CHAPTER 4

CHANGES IN VEGETATION STRUCTURE IN RESPONSE TO INVASION AND CLEARING OF EXOTIC PLANTS

4.1 Introduction

Vegetation structure is defined as the organisation of individuals in space that constitutes a stand of plants. Introduced exotic plant species or clearing of this vegetation, may influence the vegetation structure (organisation), proportional abundance of species, guilds or growth forms in that community. Communities are commonly assessed using species diversity, but change occurs at different levels of community organisation. For example, species turnover does not necessarily imply change in the physiognomy of a plant community, similarly a turnover in diversity of plant guilds or growth forms also does not necessarily illustrate a change in community diversity (Bredenkamp & Theron 1985). Hence changes to the community, brought about by clearing or invasion, may not be reflected in community diversity, but may be evident in vegetation structure.

Information on vegetation structure may reflect the extent of invasion and modification to the community caused by disturbance, and potential implications that these hold for community function and regeneration (Bredenkamp & Theron 1985; Breytenbach 1991). Vegetation structure also has an important role to play in the stability and diversity of the community (Shugart & Seagle 1985). A disturbance, such as invasion by exotic species, may influence species entering the community (Geldenhuys *et al.*1986). A loss in vegetation height class for example, may result in an alteration of under canopy species abundance and diversity. It is known that shade tolerance is important in community structure, as shade tolerance is the primary criterion used for arranging vegetation into a competitive hierarchy (Horn 1971; Keddy & MacLellan 1990). Hence, a change in canopy cover could alter community characteristics, both structurally and in terms of composition.

Possibly the greatest impact of altered vegetation structure has been observed within the eastern escarpment silvicultural zone. Here, an increased woody element formed by invasion and/or plantations has formed thickets changing the appearance and character of the landscape (Henderson & Wells 1986). Although vegetation structure may be used to measure vegetation change, vegetation biomass has been found not to be a good measure, as indigenous vegetation may have a similar biomass to exotic vegetation (Versfeld & van Wilgen 1991).

4.1.1 Effects of invasion on vegetation structure and composition

Exotic species found in the eastern escarpment silvicultural zone are mainly introduced timber species such as pine, eucalypt and acacia species, all of which are tall growth forms with high productivity and growth rate (MacDonald & Jarman 1985). Large increases in above-ground biomass have been recorded with invasion by exotic species (Versfeld & van Wilgen 1991). Shading by exotic invasive species modifies communities and it can be expected that a loss of indigenous species will occur (Midgley *et al*. 1992; Geldenhuys 1993; Holmes & Cowling 1997). Complete exclusion of all other species by exotic invader species has only been obtained in the laboratory (Gause 1934; Crombie 1947), and rarely occurs in nature (Hutchinson 1961; Miller 1967). In other situations, reductions to three and four species systems have been noted (Huston 1979). An example of this is observable in the Tzaneen area, where *Solanum mauritianum* invasion has resulted in a species poor system with a relatively open understorey (Dean 1985). In these situations, stabilisation of community structure and composition, in the opinion of Cronk & Fuller (1995), may occur with time but normally results in a reduced species stand lacking vegetation structure found in the "natural" community.

4.1.2 The effects of clearing on vegetation structure and composition

Clearing of exotic plants obviously changes vegetation structure. This is particularly true if clearing is specific for species that may constitute a community height class or occupies extensive areas. As previously mentioned, many exotic species typically found in the eastern escarpment silvicultural zone are tall growing tree forms (Midgley *et al*. 1992; Geldenhuys 1993; Holmes & Cowling 1997). The initial effect of clearing exotic vegetation is thus the opening up of the canopy, which constitutes a disturbance to the community (resulting in structural changes to the community). The opening of the canopy also creates a "window" of opportunity for establishment in an ecosystem (Geldenhuys *et al.* 1986). This is particularly true for forest and riverine vegetation, where vegetation structure plays an important role in species composition and ecosystem function (Geldenhuys *et al.* 1986).

4.1.3 The success of clearing exotic species from communities

Invasive exotic species dominate indigenous vegetation through structural (height) advantages (Rutherford *et al.* 1991). As a consequence, there is a need to completely clear invasive exotic species to allow re-establishment of original indigenous vegetation structure to occur. Using vegetation structure as a measure of disturbance, the extent of the deviation of the community through invasion clearing from that seen in "natural" communities, will enable close observation of the regeneration of the community. This should relate to successional theory of community regeneration as described by Sousa (1984) (Figure 4.1).

In order to gain an insight into the interactions of invasion and clearing on vegetation structure, the extent of modifications caused by these processes have to be identified and measured. The objective of this chapter is to determine the different levels of invasion intensity and the alterations resulting from this on vegetation structure and composition. The clearing of invasion and the subsequent affects this will have on vegetation structure will be investigated as an objective. This will entail examination of vegetation height classes, aerial cover of height classes and modifications observed for different invasion intensities. It was hypothesised that indigenous species composition and vegetation structure will differ with intensity of exotic species invasion prior to and after clearing.

4.2. Materials and Methods

4.2.1 Determination of vegetation aerial cover and height classes

Overstorey aerial cover was determined within the 20 x 50 m plots using five line transects per plot. 20 m line transects were established perpendicular to the direction of the river and placed at 10 m intervals (i.e. at 10 m, 20 m, 30 m, and 40 m distances) along the 50 m length of each plot (Figure 4.2). A 3 m ranging pole and a 50 m tape measure were used to collect the height class and spatial distribution data. The 3 m ranging pole was used to determine aerial cover height classes, and the tape measure was used to measure the extent of the aerial cover (as per the line intercept method) for each height class. Percentage vegetation cover was determined for the following three height classes: (A) Large trees (>5 m in height), (B) small trees (<5 m but >2 m) and, (C) saplings and shrubs (<2 m). The data for the sapling and shrub height class were collected for all woody species greater than 1 m in height.

4.2.2 Pre-clearing invasion intensity

Invasion intensity

Invasion intensity was measured by counting the number of individuals of *S. mauritianum, Eucalyptus* spp. and *Pine* spp. present in the 20 x 5 m (100 m^2) quadrat. The stem circumference of each individual (excluding *S. mauritianum*), felled or unfelled, above the basal bulge of the stem was measured. Stem circumference for *S. mauritianum* was not measured because of small stem circumferences, large numbers

