

Topographic controls on the invasion of *Pteronia incana* (Blue bush) onto hillslopes in Ngqushwa (formerly Peddie) district, Eastern Cape, South Africa

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Abstract

The role of topographic factors in the invasion of hillslopes by *Pteronia incana*, an unpalatable shrub, was investigated. The study combined field observations with image analysis based on high-resolution infrared imagery. A Digital Elevation Model (DEM) of 20 m spatial resolution was used to derive terrain parameters. The Topographic Wetness Index (WI), a component of the TOPMODEL, was derived from the DEM and its relationship with the spatial distribution of *P. incana* was explored. The absence/presence of *P. incana* was noted to be strongly influenced by slope angle and aspect. The probability for *P. incana* occurrence increased with slope steepness and southerly slope orientation. Abandoned and grazing lands were identified as the main invasion hotspots on hillslopes. The combined influence of slope gradient and aspect, and land use was noted to have promoted the invasion. This is borne out by the concentration of the invasion on abandoned steep slopes with a southerly orientation. The WI confirmed the bearing local topographic variations have on *P. incana* spatial distribution such that, *P. incana* was associated with the low WI values of convexities. The coupling between local topography and soil surface crusting underpins soil moisture variability. This in turn determines the competition between the patchy *P. incana* and grass species and the eventual replacement of the latter by the former. Restoration efforts of the invaded lands should focus on trapping of sediment and litter, and moisture retention on the inter-patch bare areas.

1. Introduction

Events and actions that render a given environment susceptible to invasion by non-native vegetation species have been examined by different scholars (e.g. Lonsdale, 1999; Davis et al., 2000; Buckland et al., 2001). Despite the research effort, the factors that influence the invasibility of environments and the invasiveness of certain plant species have proven elusive for ecologists (Davis and Pelsor, 2001). As to why some biomes and regions seem more susceptible to invasions is also a long way from being clarified (Lavorel et al., 1999; Lonsdale, 1999; Stohlgren et al., 1999). Defined as the degree to which a community is susceptible to the establishment of external species (Lavorel et al., 1999), invasibility is the outcome of several factors. These range from changes in disturbance regimes (Crawley, 1987; Alpert et al., 2000; Prieur-Richard et al., 2000), climatic fluctuations in a given region (Lonsdale, 1999; Sax and Brown, 2000), fluctuating resources (Davis et al., 2000; Davis and Pelsor, 2001; Kolb et al., 2002) to species diversity (Palmer and Maurer, 1997; Lavorel, 1999; Lavorel et al., 1999; Prieur-Richard and Lavorel, 2000). Invasiveness, which refers to the capacity of a species to successfully invade communities where it was previously absent (Prieur-Richard and Lavorel, 2000), is also influenced by various factors. These include: the traits of the invader, for example, low palatability or unpalatability (Buckland et al., 2001), propagule pressure (Davis and Pelsor, 2001), tolerances (Rejmánek, 1996; Sax and Brown, 2000), predation, mutualism and competition (D'Antonio et al., 1999; Richardson et al., 2000). However, as pointed out by Prieur-Richard and Lavorel (2000), invasibility is a generic characteristic that does not discriminate a priori between different types of potential invaders. Besides, the difficulty of identifying the functional characteristics of invading species has been insinuated by Crawley et al. (1996), Williamson and Fitter (1996) and Williamson (1996). This paper, however, will dwell on the characteristics of environments susceptible to invasion, rather than those of the individual invasive species themselves. A major shortcoming that can be gathered from the invasion ecology investigations cited above is the total disregard for the co-parameters of terrain and their implications for soil properties, geomorphic processes and, ultimately, the invasibility of a given environment. The lack of joint investigations between geomorphologists and ecologists engenders such critical omissions. There is a need to gain insights into the implications of geomorphic processes for invasibility. This would then provide an in-depth understanding of the underpinnings of invasibility and the interaction between invader vegetation species and geomorphic processes. The invasion of the communal lands of Ngqushwa (formerly Peddie) district, Eastern Cape, South Africa by *Pteronia incana* (Blue bush), is an environmental predicament that has been highlighted by Kakembo (2004). The invader is an unpalatable dwarf shrub indigenous to the Nama-semiarid karoo region of South Africa. The shrub is characterised by wide inter-shrub spaces and closely associated with severe erosion forms. A range of factors influencing the invasion is examined by Kakembo (2004). Amongst other factors, terrain parameters were identified as the main underpinnings of the presence or absence of *P. incana*. The coupling of topographic variables and land disturbance, particularly land abandonment, to promote the invasion is examined in this paper.

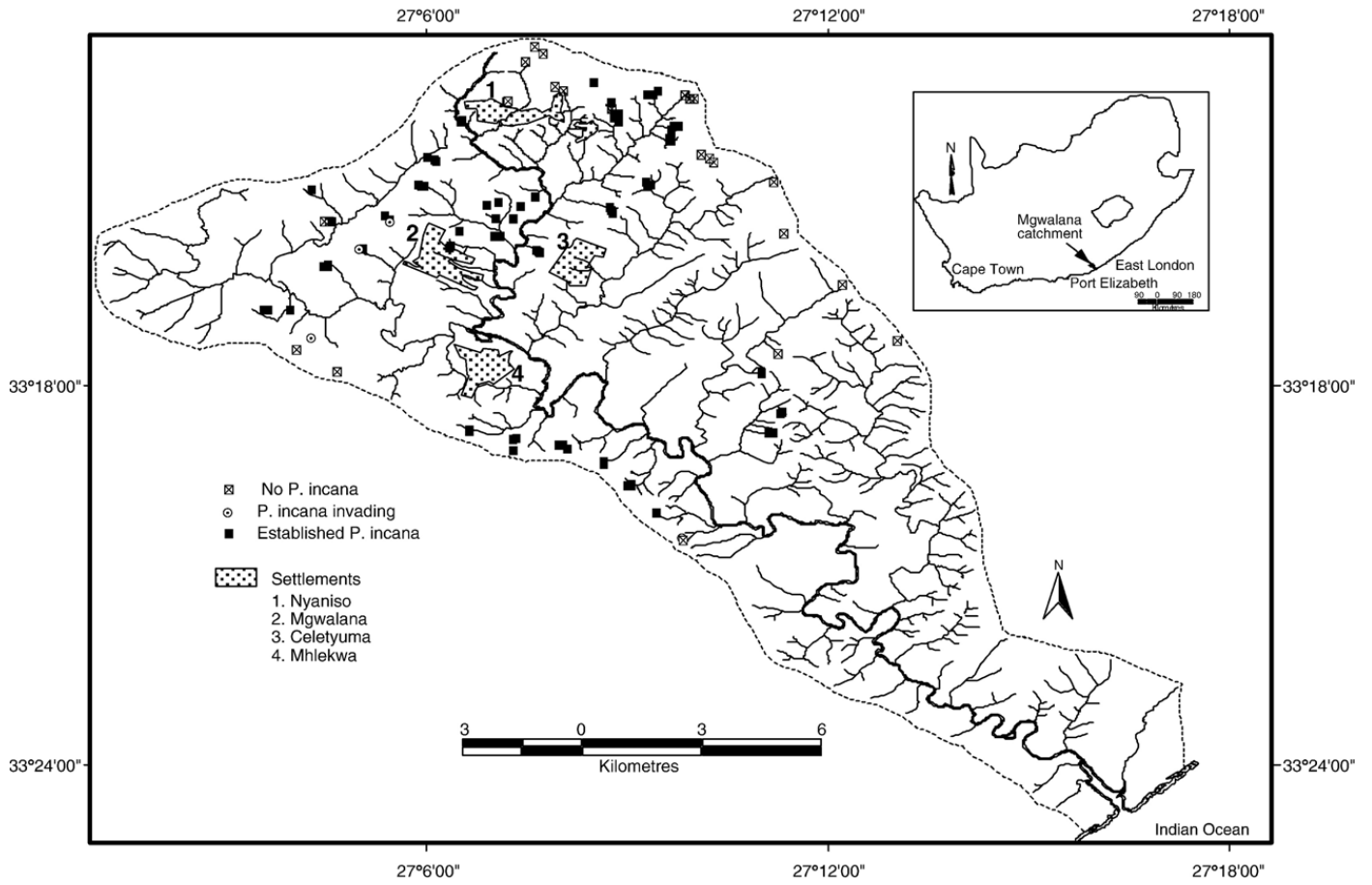


Fig. 1. Study area: a catchment survey to assess the extent of *P. incana* invasion.

