 ± 2.3^{ab}	21.8 ± 2.3^{ab}	22.6 ± 3.6^{ab}	22.6 ± 2.2^{ab}	16.4 ± 1.5^{b}
Rb (µg.g^{-1})	A	75.0 ± 16.5^{ab}	35.0 ± 14.7^{c}	87.8 ± 5.5^{ab}	39.0 ± 9.5^{bc}	66.8 ± 8.3^{ab}	69.4 ± 12.6^{ab}	76.6 ± 4.3^{ab}	99.6 ± 3.0^{a}
	B	87.4 ± 13.8^{ab}	31.8 ± 14.1^{c}	86.8 ± 6.5^{ab}	40.8 ± 11.8^{bc}	62.0 ± 10.0^{ab}	64.8 ± 13.4^{ab}	86.0 ± 4.4^{ab}	99.4 ± 3.8^{a}

(A)



(B)

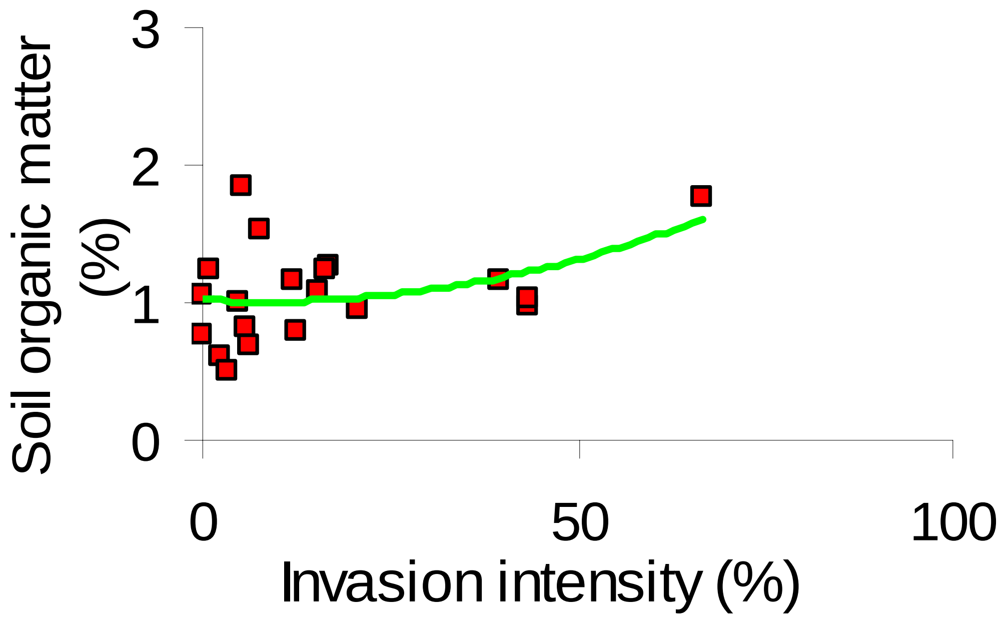


Figure 3.10 Regression of percentage soil organic matter for (A) uncleared and (B) cleared plots with increasing invasion intensity (as calculated in section 4.4.2 of the Vegetation Chapter) in the soil A horizon. Cleared (linearized) and uncleared regressions were significant at $P < 0.05$. The two regression slopes were not significant at $P < 0.05$. ⊡ indicates outliers not included in regression analyses. Regression relationships were as follows: (A) $Y = 0.4855938 + (0.00932027 * X)$ (r^2=0.49; P <0.05) and (B) $Y = -0.0002x^2 - 0.003x + 1.0212$ (r^2=0.17; P <0.05).

3.4. Discussion

3.4.1 Ground cover

The ground cover of the environment plays an important role in nutrient cycling (Theng 1980). The physical presence of ground cover has implications for the interception of rain, light, water runoff and nutrients. Typically rainfall has the most consequence, as this may result in erosion and nutrient leaching. Hence, attention is focused on the ground cover of areas cleared and under high invasion as ground cover composition and abundance is important in understanding the modification to environment being focused upon by the study.