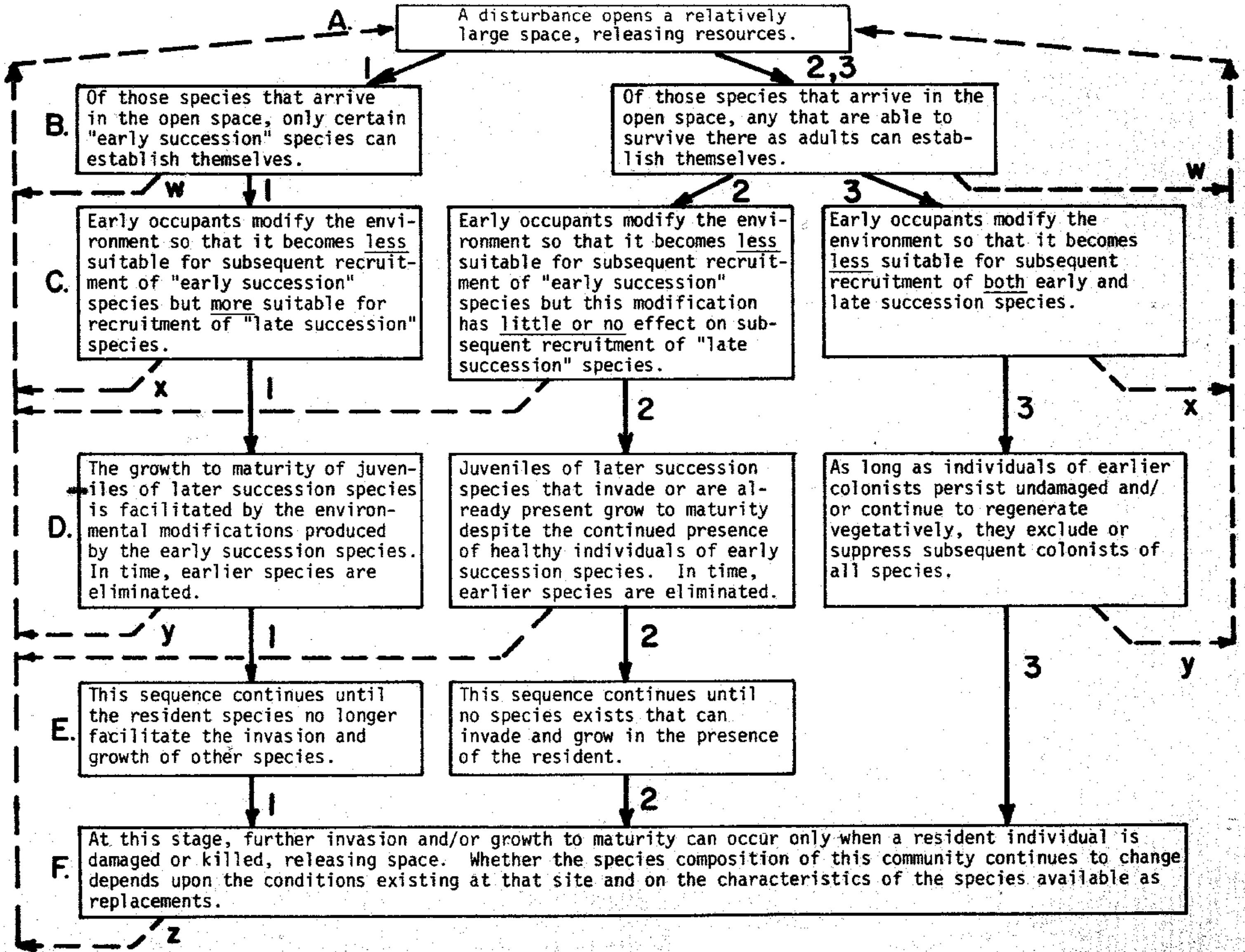


Figure 4.1 –Three models of the mechanisms producing the sequence of species in succession. The dashed lines represent interruptions of the process, in decreasing frequency in the order *w*, *x*, *y*, and *z*. From Souza (1984)

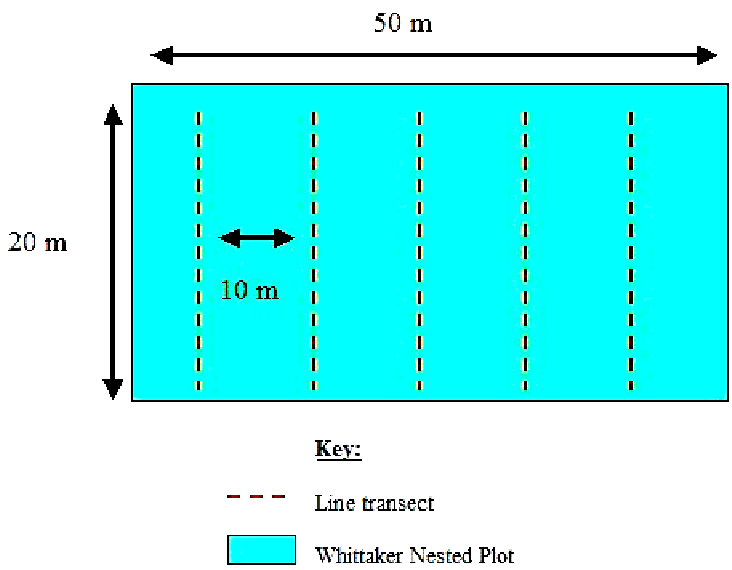


Figure 4.2 Layout of how overstorey aerial cover was determined within the 20 x 50 m plots using line transects.

of individuals and the absence of an allometric equation to determine biomass for this species. Height of each individual (for all three weed species) was determined using a clinometer and trigonometric calculations. These results were later used in the environmental modification and seed bank regression analyses.

Post clearing invasion intensity

To determine the success of clearing in clear felled plots the invasion intensity prior to clearing needed to be determined. This was accomplished by counting the number of cut stems (stumps), and measuring the circumference of each stem above the basal bulge. These circumference measurements were converted to basal diameter (BD) values using the following equation:

$$BD = \text{Circumference} / (\text{Pi})$$

These basal diameter data were regressed and a relationship determined between BD and diameter at breast height (DBH), which allowed a measure of DBH for felled individuals to be calculated (Figure 4.3). Once these data had been obtained, the volume of timber removed could be calculated for *E. grandis* and *P. patula* in the cleared plots, and a measure of previously standing invasive vegetation biomass determined. Volume of timber (ST) equations for *A. mearnsii* , *E. grandis* and *P. patula* are as follows:

$$Log_{10}SV = -4.7406+1.9532*Log_{10}(DBH)+1.2315*Log_{10}(H)...(\textit{A. mearnsii})$$

$$Log_{10}SV = -4.9819+1.9804*Log_{10}(DBH)+1.3719*Log_{10}(H)...(\textit{E. grandis})$$

$$Log_{10}SV = -5.8497+2.0696*Log_{10}(DBH+8)+1.3254*Log_{10}(H)...(\textit{P. patula})$$

Where SV is stem volume in m^3, under bark and usually to 75 mm stem tip diameter; DBH is the diameter at breast height in cm and H is the height of the tree in m (Bredenkamp 1993). Using these standard silviculture techniques, the commercial exotic vegetation biomass was calculated for each plot. Height of each individual (for all three weed species) was determined using a clinometer and trigonometric calculations, and was statistically scrutinised for all species.

Density

Density of exotic species was also used to determine the pre-clearing invasion intensity of sites already cleared. This was done by counting the number of individuals of *S. mauritianum, Eucalyptus* spp. and *Pine* spp. present in the 20 x 5 m (100 m^2) quadrat within each plot. For *E. grandis*, *P. patula* and *S. mauritianum*, the number of stems per unit area was used as a measure of invasive species density. The percentage exotic vegetation cover per plot in uncleared plots was regressed against density of invasive species. A relationship was determined for each of these species and their associated percentage aerial cover as well as total percentage invasive aerial cover. This relationship was then used to determine the percentage aerial cover in plots that were clear felled.

4.2.3 Success in clearing exotic vegetation

Invasion intensity data measured for cleared plots was compared to calculated pre-clearing invasion intensity. Invasion intensity data for cleared plots was also compared to invasion intensity of uncleared plots of the same invasion category. Both these methods were used to compare results obtained and to determine possible techniques for practical measurement of the success of clearing exotic vegetation. Other variables were also compared such as density, mean indigenous and exotic vegetation height and exotic biomass data. These were used to confirm the results obtained from the invasion intensity data analyses.

4.2.4 Plant growth forms

The growth form classes recognised were as follows: single-stemmed trees, multi-stemmed trees, single-stemmed shrubs, multi-stemmed shrubs, erect and prostrate forbs, and tufted and stoloniferous grasses. Trees were defined as multi- or single-stemmed woody plants that remain erect unassisted and are ≥ 2 m in height. A shrub was defined as a multi- or single-stemmed woody plant that remains erect unassisted with a maximum height of less than 2 m. Species growth forms were initially determined in the field during voucher specimen collection. They were later confirmed in the herbarium and species categorised as annual or perennial after identification.

4.2.5 Clearing success for *S. mauritianum*

Within the 20 x 5 m quadrats of cleared plots, for both the high and low altitude categories, a number of *S. mauritianum* plants treated by clearing operations (cut and stump capped with chopper) were randomly selected and sampled. A minimum of 100 individuals was sampled for each altitude. For each individual, the height of cut, diameter of stem at cut and the survival of the individual were determined. Two survival categories for each individual were identified, namely dead or alive. If alive, information on the individual as to whether it was resprouting or growing from seed was recorded. These data were then used to determine the relationship between survival of cleared *S. mauritianum* individuals and their size (stem diameter).

4.2.6 Statistical Analyses of Data

Univariate analysis

For each height class and total percentage aerial cover, species were categorised as indigenous or exotic. Statistical comparisons using three way ANOVA's were made between altitude, invasion intensity and clearing using indigenous, exotic and total vegetation cover for each height class and total vegetation aerial cover. Key species such as *S. mauritianum, E. grandis*, *Pinus* spp. and other dominant woody species were also compared in this manner.

The proportion of species falling into each growth form were compared between altitude, invasion intensity and clearing using three way ANOVA's. The ratios of perennial to annual species were also determined for cleared and uncleared sites of different invasion intensities. Mean height of vegetation in each plot was determined from the mean percentage of the aerial cover in each height class multiplied by the height per class.

Regression analyses of vegetation density (independent) and aerial cover (dependent) for uncleared plots were determined using SYSTAT. Comparisons were made for cleared vs. pre-cleared aerial cover and cleared vs. uncleared aerial cover of plots of the same invasion category using three way ANOVA's. Aerial cover for each height class was also analysed using three-way ANOVA.

Mean height of cleared and uncleared *S. mauritianum* individuals and mean indigenous woody vegetation height for cleared and uncleared plots were compared using *t*-tests to determine if the mean height of *S. mauritianum* differed from that of the indigenous woody vegetation under different treatments (cleared and uncleared).

Regression relationships for height of cut stem above ground, with it's diameter at the cut were obtained for both dead and resprouted *S. mauritianum* individuals. *t*-tests were used to determine if diameter of cut stem differed significantly between resprouting and dead individuals. Similarly, height of cut was tested between dead and resprouting individuals.