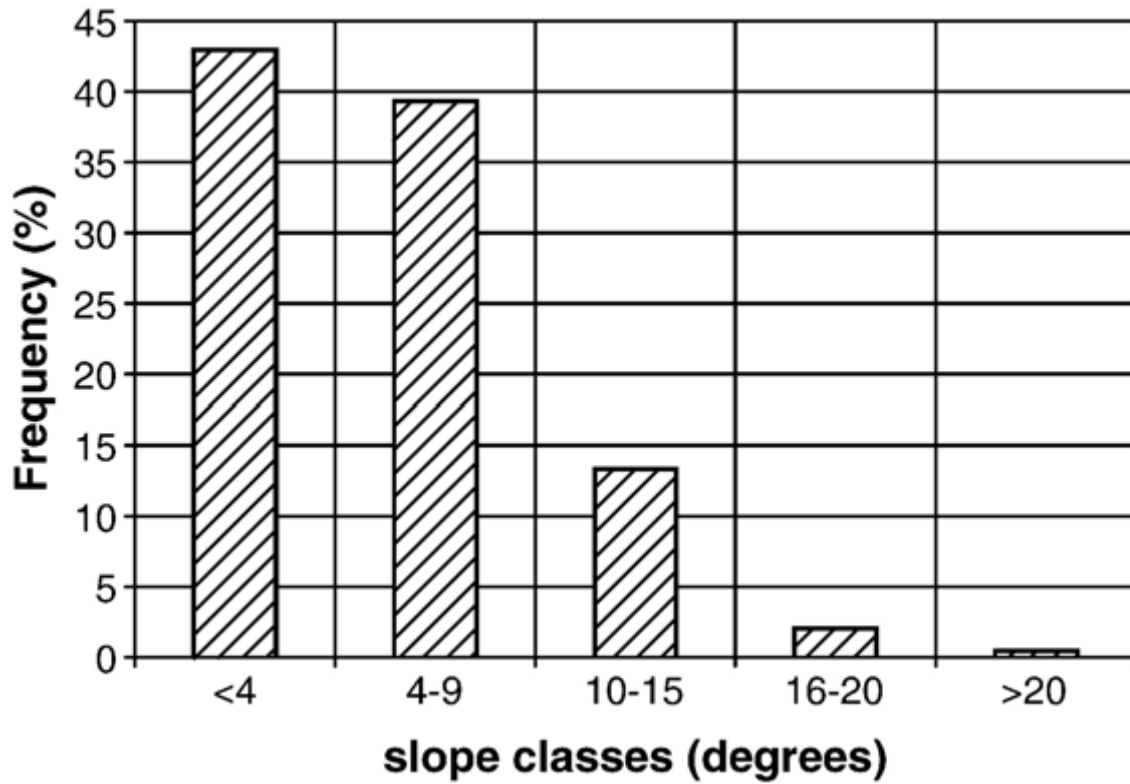


Fig. 2. Slope frequency histogram of the study area generated from the slope surface. (Slope surface calculated from a 20 m resolution DEM).

2. Study area

The upper part of Mgwalana, one of the catchments where the invasion is pronounced was chosen for the study. Communal rangelands and villages, which occupy the upper part of the catchment (Fig. 1), constitute the endemic zone for the invasion. The topography of the area is depicted by a slope frequency histogram generated from the slope surface of the catchment using a 20 m DEM (Fig. 2). Whereas slopes below 9° constitute over 70% of the catchment, most slopes facing the channels of the Mgwalana river and its tributaries characteristically rise steeply (10° and above) before they even out into gentle and extensive interfluvies. The soils of the study area are a product of the Ecca group rocks of the Karoo supergroup. Swelling hydrous mica clays with a gross structure similar to that of montmorillonite were identified from analyses of soil samples as the dominant clay mineral compounds (see Table 1). It can also be gathered from the samples that the local soils are highly sodic, as evidenced by the high sodium adsorption ratio. Such characteristics have serious implications for soil surface conditions, particularly crusting due to age-long hardening after disturbance mainly in the form of land abandonment (Fig. 3). The area has experienced a volatile land use history, characterised by widespread abandonment of cultivated land (Fig. 4), much of which has been colonised by the invader shrub. As can be noted from the figure, the abandonment is concentrated in the upper part of the catchment comprising communal villages. Grazing land has also been targeted significantly by *P. incana* invasion, leading to the loss of grazing land and increased pressure on the remaining grass species whose biomass is often reduced to ground level by browsers. The area has a mean annual rainfall of 488 mm with a bimodal distribution (October–November, March–April) and a coefficient of variation of 32%. Long-term rainfall fluctuations in the area are illustrated (Fig. 5), depicting the annual deviation of rainfall from the long-term mean, analysed using a 5-year running average. Distinct drought periods identified, for instance between the mid 1960s and early 1970s, which coincided with widespread land abandonment, may have played a role in suppressing the competitive dominance of perennial grasses and promoted invasion.



Fig. 3. Soil crusting on *P. incana* interpatch bare areas.