Rock cover

The presence of rock cover typically modifies all other ground covers to a large extent. High amounts of rock cover result in alteration of the hydrodynamics of the community through increased runoff. Rock cover also does not facilitate plant establishment and may alter the vegetation composition and density. The presence of low rock cover in all study sites enabled a number of assumptions to be made: a) firstly, a true reflection of the vegetation spatial distribution, density and composition could be obtained and; b) true distributions of other stratal cover variables could be obtained.

Litter cover

As with other research, it was found that with an increase in exotic vegetation cover there was an observed increase in litter depth and aerial cover (Jenny *et al.* 1949; Nye & Greenland 1960; Kononova 1975; Theng 1980). Increased litter retards vegetation regeneration and places chemical constraints on plant nutrition (Jackman 1964a; Jackman 1964b; Theng 1980). Hence, clearing of exotic species may reverse the impacts of increased litter deposition found under high invasion categories, but may initially compound the environmental modification by increasing the litter load.

Changes in litter cover also impact on the nutrient cycle of the community (Jackman 1964a; Jackman 1964b; Theng 1980). It was evident from the multivariate analyses that a shift in the soil nutrient status of sites occurred under different litter covers. This emphasised that nutrient availability of sites is linked to the “storage” of nutrients in the litter. Although the soil-litter relationship is clear, this is not the only variable that may explain soil chemistry, as high rainfall, among other variables, also plays a role in the soil chemistry through leaching (Scotney & McPhee 1992).

Focusing on the litter-soil nutrient relationship established, it was noted that exotic species had a higher leaf biomass than that seen for most indigenous species. It can be surmised that deposition of litter would be greater in areas with a greater invasive intensity, which correlates with the study findings. The extent of litter deposited may however also be dependent on duration of invasion within the community. Regression analysis illustrates that with increasing invasion intensity, the deposition of litter may be greater than the rate of decomposition, which could lead to an accumulation of litter on the soil surface (Jenny *et al.*1949; Stout *et al.* 1979).

As litter has a high nutrient content (Theng 1980), large amounts of litter on the soil surface would indicate available nutrients in the community being "caught" in the litter layer. Hence, high invasion sites may have nutrients immobilised in the litter, and nutrients can only to be made available by decomposition. The rate limiting factors for decomposition in these systems would include environmental conditions such as: anaerobic environments (Theng 1980), unfavourable pH (Theng 1980), high salt concentrations (Theng 1980), excessive moisture (Birch & Friend 1956; Connell & Slayter 1977; Denslow 1987), temperature (Jenny & Raychanaudhuri 1960), bacterial population (Young 1976) and nutrient status (Jenny *et al.*1949; Reeve & Sumner 1970; Theng 1980). Some of the high invasion sites illustrate rate-limiting factors such as low soil pH, low nutrient status and relatively high salt concentrations. Alternatively, low invasion sites had a lower litter deposition (as the leaf biomass of these species is less). Multivariate results and regression analysis both supported this observation for high and low invasion sites.

Clearing of exotic species however, typically also deposits a large amount of dead vegetation matter (litter). This may result in similar conditions to that in uncleared high invasion categories. This layer of dead vegetation deposited by clearing will not persist, as the exotic vegetation would have been removed (by clearing) and the litter "load" will decompose with time. The extent of deposition of litter with clearing depends on the invasion intensity in the community prior to clearing. These two factors, rate of decomposition and invasion intensity, will determine the time required for removal of litter and the return of the community to it's "original" state.

The physical effects of litter in the environment are mainly related to water. This is evident under high rainfall climates, where surface water runoff washes litter away as litter is not a stable ground cover. This generally then results in erosion, which may start as rill erosion and progress to sheet and gully erosion (Scotney & McPhee 1992). Litter was therefore considered to represent exposed soil and is further discussed in the next section.