Multivariate analysis

An identical approach to the multivariate analysis of the environmental modification data in chapter 3 was undertaken for the vegetation data in this chapter. Two approaches to determine non-essential 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 variation was accomplished using bi-plots from an initial standardized principal components analyses (PCA), and a co-variance table of vegetation variables.

The analysis of variables for the 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. 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).

4.3 Results

4.3.1 Invasion intensity

Standing exotic aerial cover or invasion intensity

Total aerial cover of sites is divided into open, indigenous and invasive species aerial cover. The percentage aerial cover of exotic vegetation was used as the invasion intensity for that study site (Table 4.1).

Pre-clearing invasion intensity (cleared sites)

Regression relationships between aerial cover, basal area and density of individuals for exotic species were determined (Figure 4.3). Best-fit significant relationships were used to calculate the pre-clearing exotic species aerial cover (invasion intensity) for cleared sites. Best-fit relationships related to aerial cover and density for all species rather than the expected aerial cover/basal area relationships (Appendix 9). Thus the calculation of pre-clearing invasion intensity in cleared sites was calculated based on the invasion intensity/stem density relationships for all species.

The calculated pre-clearing invasion intensities were statistically compared between pre-cleared invasion intensities and uncleared sites of the same invasion intensity category using a three way ANOVA for total exotic species aerial cover (Table 4.2, Appendix 10). This was repeated for both *E. grandis* and *S. mauritianum* percentage aerial cover (Table 4.1, Appendix 10). *P. patula* and *A. mearnsii* were too infrequent for these data to be compared. Pre-clearing invasion intensity was found not to be significantly different from that seen for uncleared sites of the same invasion intensity category (Table 4.1 & 4.2). Hence validating any cleared/uncleared site comparisons based on invasion intensity categories. This result was repeated at the species level for both *E. grandis* and *S. mauritianum,* although it was not significant (Table 4.2).

It was noted that *S. mauritianum* pre- and post clearing aerial cover was significantly different for different altitudes (Table 4.1), with a greater percentage aerial cover in the low altitude low invasion categories (Appendix 10). Invasion intensity (INV) for total exotic species percentage aerial cover and *E. grandis* was found to be significant at $P < 0.01$, but was not significant for *S. mauritianum*. This indicates that although there were differences in *E. grandis* and total aerial cover there are no clear differences in *S. mauritianum* invasion intensity for pre- and post clearing invasion categories.

4.3.2 Vegetation aerial cover changes with clearing and invasion

Exotic species aerial cover

Multivariate analyses of the vegetation biological data for high altitude plots separated cleared and uncleared sites based on wood biomass and invasion intensity. This was particularly visible for high invasion categories but less so for low invasion categories (Figure 4.4 & 4.5). No distinction could be inferred between high and low invasion categories based on an invasion intensity axis for high altitude plots (Figure 4.5). Low altitude cleared and uncleared sites however, although separating out on wood biomass did not do so on the invasion intensity axis (Figure 4.4). Instead low invasion cleared sites and high invasion cleared sites separated out on the invasion intensity axis for low altitude (Figure 4.4).

Significance for clearing (MAN) for calculated post clearing aerial cover compared with uncleared sites for all percentage aerial cover variables, indicated that clearing had decreased the percentage exotic aerial cover (Table 4.3 & Appendix 10). Interactions of invasion with clearing (INV*MAN) for total exotic aerial cover and *E. grandis* were significant, but not for *S. mauritianum*. Thus indicating a decrease in the percentage aerial cover of exotic species except for *S. mauritianum*, which appears not to be effectively removed by clearing operations. The persistence of this species in the community and the height of growth form showed that *S. mauritianum* overtops most indigenous vegetation even after clearing (Table 4.4). There was also a significant difference between *S. mauritianum* and the height of indigenous vegetation in cleared sites with *S. mauritianum* being significantly taller (Table 4.4).

Exotic vegetation aerial cover was significantly different with altitude for all height classes except total percentage aerial cover (Table 4.3). This indicates differential invasion intensity with altitude, but this does not alter the overall aerial cover. Significant management with invasion (MAN*INV) interactions for the exotic species aerial cover and the > 5 m height class, but not for the 2 - 5 m or < 2 m height classes were found. This, linked to the significant contribution made to the 2 – 5 m and < 2 m height class by *S. mauritianum* (78% of total aerial cover), explains the lack of change in these height classes. Clearing has thus been effective for taller height classes, which have the greatest effect on the total aerial cover (hence the significant reduction in total exotic vegetation aerial cover), but not for the smaller (shorter) height classes. Figure 4.6 illustrates the reduction of exotic vegetation aerial cover with clearing and the large reductions in the aerial cover of the > 5 m height class (Figure 4.7).

Table 4.1 Mean and S.E. for uncleared, pre- and post-clearing percentage aerial cover of total exotic vegetation (invasion intensity). Values with the same superscript letter within rows are not significantly different using Ryan's Q post-hoc test ($p < 0.05$).

Treatment	High Altitude				Low Altitude			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
% Invasion intensity	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Pre-clearing invasion intensity	72 ± 1^{a}	72 ± 8^{a}	52 ± 3^{ab}	11 ± 4^{c}	65 ± 5^{a}	69 ± 11^{a}	23 ± 10^{bc}	23 ± 7^{bc}
Post clearing invasion intensity	21 ± 12^{b}	72 ± 8^{a}	3 ± 1^{b}	11 ± 4^{b}	29 ± 8^{b}	69 ± 11^{a}	11 ± 4^{b}	23 ± 7^{b}