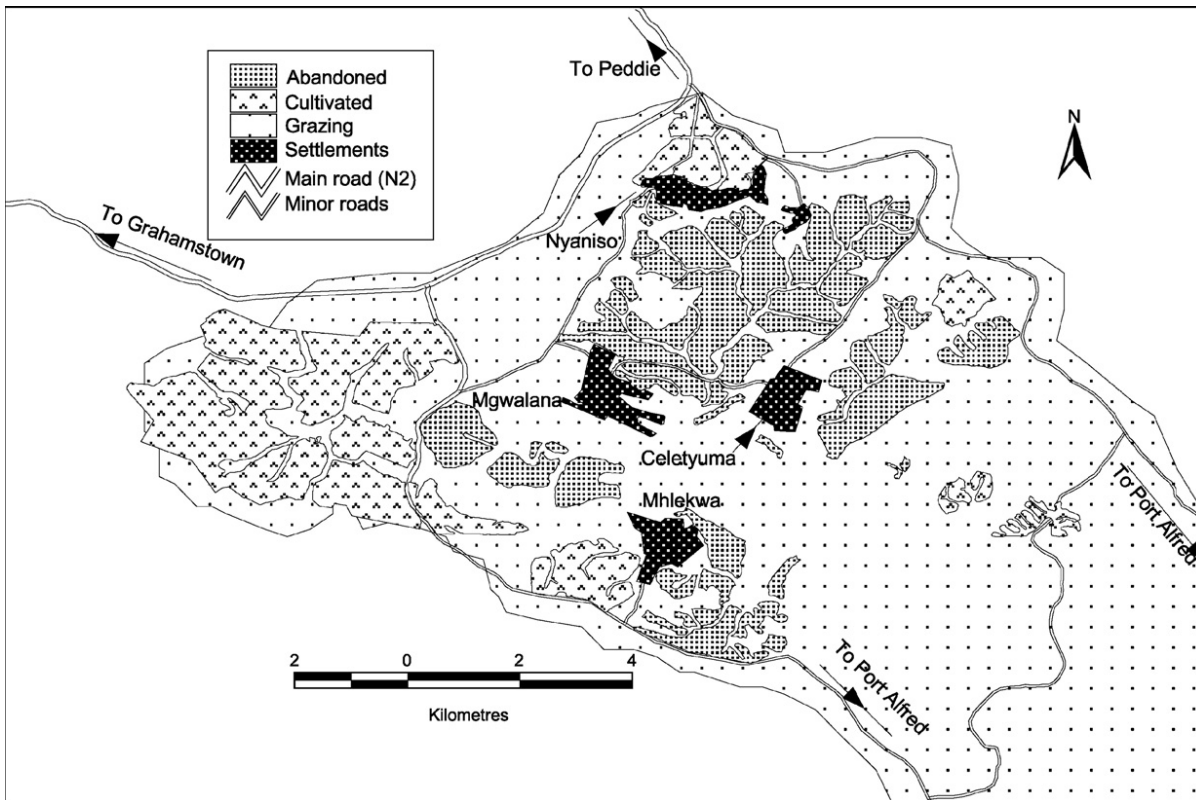


Fig. 4. Concentration of land abandonment in the upper part of the catchment comprising communal lands (mapping based on 1988 orthophoto maps).

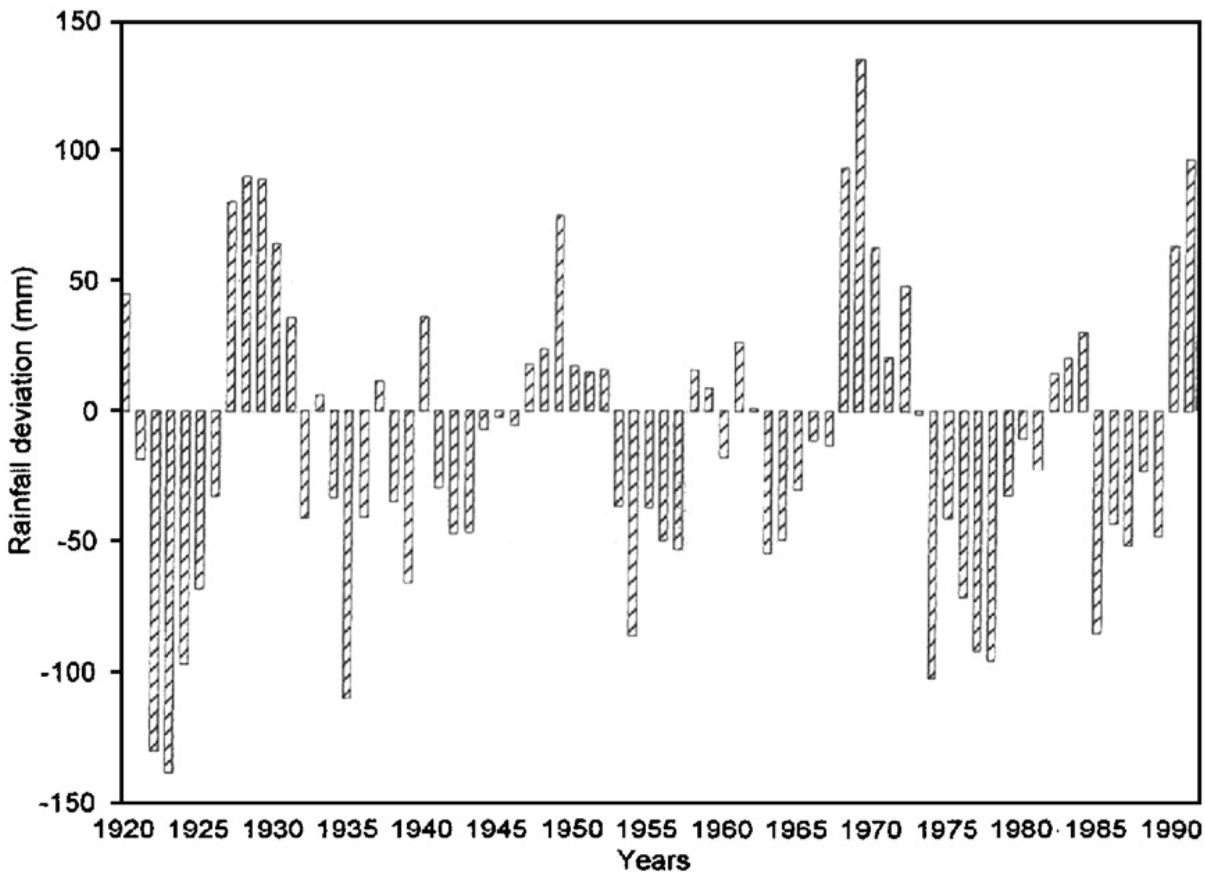


Fig. 5. Annual deviation of rainfall from the long-term mean (5-year running mean).

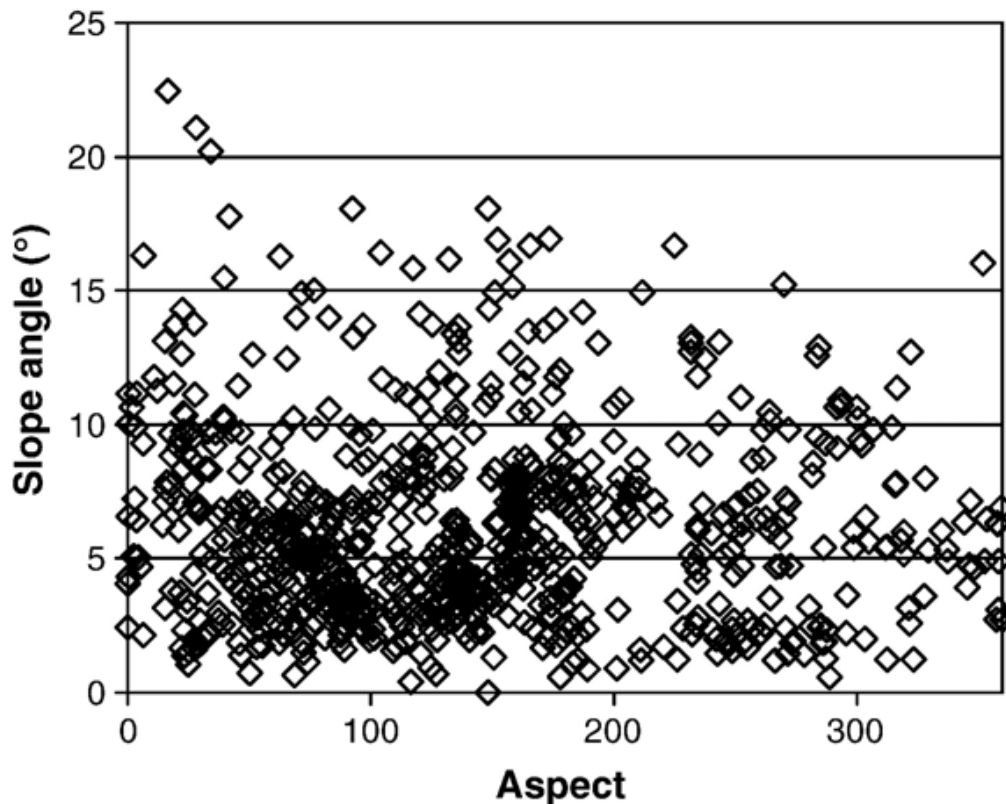


Fig. 6. Non-collinearity between slope angle and aspect as independent variables.