Exposed soil

Exposure of soil to the physical elements has a number of implications. Firstly, the soil surface offers no haven for seed deposition, burial and persistence in a soil seed bank (Garner & Witkowski 1997).

Secondly, the exposed soil surface is open to erosion and compaction (van Outshoorn 1992). Thirdly, exposed soils are given to lower organic matter inputs, ultimately resulting in nutrient deficiencies (Jenny *et al.* 1949; Brams 1971; Theng 1980). Areas cleared of exotic species typically had higher percentages of exposed soil, particularly the low invasion sites, and sites where lower litter deposition occurred. As mentioned in the previous section however, litter is not a stable soil cover and masks the potential effects of erosion. This is what was observed for the high invasion cleared and uncleared sites, as an increase in bare soil was expected but not measured.

Considering all ground cover with litter to be synonymous to exposed soil, the combined soil/litter cover reflects the true area exposed to the increased risk of erosion. This was best observed for the high invasion uncleared sites where in excess of 95% of the ground cover was comprised of soil/litter. The implications are that modification to the vegetation by invasion leads to the increased risk of soil erosion. This is exemplified with clearing of high invasion sites, where the vegetation has also been removed and the soil surface disturbed. This has been observed both in the Mpumalanga and KwaZulu-Natal silvicultural zones (A. Poulter *pers. comm*. 1997; D. Salmon *pers*. *comm*. 1998).

Vegetation cover

Typically, in plant community succession, herbaceous or weedy species colonise the disturbed areas first (Stohlgren *et al.*1995). Grasses and other species generally follow on from weed species in the successional sequence (Connell & Slatyer 1977; Geldenhuys 1995). Grasses and smaller growth forms may however, be replaced in the community once tree cover becomes dominant and shading effects take place (Connell & Slatyer 1977; Denslow 1987; Geldenhuys 1995). From the vegetation cover results, it was evident that the extent and duration of invasion plays a role in the vegetation cover but was uncorrelated with any variable measured. Vegetation cover can however, be broken into two types, herbaceous and grass cover. Grass cover was found to behave differently with altitude as grass species dominate the high altitude sites (Van Oudtshoorn 1992; Rutherford and Westfall 1994).

Using forb vegetation cover (i.e. herbaceous cover less grass cover) as an indicator of disturbance, illustrated a distribution pattern for sites related to disturbance caused by clearing and invasion. This pattern of sites related particularly to increased herbaceous vegetation cover in cleared sites, illustrating that removal of individuals from the environment results in “forest gap” formation exposing the lower growing vegetation types to light resources (Shugart & Seagle 1985; Geldenhuys 1995). Hence, clearing operations modify the environment, and by virtue of this, change the vegetation cover.

A decrease in the herbaceous vegetation cover occurred with invasion. Exotic species, which are tall growing, reduce light penetration to the ground, thus limiting light to the under canopy. Herbaceous species do not proliferate or typically colonise these areas, hence a decrease in the herbaceous ground cover was observed.

From the results obtained in this study it can be noted that different disturbances to the vegetation community result in different vegetative cover responses. Grass cover did not show any pattern with disturbance due to associations with the overlapping savanna and grassland biomes that occurred with altitude. A clear separation of cleared and uncleared sites at high invasion could be made however, using herbaceous vegetation cover.

3.4.2 The soil environment

Soil physical properties and their relationship to clearing and invasion

Soil physical attributes are highly unlikely to have been altered by the disturbances discussed in this study. The only possible changes that may have been imposed on soil structure through clearing and/or invasion are: a) the possible lack of distinction between soil horizons, with a shift towards coarse soil textures as finer soil materials are eroded away and; b) the possible loss of finer soil textures with increased erosion on cleared sites and areas with high invasion. There was some grouping of high altitude sites using multivariate analyses of soil physical characteristics, but these were weak and all other sites illustrated no associations between plots of different treatments. Univariate analyses of soil physical structure supported this as no statistical differences could be determined. This lack of difference between sites based on soil physical properties has two implications. Firstly, the data illustrate that both invasion and clearing of exotic species do not influence the soil physical structure. Secondly, it indicates that sites were not biased by the study design or site location, and thus would not influence other variables being observed in the study (i.e. biological analyses and soil chemical analyses). It must be noted that riverine sites are highly disturbed by flooding and the floods which occurred in the 2000 rainy season resulted in large erosion, deposition of soils and loss of the permanent plot concrete works.