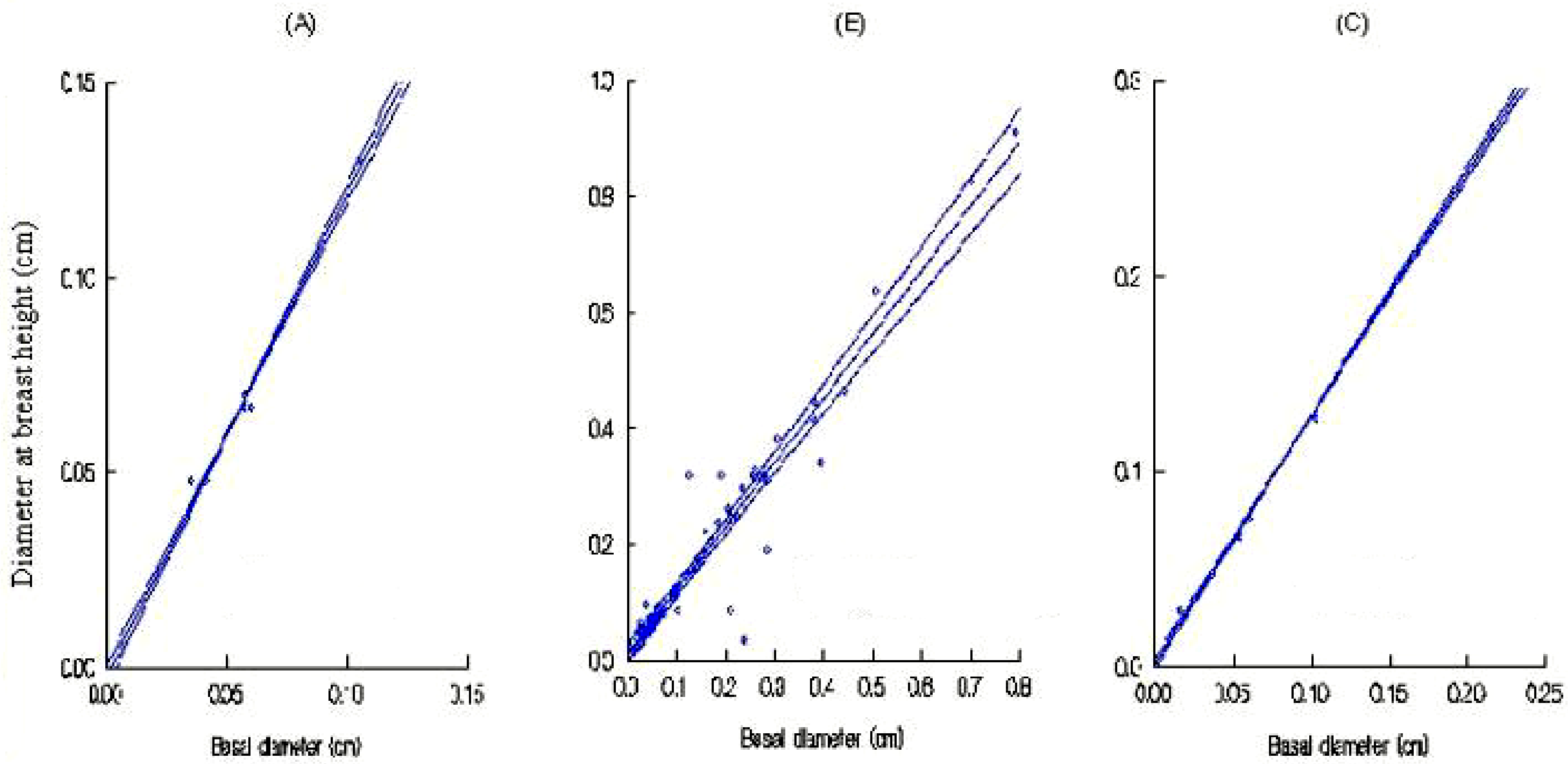
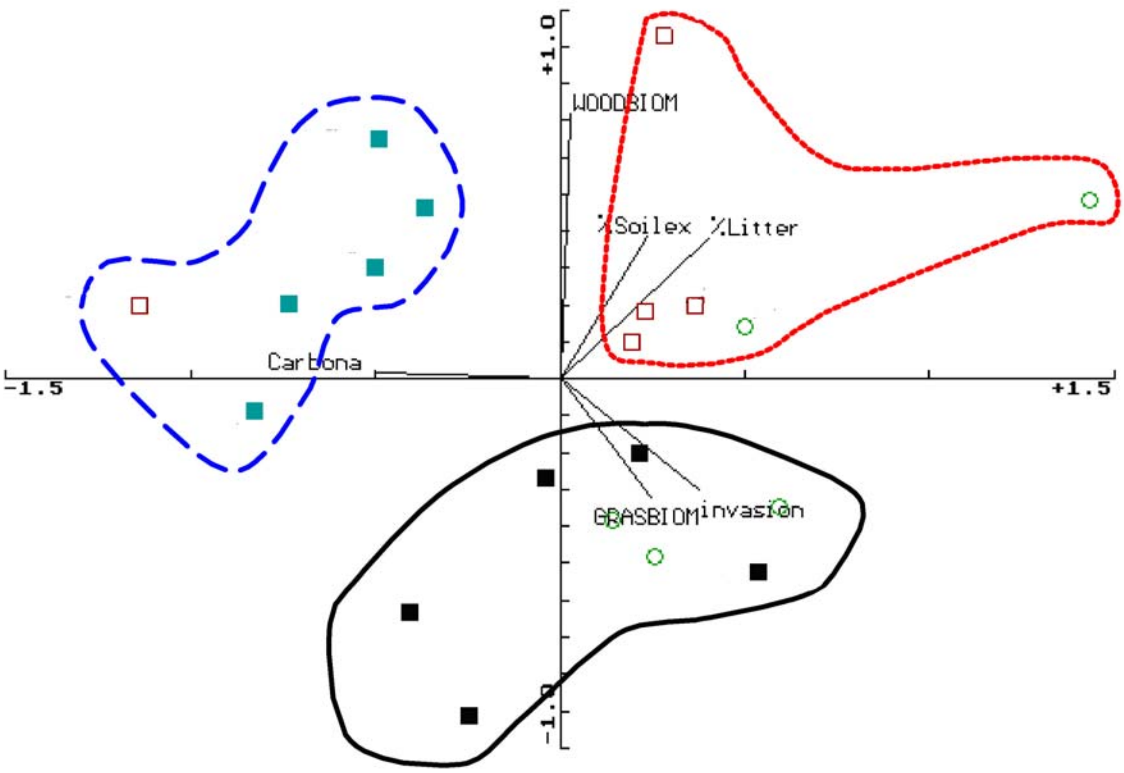


Figure 4.3 Regressions of diameter at breast height (DBH) verses basal diameter (DB) with 95% standard error lines for *Acacia Mearnsii* (A) (Y = 0.833 * (X); r^2= 0.904), *Eucalyptus grandis* (B) (Y = 0.732 * (X) + 6.94 * 10^3; r^2= 0.92) and *Pinus patula* (C) (Y = 0.853 * (X) – 3.2 * 10^{-3}; r^2= 0.993), used to determine biomass of felled individuals in cleared sites.

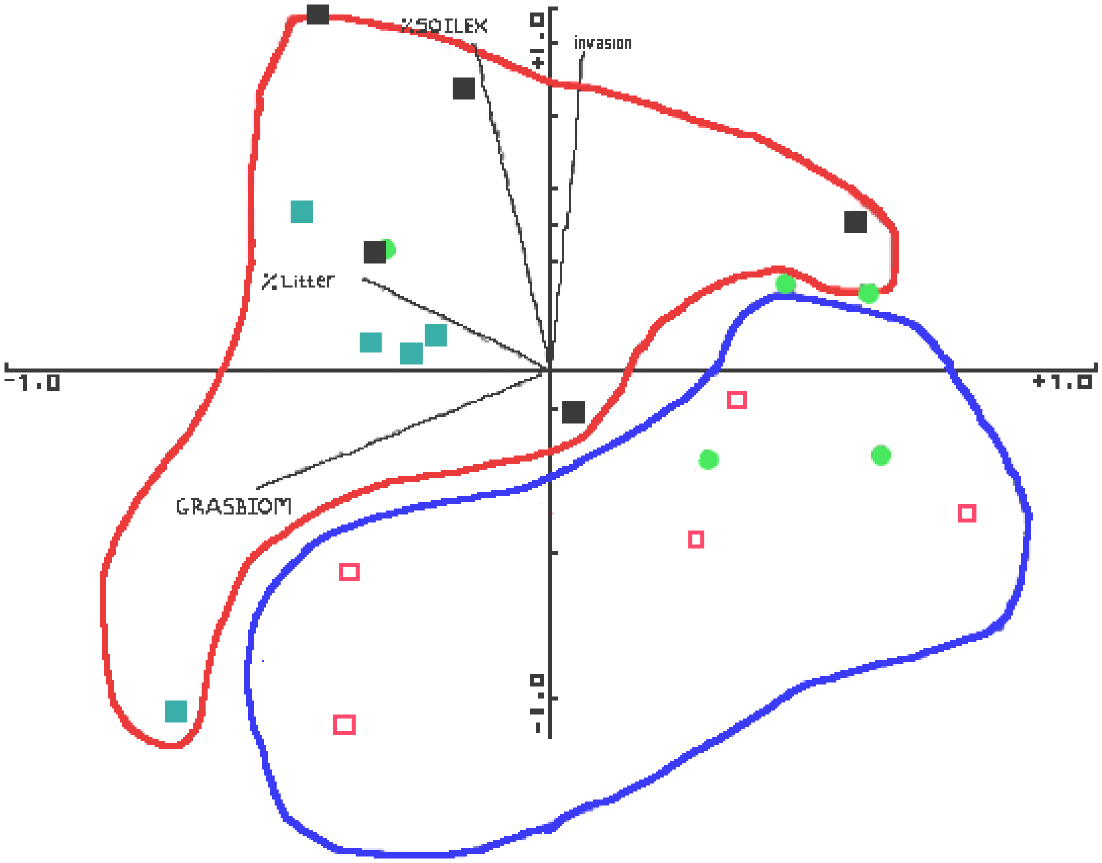
Table 4.2 Probability values for pre- and post-clearing aerial cover from the three way ANOVA's for total exotic vegetation, *E. grandis* and *S. mauritianum*, in relation to invasion (INV), altitude (ALT) and management / clearing treatment (MAN). *d.f.* = 1,32 for all main effects and interaction terms.

Species / Treatment	Pre-clearing exotic aerial cover (%)	Post clearing exotic aerial cover (%)	Pre-clearing *S. mauritianum* aerial cover (%)	Post clearing *S. mauritianum* aerial cover (%)	Pre-clearing *E. grandis* aerial cover (%)	Post clearing *E. grandis* aerial cover (%)
ALT	0.2284	0.3571	**0.0328**	0.0346	0.2853	0.0707
INV	**0.0001**	**0.0001**	0.0516	0.0729	**0.0001**	**0.0001**
MAN	0.2291	**0.0001**	0.2181	**0.0460**	0.2198	**0.0002**
ALT*INV	0.7921	0.5861	0.2457	0.5371	0.3066	0.1011
ALT*MAN	0.0506	0.8492	0.4243	0.3483	0.0833	0.1383
INV*MAN	**0.0247**	**0.0016**	0.5523	0.3906	0.7999	**0.0014**
ALT*INV*MAN	0.1580	0.5930	0.4478	0.8475	0.1667	0.2369



Key:
High Invasion Cleared Sites ■ **Low Invasion Cleared Sites** ■
High Invasion Uncleared Sites ○ **Low Invasion Uncleared Sites** □

Figure 4.4 Centered and standardized PCA representation of low altitude study site relationships in ordinal space based on “biological” transient variables. Three groupings discernable are (A) Blue – Low Invasion Cleared sites, (B) Red – Uncleared sites (mainly Low Invasion), and (C) Black – High Invasion Cleared sites. 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: GRASBIOM – Grass Biomass; invasion – Invasion intensity (%), % Soilex – Percentage soil surface exposed; % Litter – Percentage Litter cover; WOODBIOM – Wood Biomass (Ton); Carbona – Carbon content of A-soil horizon (mg).