3. Methods

3.1. High resolution imagery, aerial photos and orthophoto maps Ten high resolution (1×1 m²) near infra-red aerial photographs depicting different degrees of *P. incana* invasion were captured in March 2001 using a Kodak DCS420 digital camera. The images were converted into three digital colour band images; the infrared, red and green using Idrisi Kilimanjaro GIS. Based on a priori field surveys, the images were classified using a supervised procedure and *P. incana* boolean images were created (Kakembo, 2004). Abandoned cultivated lands, many of which are truncated by severe rills and gullies, and grazing land were identified from aerial photographs and orthophoto maps of 1975 and 1988, respectively. Using the orthophoto maps as a backdrop, these details were captured onto a GIS in PC ARC/INFO format and the relevant thematic maps were produced in ArcView.

3.2 (Fig. 4). In order to highlight and quantify the link between *P. incana* and past and present land use practices, shapefiles of abandoned and grazing lands were exported to Idrisi GIS from ArcView in vector format. They were rasterised and overlaid on the 2001 images of *P. incana* distribution. It was thus possible to determine from each image the area of abandoned and grazing land invaded by *P. incana*. The extent of invaded abandoned and grazing lands within designated slope angle and aspect categories was established by overlaying the rasterised surfaces with boolean images of the slope categories.

Table 2
Classification table for absence and presence of *P. incana*

		Predicted		% Correct
		0	1	
Observed	0	291	100	74.4
	1	136	255	65.2
Overall percentage correct predictions				69.8

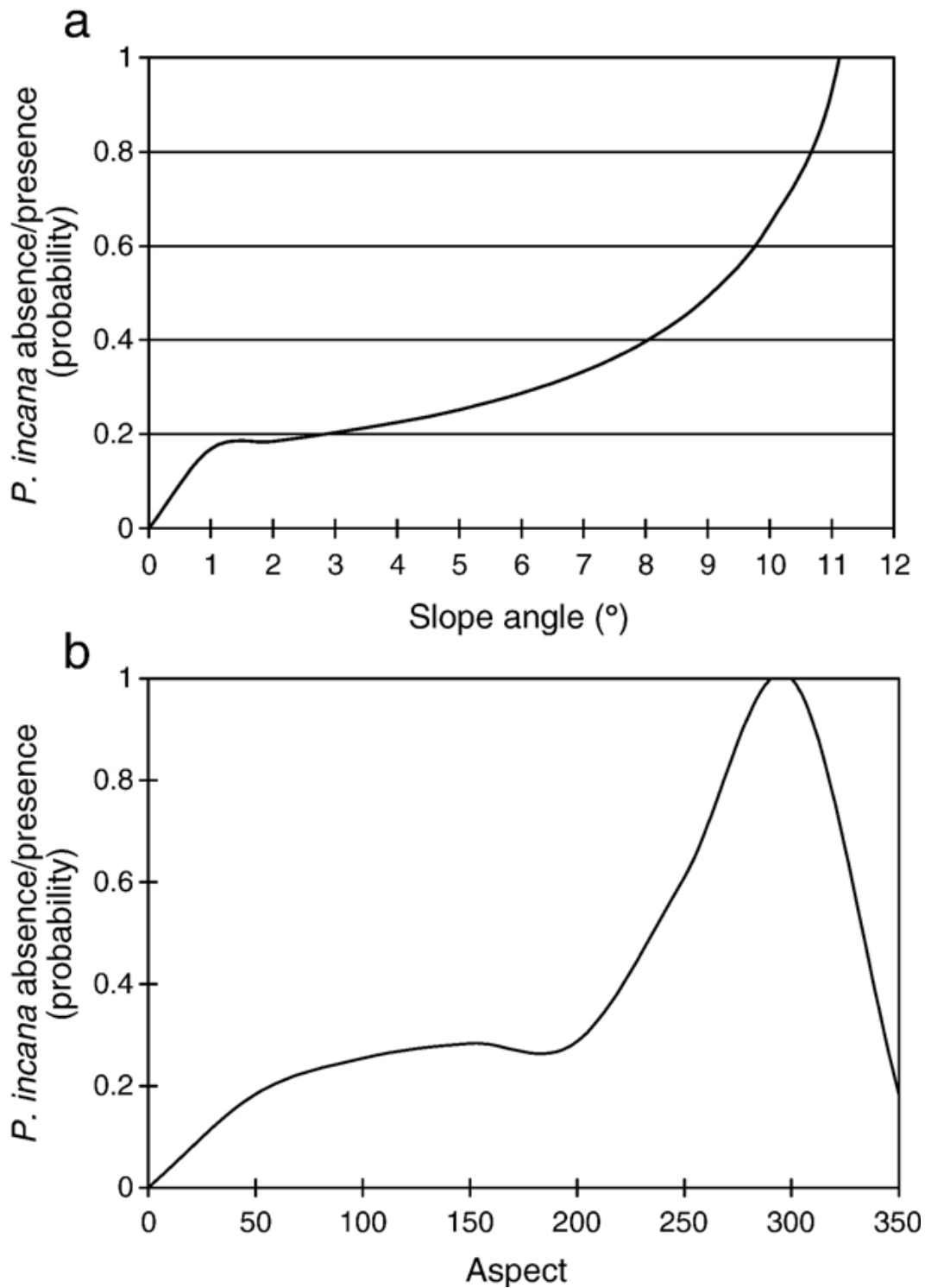


Fig. 7. (a, b) Logistic regression curves for slope and aspect.

3.2. Digital Elevation Model (DEM)

An intermediate resolution DEM of 20 m was used for the derivation of slope and aspect topographic parameters. DEM resolution significantly affects the computed topographic parameters and related hydrological models (Zhang and Montgomery, 1994). The representation accuracy decreases moderately at an intermediate resolution, but sharply at coarse resolutions. This observation is supported by Hickey (2000) who states that, with typically low

resolution of DEMs, for instance the 30 m for 7.5 min USGS DEMs, micro-features critical for hydrological modelling are lost, resulting in significant error. As DEM resolution and accuracy increase, the landscape will be more accurately represented and topographically driven hydrologic models will approach actual values. If a DEM has a coarser resolution than the image used, it is necessary to resample the DEM to match the resolution of the image, especially in places of very steep relief. In areas where slopes are not very steep, for instance less than 25°, the DEM resolution can stay lower than 2–3 times the image resolution (Geosystems, 2003). Gentle slopes constitute 70% of the study area (Fig. 2). As recommended by Geosystems (2003), a DEM lower than 3 times the image resolution would suffice for slope and aspect calculation. The quality of the 20 m DEM used in this study was compared with field slope angle and aspect data collected during field surveys using an Abney level and a Global Positioning System (GPS), respectively. The data were collected from 50 sampling points at intervals of 1 km on slope elements adjacent to the roads and tracks that traverse the catchment. When matched with the same geographic locations on the DEM derived surfaces, slope angle and aspect at all 50 sampling locations were correctly predicted.