Soil nutrients and their modification by clearing and invasion

The separation of cleared and uncleared sites using multivariate analyses indicates that changes in the soil chemical environment occurred as a consequence of clearing of invasive species. The soil chemical attributes shift after clearing towards the less modified state seen in low invasion categories. This was supported by changes observed in the P and Ca concentrations in the soil. This has consequences for vegetation after clearing, as P in the form of phosphate is a vital plant nutrient which, causes growth reduction in plants when limited (Reeve & Sumner 1970; Bell 1982). Ca plays a role in cation exchange and availability of nutrients, while also influencing soil pH (Theng 1980).

Due to the modification of soil chemical attributes being indirect, there are other variables that may need to be considered. Sandy alluvial soils, such as those found in the study region, are typically low in nutrients due to low organic content, and consequently have slower nutrient cycling (Bell 1982). Sandy soils also leach nutrients earlier, leading to a nutrient cycle similar to that seen in tropical rain forests of South America (Theng 1980). From the study, high invasion typically results in high vegetative biomass. This high plant biomass places pressure on the acquisition of nutrients from the habitat (Bell 1982). Multivariate and univariate analyses indicate that the increased nutrient demand from high vegetation biomass appears to be corrected by the clearing of exotic species, although no particular nutrient species came to the foreground as an indicator of this process.

3.4.3 The "biological" environment

Direct effects of clearing and invasion intensities were seen in the "biological" multivariate analyses. The patterns obtained indicate a decrease in the vegetative cover of sites with clearing and with high invasion. "Biological" variables such as percentage herbaceous vegetation cover, which separated the high invasion cleared sites, can be explained by successional theory (Connell & Slayter 1977; Denslow 1987; Geldenhuys 1995). These sites have been successionally "re-set" to the primary successional stage where herbaceous weedy species pre-dominate (Geldenhuys 1995). In high invasion sites, clearing has "re-set" the majority of the site with little area remaining in a tertiary state. However, in low invasion cleared sites, an island effect exists, where cleared areas are broken by islands of original indigenous vegetation (Shugart & Seagle 1985).

In high invasion uncleared sites, the community relates closely to a tertiary successional community. Low vegetation cover with high woody biomass can be seen as the defining variable of this successional stage. This was verified by the PCA analyses where uncleared sites separated out using these two variables. Low invasion cleared and uncleared sites both have lower biomass and an increased vegetation cover. This fits into the secondary successional community as explained by Geldenhuys (1995), and is also where maximum diversity is expected. The results of the PCA analyses concur with this theory, and only the percentage soil exposed by clearing distinguished cleared from uncleared sites.

3.5 Conclusions

From this chapter is can be concluded that sites selected for the study were not biased by any fundamental environmental variables such as soil texture or ground cover. This reduced complications in interpretation of clearing and invasion effects on community composition, soil seed banks and community structure.

What was also evident in this chapter was that clearing resulted in alteration of both soil chemical attributes and vegetation cover. Similarly, invasion also altered the environment through modifications to ground cover, particularly vegetation and litter. The extent of these modifications was found to be dependent on extent of invasion. This is also true for disturbances caused by clearing, as this disturbance is a consequence of invasion (and its intensity).

Considering modifications to the environment caused by clearing and invasion, the disturbances can be ordered as follows in declining extent of disturbance severity: 1) high invasion cleared sites; 2) high invasion uncleared sites; 3) low invasion cleared sites; and 4) low invasion uncleared sites.