Key:

High Invasion Cleared Sites ■ **Low Invasion Cleared Sites** ■

High Invasion Uncleared Sites ○ **Low Invasion Uncleared Sites** □

Figure 4.5 Centered and standardized PCA representation of high altitude site relationships in ordinal space based on "biological" transient variables. Two groupings were identified (A) Red – Cleared plots, and (B) Blue – Uncleared plots. Eigenvalues for 1st and 2nd axes are 0.481 and 0.197 respectively, representing 67.8% of the cumulative variance of species data. KEY: GRASBIOM – Grass Biomass; invasion – Invasion intensity (%), % Soilex – Percentage soil surface exposed; % Litter – Percentage Litter cover; WOODBIOM – Wood Biomass (Ton); Carbona – Carbon content of A-soil horizon (mg).

Table 4.3 Probability values of the three way ANOVA's of the percentage aerial cover for exotic vegetation, *Eucalyptus grandis*, *Solanum mauritianum* and indigenous vegetation at three height classes (> 5 m; 2 - 5 m; < 2 m) for each site in relation to invasion (INV), altitude (ALT) and management / clearing treatment (MAN). *d.f.* = 1,32 for all main effects and interaction terms.

% aerial cover	Species	ALT	INV	MAN	ALT*INV	ALT*MAN	INV*MAN	ALT*INV*MAN
Total	Total	0.1039	0.6472	**0.0099**	0.3208	0.4964	**0.0226**	0.9766
	> 5 m	0.5132	0.5866	**0.0188**	**0.0025**	0.6277	**0.0011**	0.0949
	2 - 5 m	**0.0007**	0.9588	**0.0155**	0.5742	0.2006	0.0595	0.0576
	< 2 m	0.4938	0.3996	0.4476	0.1194	0.1130	0.1693	0.6822
S. mauritianum	Total	**0.0346**	0.0729	**0.0460**	0.5371	0.3483	0.3906	0.8475
	> 5 m	-	-	-	-	-	-	-
	2 - 5 m	0.0587	0.0830	**0.0230**	0.4691	0.3474	0.1974	0.8561
	< 2 m	0.1112	0.1147	0.2797	0.8213	0.5277	0.1894	0.2203

Table 4.3. Continues …….

	Species	ALT	INV	MAN	ALT*INV	ALT*MAN	INV*MAN	ALT*INV*MAN
% aerial cover								
E. grandis	Total	0.0707	**0.0001**	**0.0002**	0.1011	0.1383	**0.0014**	0.2369
	> 5 m	-	-	-	-	-	-	-
	2 - 5 m	-	-	-	-	-	-	-
	< 2 m	-	-	-	-	-	-	-
Indigenous	Total	0.3961	**0.0001**	0.5342	0.6316	0.5378	0.9726	0.6749
	> 5 m	0.2360	**0.0057**	0.6673	0.1078	0.4624	0.1641	0.4109
	2 - 5 m	0.1203	**0.0014**	0.8545	0.3726	0.9076	0.6924	0.1974
	< 2 m	0.1585	0.1179	0.1798	0.2719	0.2630	0.3330	0.4496
Exotic	Total	0.3571	**0.0001**	**0.0001**	0.5861	0.8492	**0.0016**	0.5930
	> 5 m	**0.0238**	**0.0001**	**0.0001**	**0.0076**	0.1252	**0.0009**	0.1539
	2 - 5 m	**0.0066**	**0.0005**	**0.0018**	0.1034	0.1021	0.0567	0.3550
	< 2 m	**0.0264**	**0.0267**	0.0738	0.1142	0.1070	0.1635	0.2897

Stacked bar charts graphically illustrate the vegetation structural changes with clearing in each experimental category for each height class (Figure 4.6.). Cleared sites have a greater "open" category (no aerial cover > 1 m) than do uncleared sites, which would result from the removal of exotic vegetation. However, differences in percentage aerial cover in the "open" categories after clearing is less between low invasion sites where disturbance to the vegetation can be expected to be minimal (Figure 4.6.). A trend of decreasing aerial cover in the tall height class (> 5 m) and increasing aerial cover in the smaller height classes (2 - 5 m & < 2 m) with clearing treatment was also observed (Figure 4.7.)

Table 4.4 *t*-tests and mean ± S.E. for *S. mauritianum* and indigenous vegetation height (m) in both cleared and uncleared plots.

	S. mauritianum		Indigenous Vegetation	
	Cleared	Uncleared	Cleared	Uncleared
Mean ± S.E.	2.816 ± 0.575	4.297 ± 0.553	2.249 ± 0.553	5.265 ± 1.583

	d.f.	*t*	*P*
S. mauritianum Cleared vs. Indigenous Cleared	15	0.728	0.446
S. mauritianum Cleared vs. Indigenous Uncleared	15	1.329	**0.203**
S. mauritianum Uncleared vs. Indigenous Cleared	15	2.483	0.025
S. mauritianum Uncleared vs. Indigenous Uncleared	16	0.598	0.558

Indigenous vegetation aerial cover

There were no significant differences for the indigenous percentage aerial cover with altitude, management and interactions between them (Table 4.3; Appendix 11). Invasion intensity did however, have a significant effect on the total percentage aerial cover for vegetation in the > 5 m, 2 - 5 m and overall height classes (Table 4.3). Figure 4.6 illustrates the difference in overall indigenous aerial cover with invasion intensity in low invasion categories compared to that in high invasion categories. In the smallest height class, < 2 m, there were no significant reductions in the indigenous aerial cover with invasion intensity (Table 4.3).

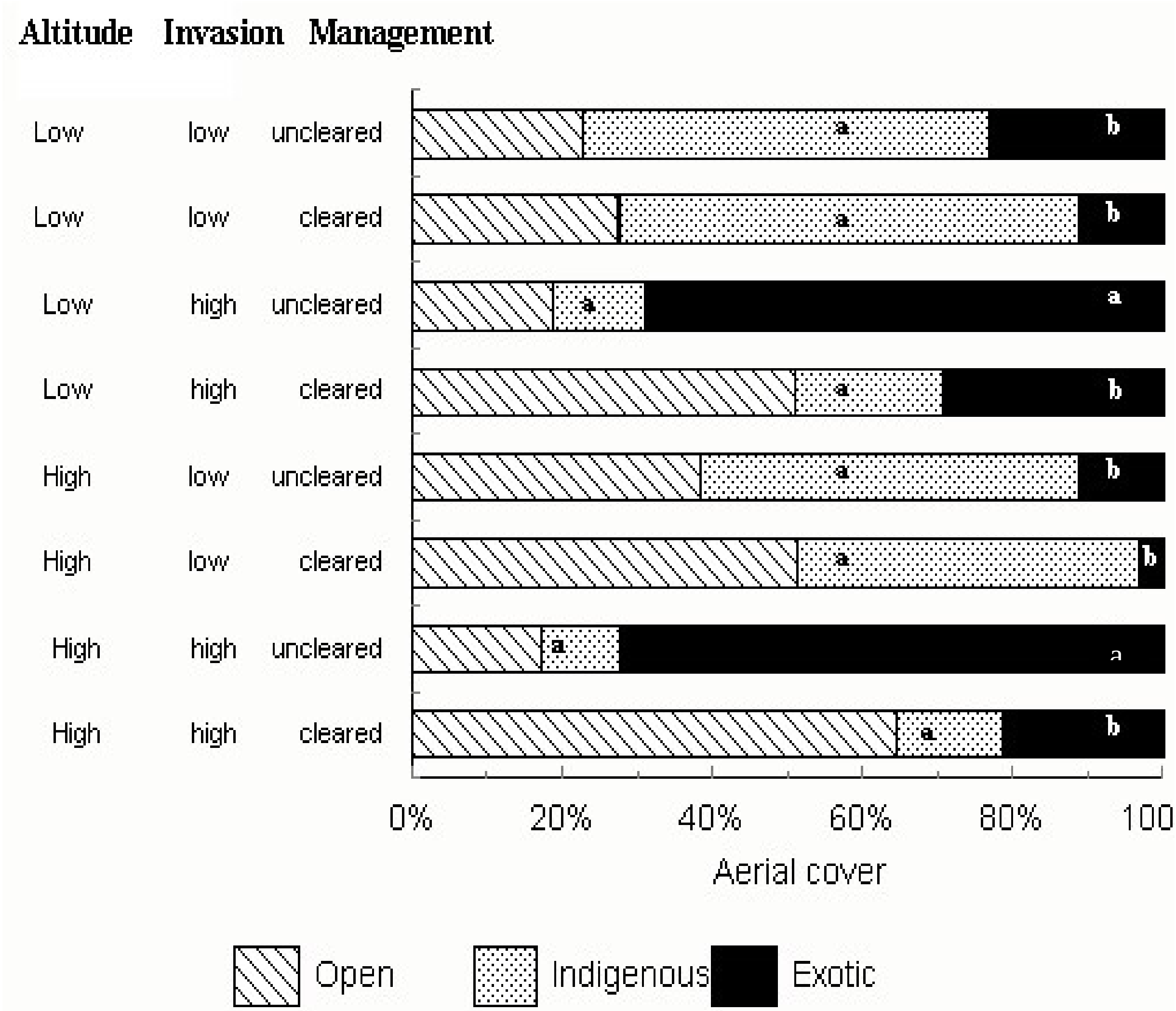


Figure 4.6 Mean aerial cover of indigenous and exotic species for each altitude, invasion intensity and management category showing high exotic species aerial cover in uncleared study sites and extent of vegetation aerial cover loss in cleared study sites. Different letters within categories denote statistical differences between treatments (P<0.05).