Geographic windows of the same resolution as the DSC420 derived classified images were created from the DEM to enable overlay with *P. incana* distribution images. Boolean images representing the cardinal points of slope direction and desired categories of slope angle were then prepared from the DEM windows. Direct overlays with *P. incana* images were made possible by digitising and rasterising outlines of the relevant slope and aspect categories, using parameters copied from the *P. incana* images. The area (m²) of the overlap zone of the *P. incana*, and the aspect and slope masks was divided by the relevant image mask to obtain *P. incana* density. The number of pixels with *P. incana* was used as a surrogate for its concentration. Given that the respective images represent varying *P. incana* invasion scenarios in relation to slope angle and aspect, *P. incana* density was calculated for all the images.

3.3. Wetness index derivation

The Wetness Index (WI), which is one of the major topographically driven derivations strongly related to spatial soil moisture variations (Beven, 1997; Quinn et al., 1995; Asserup and Eklöf, 2000), was calculated for the respective DEM windows. The index demonstrates the soil moisture dependencies for shrubs and grass species, and their implications for competition and replacement of the latter by the former. The WI was derived using the formula:

$$WI = \ln(A_s / \tan\beta) \quad (1)$$

where A_s is the specific catchment area, being the local upslope contributing area to a specific point in the catchment, and β is the local slope. Soil moisture variations as depicted by the WI were corroborated by way of extensive soil moisture surveys. 38 adjacent grass patches and *P. incana* clusters that spanned the study area were identified from the images. The Normalized Difference Vegetation Index (NDVI) calculated from the red and near infrared bands provided a distinct spectral separation between grass and *P. incana* cover. Soil moisture data at the sites were collected in the field up to the depth of 7 cm using a calibrated Delta-T Theta Probe ML2 moisture meter. Soil moisture conditions for the sites were determined by averaging moisture readings taken at each site on eight field visits conducted during the month of March 2002, which was relatively dry. Multiple visits were made for purposes of getting a consistent picture of the moisture variability.

3.4. *P. incana* presence/absence

In order to establish a generic relationship between the occurrence of *P. incana* and slope angle and direction, 80 sampling points representing the presence or absence of *P. incana* in equal proportions were digitised from each of the 10 classified images. The dichotomous sampling points were converted to raster image masks by means of the POINTRAS module in Idrisi. Using the image masks as the feature definition files, values files representing the *P. incana* dichotomy were extracted from slope and aspect boolean images described earlier. 18 sampling points out of the total of 800 extracted were identified as overlapping and were thus discarded. The values files were readily exported to Excel spreadsheets where the data were assembled and *P. incana* absence and presence were coded as 0 and 1, respectively.

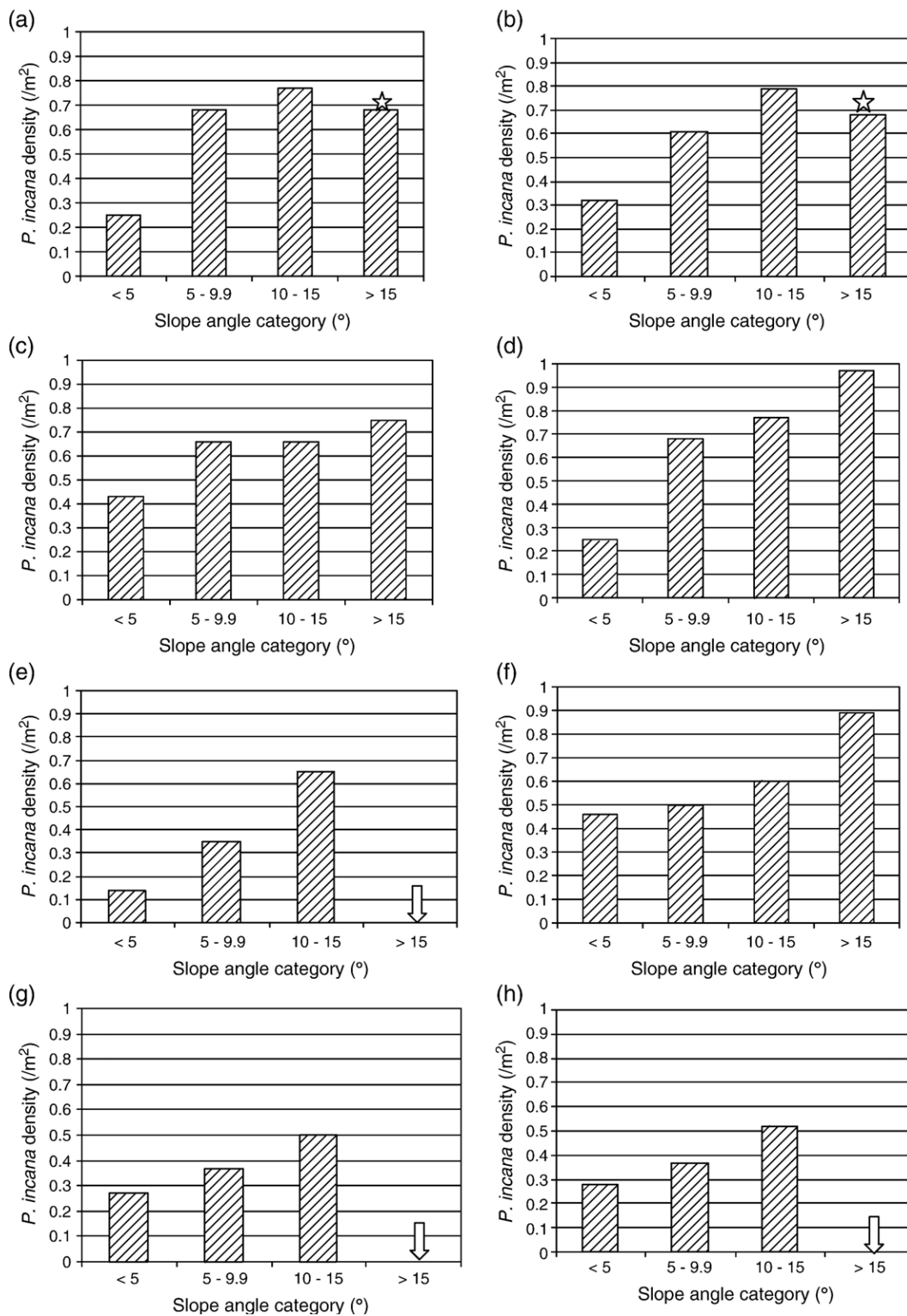


Fig. 8. (a)–(j) Histograms showing *P. incana* density variations with slope angle categories for the respective images (1–10). Block arrows indicate absence of slope category in the area depicted by the image. ☆ denotes considerable bare surfaces and erosion in slope category and hence lower *P. incana* density.