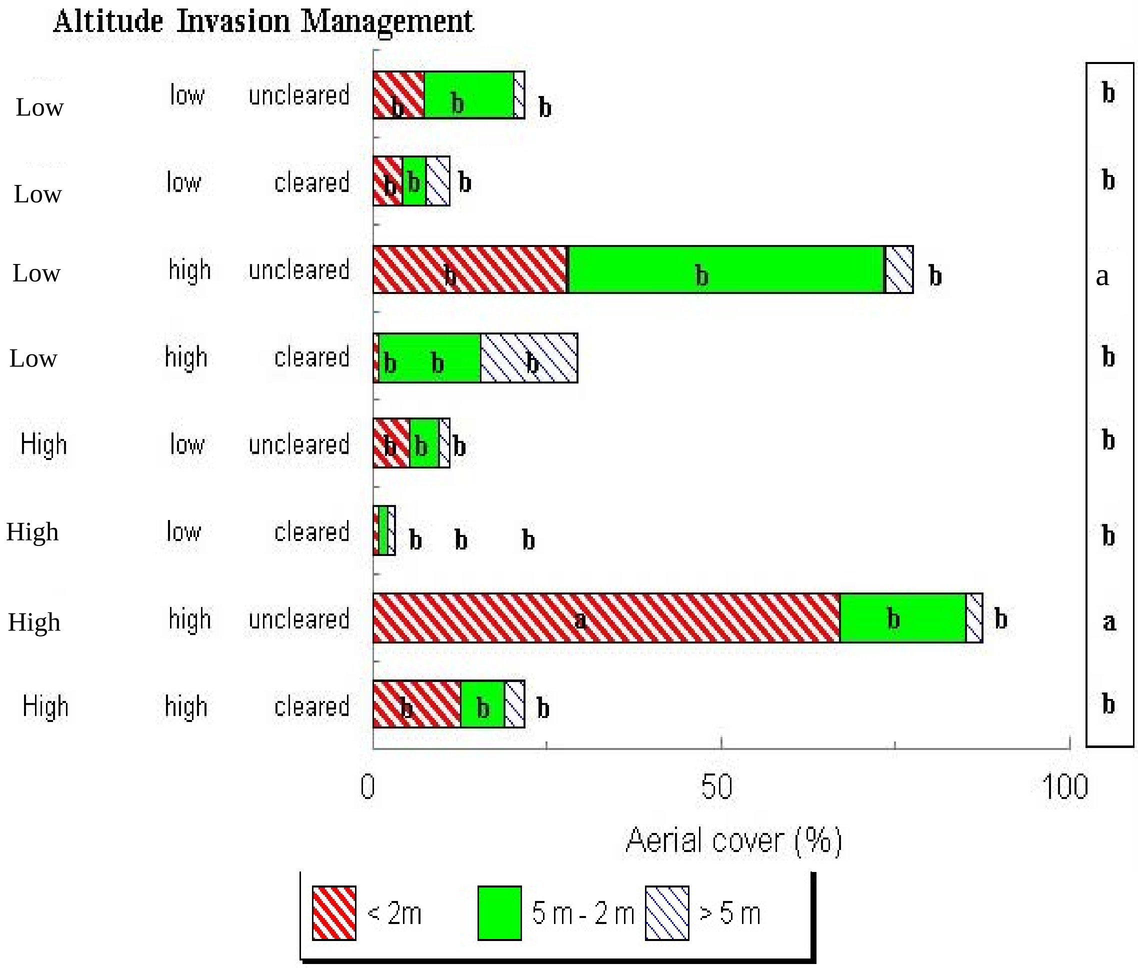


Figure 4.7 Mean percentage aerial cover of exotic species in three observed height classes and total aerial cover for altitude, invasion intensity and management experimental categories. Different letters within categories denote statistical differences between treatments (P<0.05). Statistical differences for total aerial cover are depicted by the boxed letters.

Figure 4.8 shows the differences in vegetation aerial cover for each height class comprising the indigenous vegetation aerial cover. No differences occurred within clearing treatments (MAN) for indigenous aerial cover (Table 4.3, Appendix 11) indicating inconsequential changes to the indigenous vegetation by clearing operations.

Total species vegetation aerial cover

Percentage aerial covers for all species in the total, > 5 m and 2 - 5 m height classes were significantly different for clearing treatments (MAN), thus indicating that clearing operations have changed height class structure (Figure 4.6). For the < 2 m height class however, no significant differences occurred (Table 4.3).

This may be due to no significant difference in the exotic vegetation structure in this height class (Table 4.3), and particularly that of the < 2 m vegetation height class for *S. mauritianum*.

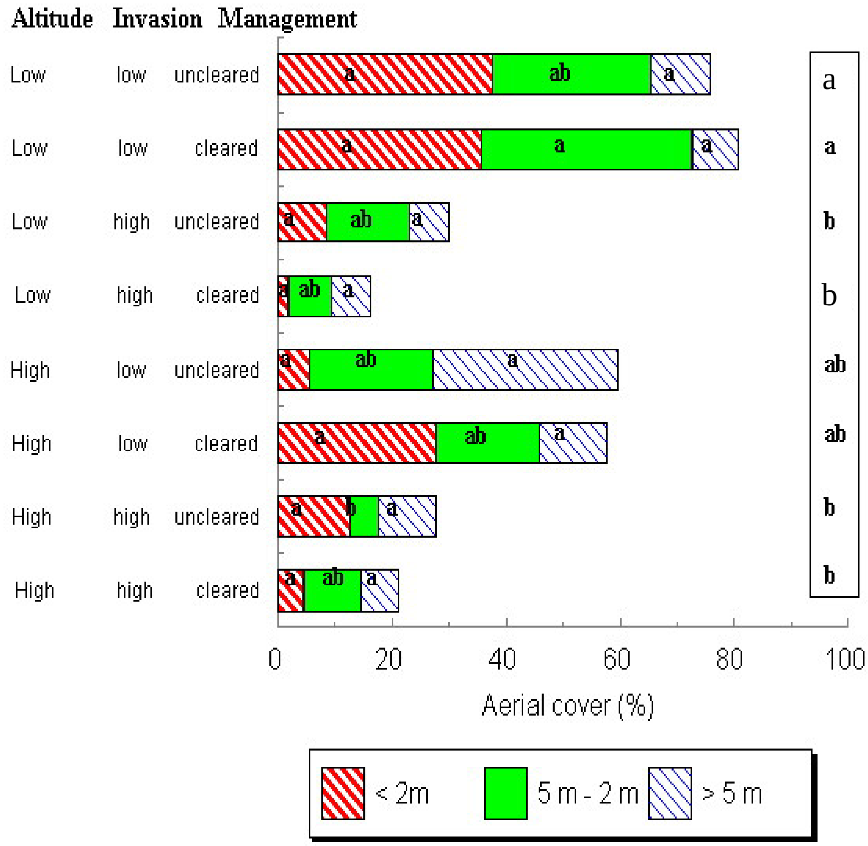


Figure 4.8 Mean percentage aerial cover of indigenous vegetation in three observed height classes for altitude, invasion intensity and management categories. Different letters within categories depict statistical differences. Statistical differences for total aerial cover are depicted by the boxed letters.

4.3.3 Vegetation structure differences with invasion and clearing

Timber volume

As covered in the section on exotic species aerial cover, woody biomass plays a major role in separating cleared from uncleared sites both on the high and low altitudes (Figures 4.4 & 4.5). There was too little data for detailed statistical analyses, but trends indicated that a higher invasive standing timber volume exists at high altitudes in high invasion sites. For low altitude sites, the high invasion intensity category had a marginally greater standing timber volume. The lack of difference was due to a number of *P. patula*

Table 4.5 Standing timber volumes (m^3/ha) (mean ± S.E.) for the species *E. grandis*, *P. patula* and *A. mearnsii* and total timber for each altitude, invasion intensity and management/treatment.