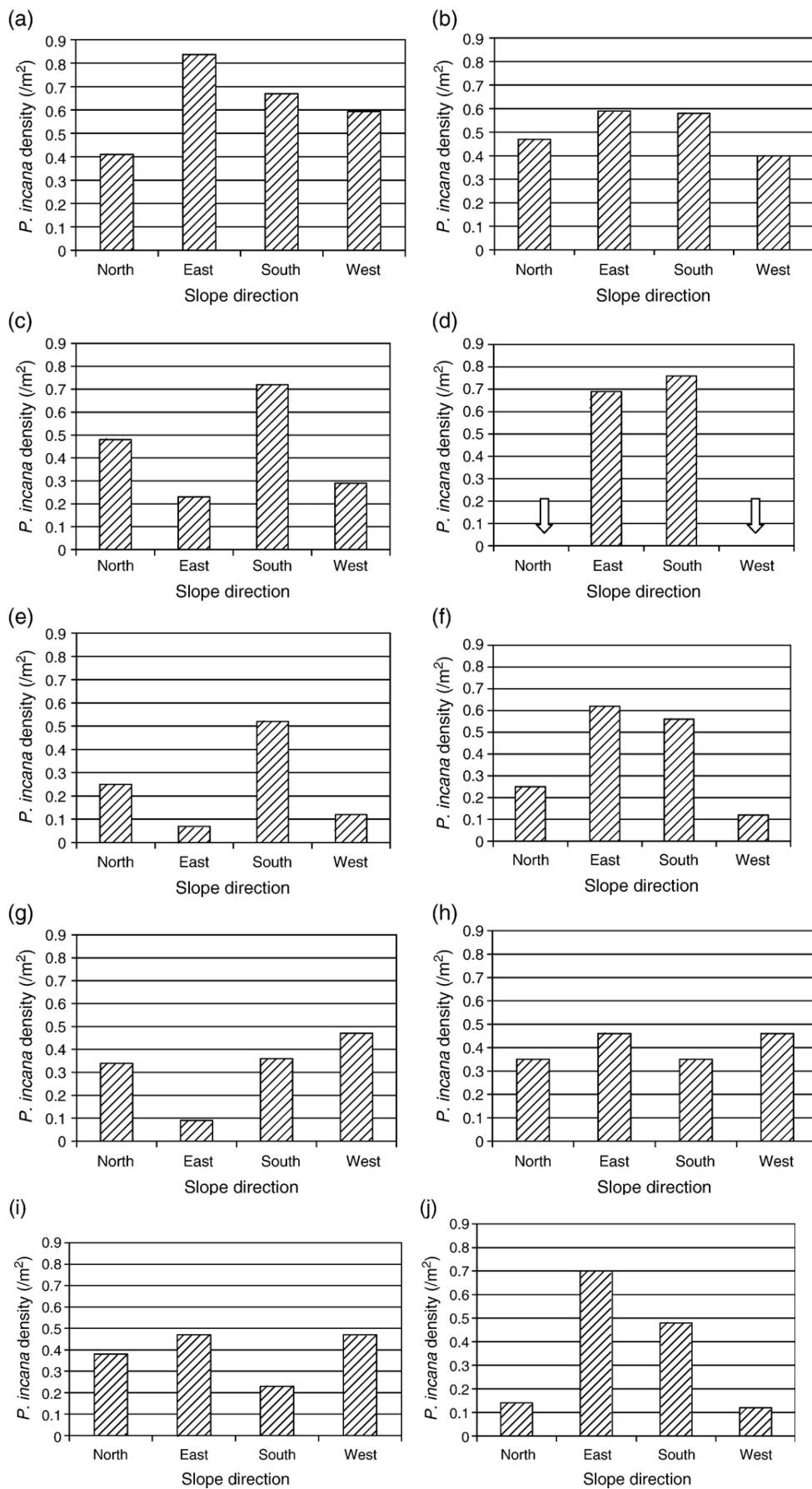


Fig. 9. (a–j) Histograms showing *P. incana* density variations with slope direction for the respective images (1–10). Block arrows indicate direction of slope occupied by settlements.

According to Quinn and Keough (2002), when a dependent model is categorical (with two levels, 0 and 1), the Binary Logistic Regression (BLR) is best suited to model such response variables that are binary, e.g. presence/absence. It is suited to models where the dependent variable is dichotomous and hence discrete (0, 1). The model's success can be assessed by looking at, among other things, the classification table showing correct and incorrect classifications of the dichotomous dependent variable (Garson, 2002). In the present model, the "Percent Correct Predictions" (PCP) statistic is used. The statistic assumes that if the estimated probability is greater than or equal to 0.5, then the event is expected to occur. High percentage correct predictions signify model effectiveness. The Maximum Likelihood Estimation (MLE), which is the distributed Chi-square with degrees of freedom being the number of independent variables, is also employed. The overall Chi-square is used to determine whether the overall model is statistically significant.

SPSS version 10.0 statistical package was used to analyse the data. The *P. incana* dichotomy was entered as the dependent variable while slope angle and aspect as the independent variables. Before the BLR is run, there is a need to check for collinearity – an undesirable situation where the correlations among the independent variables are strong. A very weak correlation ($R^2 = 0.0006$) between the two independent variables revealed non-collinearity between them (Fig. 6). The point of departure was setting the null hypothesis (H_0) that there is no relationship between the absence or presence of *P. incana* and slope angle and aspect.

3.5. Logistic regression model

In a dichotomous scenario, we model the probability that $Y=1$ for a given value of X . The logistic regression predicts group membership as a sigmoidal probabilistic function for which the prediction switches from one group to the other at a critical value, specified as an inflection point where the probability (P)=0.5 (Quinn and Keough, 2002). Instead of least squares regression, different authors (Whitehead, 1998; Garson, 2002; Quinn and Keough, 2002) recommend alogistic regression model for binary data.

The logistic model is derived thus:

$$\pi(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}, \tag{2}$$

where β_0 and β_1 are the intercept and slope, respectively. Given the categorical nature of the dependent variable (0, 1), a log transformation of $\pi(x)$ (commonly known as the 'logit') is carried out thus:

$$\ln\left[\frac{\pi(x)}{1-\pi(x)}\right]. \tag{3}$$

The logit transformation is modelled against the predictor variable using the simplified equation:

$$g(x) = \beta_0 + \beta_1 x_1, \tag{4}$$

where $g(x)$ is the logit/natural log of the odds that $y=1$ relative to $y=0$. β_0 and $\beta_1 x_1$ are the constant (intercept) and the product of the regression coefficient (β_1) and the value of the independent variable. Whereas the $\pi(x)$ is constrained to between 0 and 1, the logit transformation values range between $-\infty$ and $+\infty$ (Quinn and Keough, 2002).

4. Results

4.1. PCP and MLE statistics

Table 2 presents the PCP statistic. According to the classification table, the model predicts 70% of the *P. incana* occurrences correctly. Implicit in this prediction is that slope angle and aspect do significantly influence the absence or presence of *P. incana*. The selected summary statistics of the MLE of the model parameters are presented in Table 3. As can be gathered from Table 3, the Chi-square is well above the critical value and hence statistically significant at the given level. Likewise, the Hosmer and Lemeshow Chisquare statistic is also well above the critical value, denoting statistical significance. On the strength of the Percent Correct Predictions and the Chi-square test statistics, the null hypothesis is rejected. Slope angle and aspect do have a strong influence on the presence and absence of *P. incana*.