Treatment	High Altitude				Low Altitude			
	High invasion		Low invasion		High invasion		Low invasion	
Timber volume	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Total	0.0128 ± 0.0128	0.0095 ± 5.0136	0.0001 ± 0.0084	0.0148 ± 4.6228	0	0.0002 ± 0.2149	0.0001 ± 0.0004	0.0093 ± 9.2593
A. mearnsii	0	0	0	0	0	0.0001 ± 0.00773	0	0
E. grandis	0.0128 ± 0.0128	0.0021 ± 2.0634	0.0001 ± 0.0084	0.0102 ± 0.0102	0	0.0002 ± 0.2146	0.0001 ± 0.0004	0
P. patula	0	0.0074 ± 7.3471	0	0.0046 ± 4.6238	0	0	0	0.0093 ± 9.2593

individuals in the low invasion sites (Table 4.5). Thus standing timber volume corroborates the invasion intensity differences found for the aerial cover data (invasion intensity) (Table 4.2 & 4.3).

Woody vegetation density

At high invasion intensity, density of woody vegetation in cleared sites was significantly different from the density of woody vegetation in uncleared sites (this was true for both high and low altitude). Invasion resulted in a significant increase in the density of the woody vegetation (Table 4.6). Woody vegetation density was higher in cleared sites although not significantly so for the lower invasion categories (Table 4.6). Only woody vegetation density in the low altitude; low invasion category did not exhibit this trend.

Table 4.6 Woody vegetation density with invasion and clearing of exotic vegetation. Data used from the 1 m^2 plots. Significance using *t*-tests, *d.f.* = 38.

Site description	*t*	*P*
Clearing effects		
HHC vs HHU	4.316	**0.024**
HLC vs HLU	0.047	0.341
LHC vs LHU	4.679	**0.043**
LLC vs LLU	0.082	0.491

Key: HHC - High Altitude, High invasion, Cleared
HHU - High Altitude, High invasion, Uncleared

Vegetation growth forms

Growth form data illustrated that a higher grass and sedge species and herbaceous species number occurred with clearing (Table 4.7). For species falling within the shrub growth forms there was no trend in the number of species comprising the community with clearing or invasion. The number of species in the tree growth form category decreased with clearing except for low invasion sites where the opposite was observed (Table 4.7). High invasion category sites had detrimental effects to the smaller growing growth forms. The reason for this could be attributed to competition for light and the fact that exotic vegetation has a taller growth form than most indigenous species (Table 4.4). This was particularly clear for the high altitude categories where the loss in number of species comprising the different growth forms corresponds with a loss in the percentage aerial cover for the middle height class (5 m < x < 2 m).

Clearing of exotic vegetation had the expected effect of reducing the number of species in the tree growth form and increasing the number of species comprising the grass, herb and shrub growth forms (Table 4.7). Low invasion cleared and uncleared sites did not however, show any major changes to the species number comprising the growth form composition of the vegetation except for an increase in the number of species in the herb growth form category (Table 4.7).

Table 4.7 List of plant growth forms (grass, herbaceous, shrub and tree) found in riverine habitats along the Sabie River. Grass, herbaceous, shrub, tree and total species number per category and proportional composition for each experimental category is given.

Species	Total	High altitude				Low Altitude			
		High Invasion		Low Invasion		High Invasion		Low Invasion	
		Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Grass and Sedge - number of species	19 (11%)	12 (17%)	7 (10%)	14 (16%)	10 (15%)	9 (15%)	4 (7%)	9 (12%)	9 (12%)
Herbaceous - number of species	74 (45%)	37 (52%)	33 (48%)	40 (44%)	29 (45%)	26 (44%)	21 (39%)	27 (36%)	26 (35%)
Shrub - number of species	44 (27%)	16 (23%)	16 (23%)	24 (27%)	18 (28%)	17 (29%)	15 (28%)	22 (29%)	24 (33%)
Tree - number of species	29 (17%)	6 (8%)	13 (19%)	12 (13%)	8 (12%)	7 (12%)	14 (26%)	17 (23%	15 (20%)
Total species number	164	71	69	90	65	59	54	75	74

4.4 Discussion

4.4.1 The effect of invasion on aerial cover

Invasion by exotic species resulted in alteration of vegetation height class distribution, and various components of the vegetation structure. The extent of this alteration was found to be dependent on the invasion intensity and the height class in question.

Aerial cover analysis indicated that the invasion of indigenous communities by exotic vegetation resulted in both the domination of, and an increase in the tallest aerial cover category. This was attributed to the fact that the exotic species (pine, eucalypt and wattle trees) were of larger growth form than that of indigenous species. These exotic species outgrow (in both growth rate and height) those species indigenous to the community and were observed to also have a taller and more full aerial cover. Hence, in the upper canopy, indigenous species have been overtopped by the taller-growing exotic species. Many of these indigenous species are typically light seeking, and may be shaded out if the exotic species upper canopy is extensive (Henderson & Wells 1986).

The increases in aerial cover of the tallest category had an associated negative impact on the mid- and lower aerial cover categories. The effects of this impact however, were variable for the mid-level aerial cover, with no clear trends being observed for the different invasion categories. Further investigation revealed that this was due to domination of the 2 m to 5 m height class by the woody exotic species *Solanum mauritianum*, usually a single stemmed shrub. The lack of differences between high and low invasion categories for *S. mauritianum*, both in density and aerial cover, indicates the extensive invasion of this species within the riverine community. Only in extremely high invasion intensities, where almost 100% aerial cover in the upper aerial cover category occurred (i.e. plantation-like vegetation stands), was a decline in the aerial cover of *S. mauritianum* observed. This species however, still comprised the majority of remaining mid- and lower height class's aerial cover. In the sites with very low invasion, a certain amount of exclusion of *S. mauritianum* was observed. This was not total exclusion however, and a number of isolated individuals were noted during the fieldwork in all sites.

The aerial cover of the smallest height class (< 2 m) revealed an expected decline with invasion and an inverse relationship to the increasing aerial cover in the upper height class. This was attributed to the shading out effect of the upper height classes, which increased with invasion intensity. A decline in the lower aerial cover indicates that either a change in the species composition occurs with shading out of the smaller growth forms, or that there is a decline in the number of young individuals of the taller height class. The growth form data for species in the higher compared to lower invasion categories, illustrates that a general decline in the number of species comprising the shorter growing growth forms occurs with increasing invasion.

The overall aerial cover of communities increased with invasion, which indicated that the exotic vegetation tended to have a more dominant canopy compared to that seen in uninvaded indigenous vegetation or low invasion categories. The vegetation aerial cover supported this when looked at in two separate categories, namely indigenous and exotic vegetation. In highly invaded areas the upper height classes were dominated by exotic species. This illustrated the out-competing of the indigenous vegetation by exotic species, and the overall increase in vegetation aerial cover.

4.4.2 Clearing effects on aerial cover

The following section is split into high and low invasion categories, as various responses occurred with clearing.

Clearing of high invasion sites

The clearing of exotic vegetation from high invasion intensity sites had significant implications for aerial cover. Because exotic vegetation dominates the aerial cover and biomass of the upper height class, its removal resulted in a drastic reduction in both of these variables. The aerial cover of lower height classes was not reduced as much as that of the upper height class. This was attributed to a lack of effective removal of exotic species from the lower height class. This left a number of individuals within the community to either coppice, establish from seed or continue growing. With the time interval between clearing and sampling being in the region of 12 – 24 months, there was adequate time for growth into these height class categories. Hence the observation that the majority of the remaining aerial cover was exotic, being principally composed of *S. mauritianum*, which was not effectively removed by the clearing program.

In high invasion categories, the shortest aerial cover height class (< 2 m), illustrated an expected increase in aerial cover after clearing. This was attributed to the establishment of pioneer species and young individuals (supported by the basal cover data for herbaceous species and species growth form data), and the growth of individuals that were established within the community but had been suppressed by the canopy prior to clearing. There was however, similar to the middle height class (2 – 5 m), a dominance of exotic vegetation in the aerial cover, indicating a re-invasion by exotic species. Once again this is attributed to ineffectual removal of *S. mauritianum*.

Although altitude did not appear to play a major role in the effects of invasion or clearing of exotic vegetation in the high invasion plots, it was noted that higher altitude sites were associated with lower total aerial cover. These differences in aerial cover were attributed to species composition and dominant vegetation type (grassland vs. bushveld or savanna). This was reflected by the growth form data where the proportion of grass and herbaceous species comprising the community increased and the shrub and tree composition decreased.