In the present model, the natural log of the odds that *P. incana* is present relative to being absent at a given slope angle and aspect was calculated. The logit coefficients in the SPSS statistical software output were provided as 0.178 for slope and 0.007 for aspect, with 1.982 as the intercept. The log odds ratios calculated using Eq. (3) were then translated back into predicted probability values using the equation:

$$P = 1 / (1 + e^{-(\beta_0 + \beta_1 x_i)}) \quad (5)$$

Logistic regression curves for slope and aspect are provided (Fig. 7a and b). The probability for *P. incana* presence or absence was calculated using formula (4). As can be noted from Fig. 7a, the critical slope angle represented by the inflection point where $P=0.5$ is about 9° . This signifies the threshold slope for *P. incana* absence or presence. South-facing slopes (particularly SW oriented) are also identified in Fig. 7b as the point at where the probability that *P. incana* is present is greater than that of its absence. There is a need, however, to obtain the finer details of the observed relationships, as the regression model only reveals that slope angle and aspect do have a statistically significant influence on *P. incana* occurrence. The details of the relationship are explored in the sub-section below.

4.2. *P. incana* density variations with slope angle and aspect The statistical test above does not reveal and account for the spatial variations in the density of the species with the different components of slope direction and categories of slope angle. In order to establish whether the invader species do have preferential categories of slope angle and elements of slope orientation, *P. incana* density images were overlaid with slope angle and aspect boolean surfaces. Fig. 8 (histograms a–j) presents *P. incana* density variations with slope angle category. An increase of *P. incana* density with slope angle can be identified from histograms a–j, with the highest density noted in the slope categories above 10° . The low density in the $N15^\circ$ category as illustrated by histograms a and b is explained by the existence of severe forms of erosion and extensive bare surfaces at specific sites in this slope category for the two cases. Extremely high *P. incana* densities of up to $0.9 \text{ m}^2/\text{m}^2$, depicted by histograms a to f, signify cases of blanket invasion.

Slope angle alone however, cannot explain the observed differences in *P. incana* invasion and density. *P. incana* density variations with the co-parameter of slope aspect are presented (Fig. 9, histograms a–j). It is noticeable from histograms a–f that slopes with a southerly orientation have the highest *P. incana* density ($0.63/\text{m}^2$ on average), followed closely by the easterly oriented ones ($0.506/\text{m}^2$). The latter group of histograms (g–j) represents an area with gentle slopes. By implication, topographic variations in terms of slope direction would not play a significant role in influencing *P. incana* invasion and density variations. The influence of slope angle and aspect cannot be examined in isolation if *P. incana* invasion dynamics are to be clearly understood. As pointed out earlier, most of the abandoned lands have been colonised by the invader shrub. It is therefore necessary to explore the combined influence of land use as an important co-parameter and terrain factor.

4.3. *P. incana* invasion and land use

The relationship between *P. incana* invasion and land use is provided (Fig. 10). This confirms that blanket invasion of abandoned lands by *P. incana* is a prominent phenomenon in the area. The small percentage of these lands not under *P. incana* cover is in most instances bare and gullied land. On the other hand, partial invasion on the grazing lands is noticeable from the figure. Abandonment per se may not explain the invasion. It would be useful to establish how much of the invaded abandoned and grazing lands are within the respective slope angle and aspect categories. Fig. 11 illustrates the acreage of invaded and remaining abandoned and grazing land in the respective slope categories. It is noticeable that the most invaded abandoned land area is in slope category 5° – 9.9° . A considerable invaded area is also noted in the 10° – 15° and $N15^\circ$ categories, especially considering that their frequency in the entire catchment is only 13% (see Fig. 2). By implication, the land abandonment– slope angle interaction has a strong bearing on *P. incana* invasion.

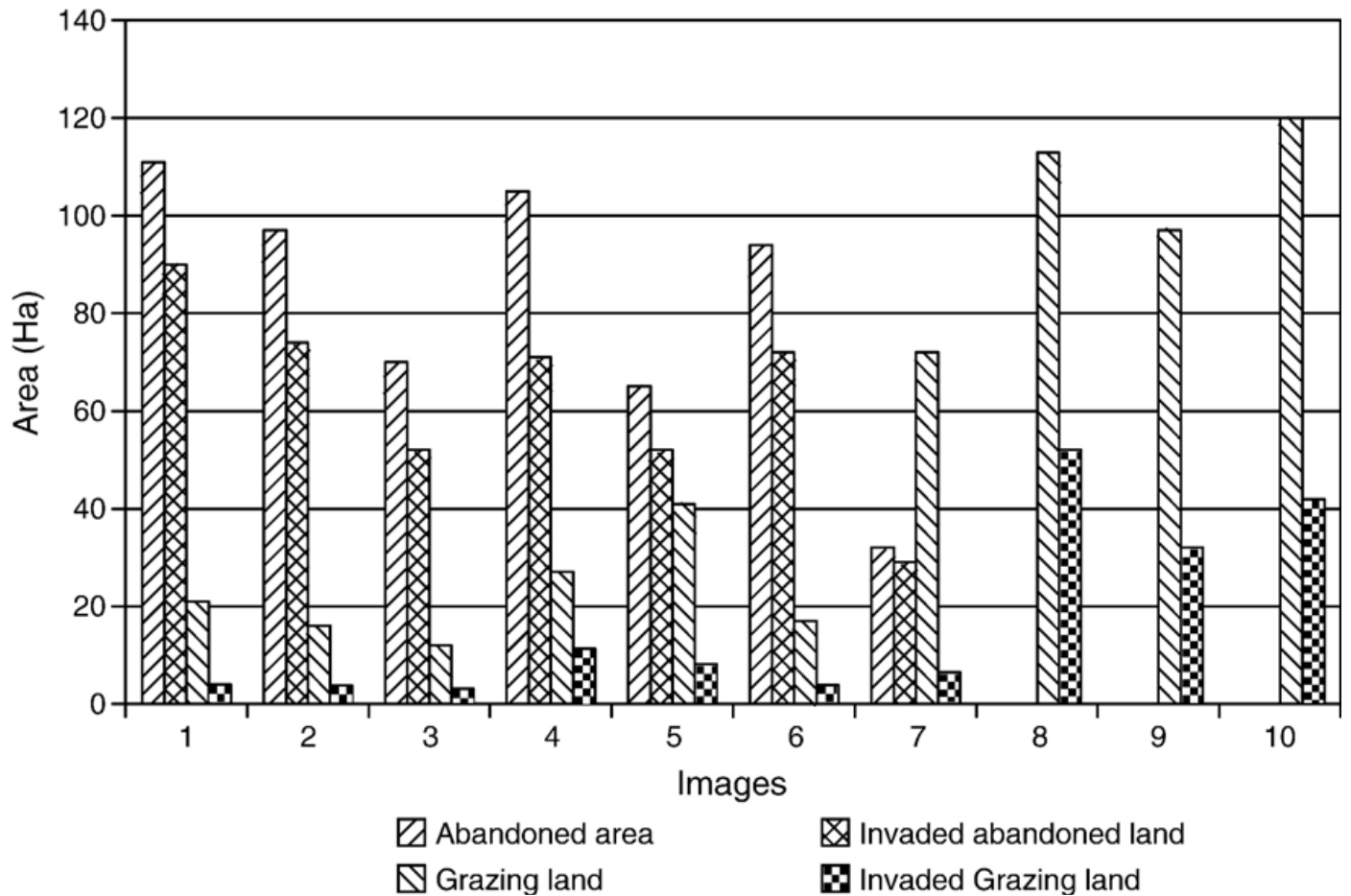


Fig. 10. Area in hectares of abandoned and grazing land invaded by *P. incana*.