Clearing of low invasion sites

Low invasion categories exhibited a similar reduction in the upper canopy aerial cover with clearing as seen in high invasion categories. The reduction in overall aerial cover was however, far less after clearing as the dominant vegetation of the tall height category was indigenous. Hence, the reduction in the vegetation biomass of the community and the opening up of the vegetation canopy was less prominent.

The reduced impact on the total vegetation aerial cover was reflected in the other height classes. Only the smallest height class (< 2 m) showed a marginal increase in aerial cover. This was attributed to the reduced disturbance caused by clearing, resulting in an opportunity for new individual establishment, which is reflected in the lower height class. The proportional reduction in exotic composition of the height class in the low invasion cleared sites also indicates a more successful removal of exotic vegetation.

Although there was a minimal disturbance in the low invasion category with clearing, there was an increase in the vegetation density. The number of individuals per unit area increased dramatically after clearing and was attributed to the increase in pioneer species (herbaceous spp.) establishing in disturbed areas caused by clearing. This was supported by the species data where a notable increase in grasses, sedges and herbaceous species occurred with clearing as has been noted by other authors such as Sousa (1984). As a consequence, vegetation growth form composition in the low invasion categories appears to be more evenly spread across the growth form classes and not biased towards either the lower or higher growth forms as was observed in the high invasion sites.

Implications of the reduced re-invasion of low invasion intensity sites are that clearing of areas with low invasion causes less disturbance and modification to the vegetation structure. This in turn results in less re-invasion or re-establishment of exotic species into the community. Hence maintenance of the invasion intensity in the low invasion category is a more successful and sustainable approach to weed control. From the observations made for high invasion sites, a high frequency of follow up operations will be required to prevent re-invasion by exotic species. This will however, reduce with time once the indigenous vegetation has once again become dominant and a similar effect as was seen for low invasion sites can be followed.

4.4.3 Exotic species eradication by clearing

The success of clearing exotic vegetation was raised as a concern by the aerial cover data, as there were unexplained increases in exotic vegetation cover in mid- and lower height classes. The aerial cover of indigenous vegetation compared to exotic vegetation, both before and after clearing, illustrated that exotic vegetation still contributed largely to the aerial cover in the mid- and lower height classes.

The removal of the taller exotic vegetation (species such as eucalypt, pine and wattle) appeared effective, with almost 100% eradication of these species. This is attributed to the easy location and minimal coppicing in larger individuals. The removal of the smaller exotic growth forms, including species such as *Chromolaena odorata* and *S. mauritianum*, was not as successful. These species are far more difficult to locate in dense vegetation and also have extensive regenerative capabilities, which are facilitated by the disturbance caused by clearing (Witkowski & Wilson 2001). This can result in extensive re-establishment, as was observed in the lower height categories after clearing. Field observations also showed that a large number of the coppicing *S. mauritianum* individuals were not properly cut and treated with herbicide, which would have resulted in increased success in removal of this species.

A consequence of this ineffectual clearing/eradication of exotic vegetation is that an extensive follow-up clearing programme will have to be implemented, once again disturbing the plant community. In addition, the previously cleared and regenerating individuals will be smaller in size and more difficult to locate in the dense vegetation of the study area. This means that the follow up clearing programme may not be as effective as originally anticipated.

4.4.4 *S. mauritianum* clearing

The successful clearing of *S. mauritianum* appears not only to be linked to the effective location of individuals, but also the correct application of the method of clearing. Sites cleared of exotic vegetation in the study area were treated with a herbicidal mix of 50% Garlon and 50% diesel. With the high density of vegetation in some sites it is difficult to apply this method, hence the unsuccessful eradication of *S. mauritianum* individuals (this is further discussed in Chapter 5).

Coppicing individuals of *S. mauritianum* have shown an exceptionally fast growth rate, which is seldom surpassed by indigenous vegetation (MacDonald & Jarman 1985). This has implications for post-clearing vegetation, where *S. mauritianum* can become the dominant vegetation cover. This is a possibility as the mean height of the *S. mauritianum* vegetation can be taller than that of the indigenous vegetation in the riverine communities studied. This may once again lead to shading out of indigenous vegetation in high invasion categories and result in the total domination of the vegetation biomass, composition and structure by *S. mauritianum*, as was observed in the Tzaneen reserve (Dean 1985).

Should the re-establishment of *S. mauritianum* not totally dominate the upper canopy of the vegetation community, it may still detrimentally change the structure of the vegetation. This would result in the modification of the ground cover by changing the foliage profile, and increasing the leaf area index in this (*S. mauritianum*) height class (Versfeld & van Wilgen 1991). Thus the effect of this species remaining in the vegetation/community after clearing appears to be potentially disastrous.

4.4.5 Vegetation structure variables affected by clearing

Biomass

The clearing of exotic vegetation also had impacts on vegetation structural variables such as the vegetation biomass. These measures are typically useful for silvicultural activities. They may be of value in determining the quantity of wood material obtainable out of an invaded community. Biomass is closely linked to the invasion intensity and thus the exotic aerial cover. The exotic vegetation being of generally large growth form explained this. The calculation of biomass is however, more difficult to measure than measuring aerial cover. There are also not equations for all the exotic plant species within the community and the existing equations are for wood biomass and not total biomass as would be of interest from an ecological perspective. For the purpose of defining impact to the community it is proposed that future measurements use only invasion intensity calculated from aerial cover.

Biomass does however have the implication of adding litter and other combustibles to the community. Should a fire pass through a community with an elevated biomass of exotic vegetation the consequences may be disastrous to indigenous vegetation structure and function. This however, was beyond the scope of this study and can only be reflected upon.

Vegetation density

Vegetation density, another variable linked to aerial cover, also illustrated a relationship with invasion intensity. In this case, the density of vegetation was inversely related to the invasion intensity but only in uncleared plots. This was due to the shading out of many individuals by the taller growing exotic vegetation. In cleared plots the reverse was noted, the higher the invasion, the greater the density. This was attributed to the opening up of the canopy, which resulted in vegetation establishment. In lower invasion intensity sites clearing did not allow for the same degree of establishment as there were less (smaller) areas of disturbance and thus less opportunity for vegetation establishment.

Vegetation Growth Form

The alteration of the proportion of species in each growth form with clearing and invasion shows the extent to which vegetation structural components may be altered. The decline in species comprising the herbaceous and grass growth forms found within the community with invasion supports the shading out of species with increased canopy cover of exotic species. The disturbance caused by clearing the community of exotics is also reflected in growth form changes within the community as many of the pioneer species that first establish after disturbance are of smaller growth form.

The proportion of species comprising the growth form of the community is, however, subject to biome type. This was seen in the high altitude sites where more grass and less tree species occurred than in the low altitude sites. If this is related to the biomes in which these two categories are located, it is found that the high altitude category, although in riverine bushveld, is located within the grassland biome. The low altitude category is within the savanna biome, a woodier biome than that of the grassland biome.

4.5 Conclusion

Invasion of the riverine community by exotic vegetation creates a disturbance and alters the vegetation structure. This was less pronounced in the low invasion categories, but became more extensive in high invasion categories. The consequences of exotic invasion are closely linked to the exotic species (and their growth form) invading the community. Some of the species observed during sampling were of tall growth form and dominated the upper canopy, which in high invasion categories resulted in shading out of smaller growth forms and alteration to the under canopy.

Clearing of invasive vegetation resulted in a decrease in the total vegetation aerial cover and a disturbance to the vegetation height classes. This disturbance was proportional to the invasion intensity of the plots prior to clearing. The upper vegetation height category was the most impacted upon. The reason for this was the large growth form of the exotic vegetation. Clearing of exotics had different consequences for vegetation structure depending on the invasion intensity. In high invasion categories, where the vegetation structure had already been altered by the presence of exotic vegetation, the vegetation structure was drastically altered. This was a result of the majority of the vegetation being composed of exotic species, thus their removal significantly reduced the overall biomass and aerial cover. In a sense, the high invasion sites cleared of exotic vegetation were almost re-set in terms of successional sequence and the majority of colonising vegetation was observed to be primary successional species.

Low invasion plots cleared of exotic vegetation illustrated little modification to the vegetation structure. This was due to the localized nature of the disturbance and the availability of indigenous species to utilize the gaps and resources exposed by the exotic species removal. Clearing at this invasion intensity is preferred, as the disturbance to the community was minimal and allowed for indigenous vegetation recovery.

Success in clearing (eradication) of exotic species had mixed results across invasion categories. Clearing of high invasion sites appears to have been successful in the short term. In low invasion categories however, due to the remaining indigenous vegetation, a number of exotic individuals were missed during clearing. In both high and low invasion categories, there were problems with the eradication of species such as *S. mauritianum*, which regenerated at a fast rate and was not eradicated by clearing applications. Investigations indicate that the methods applied would be more successful if more stringently applied both in terms of physical cutting and herbicide application. This is important as areas cleared of exotics have been extensively disturbed and are open to re-colonization by exotic species.