The area of invaded abandoned and grazing land in relation to slope direction is provided (Fig. 12). It is evident that 71% of the invaded abandoned land is located on the south-facing slopes. It also follows that the south-facing slopes were by far the most farmed before abandonment, given that 77% of the previously farmed land is already invaded by *P. incana*. The following observations pertaining to slope angle and aspect on the one hand and the invasion of abandoned and grazing land on the other can be made:

- Steep slopes in the category 10°–15° and N15° have the highest *P. incana* density (Fig. 11).
- *P. incana* density is highest on the south-facing slopes (Fig. 12).
- Invaded abandoned land with high *P. incana* density is predominantly located on steep south-facing slopes with slope angles above 5° (Figs. 11 and 12).
- Steep slopes in the category 10°–15° and N15° have the highest *P. incana* density (Fig. 11).
- *P. incana* density is highest on the south-facing slopes (Fig. 12).
- Invaded abandoned land with high *P. incana* density is predominantly located on steep south-facing slopes with slope angles above 5° (Figs. 11 and 12).
- Invaded grazing land with low *P. incana* density is located mainly on gentle slopes below 5° with a north, south and west orientation (Figs. 11 and 12).

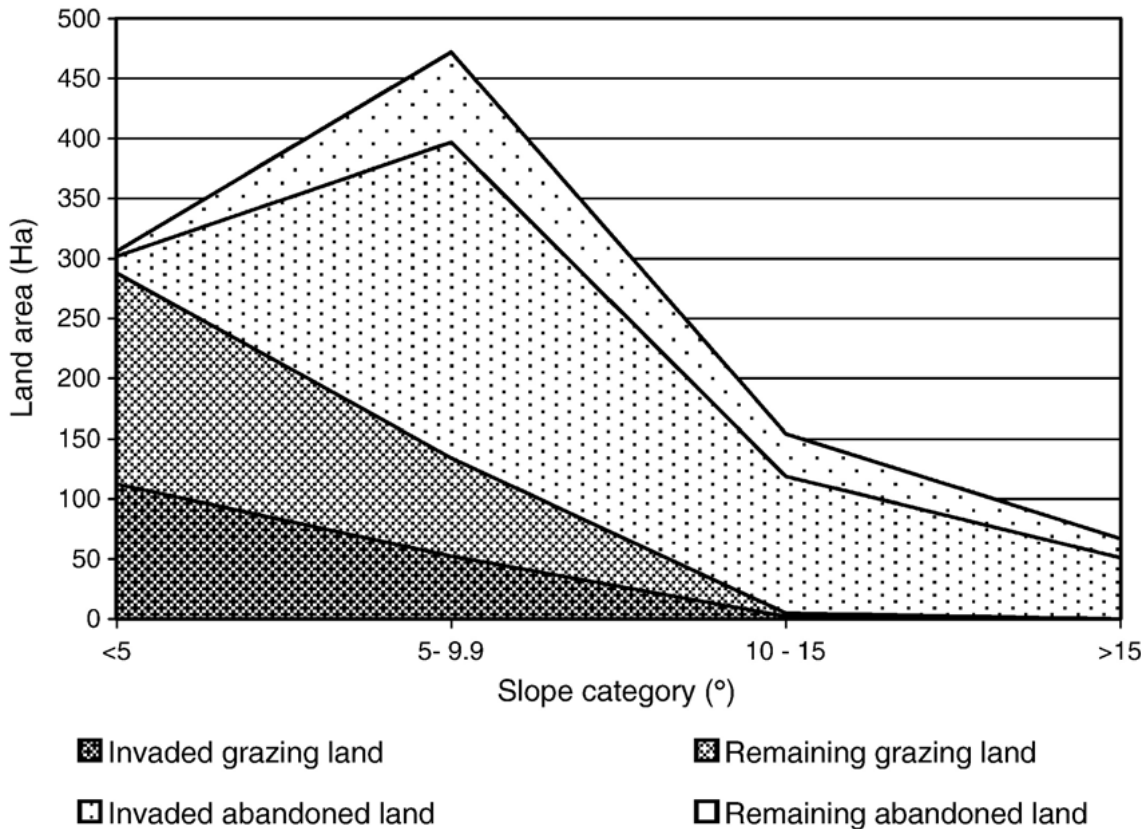


Fig. 11. Invaded and remaining abandoned and grazing land per slope category.

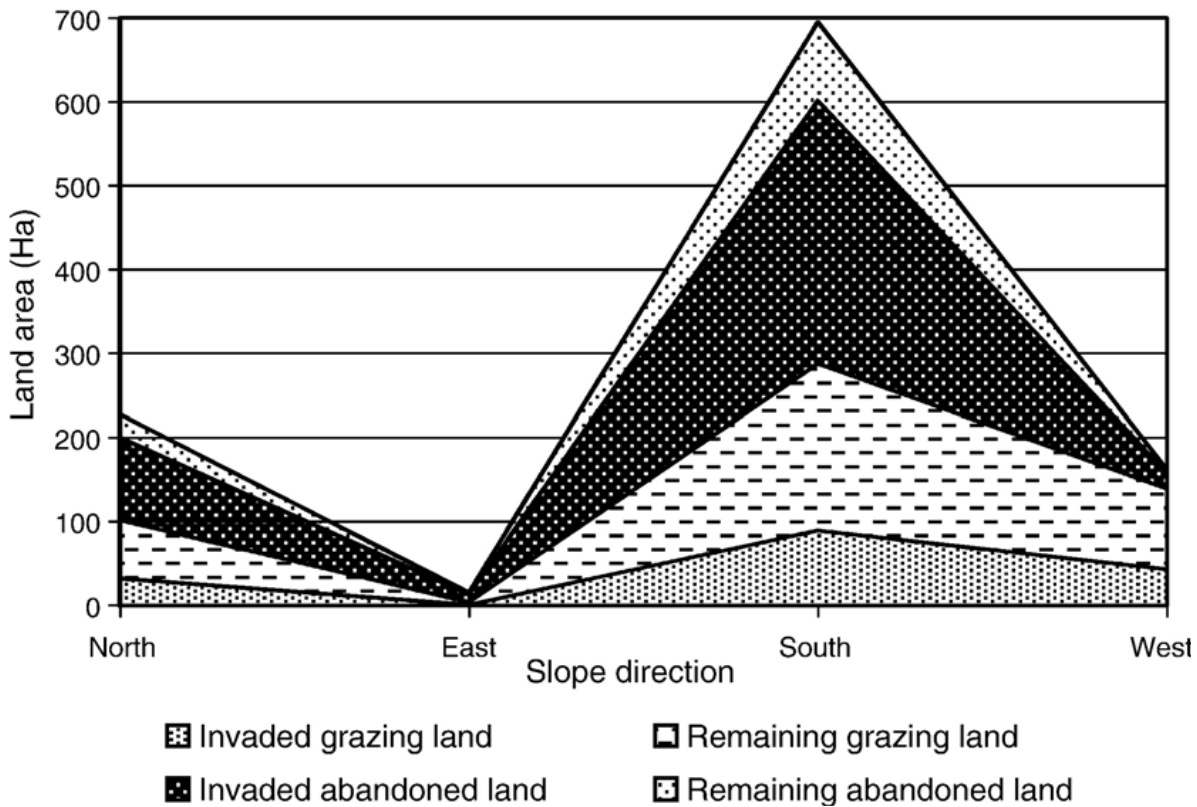


Fig. 12. Invaded and remaining abandoned and grazing land in relation to slope direction.

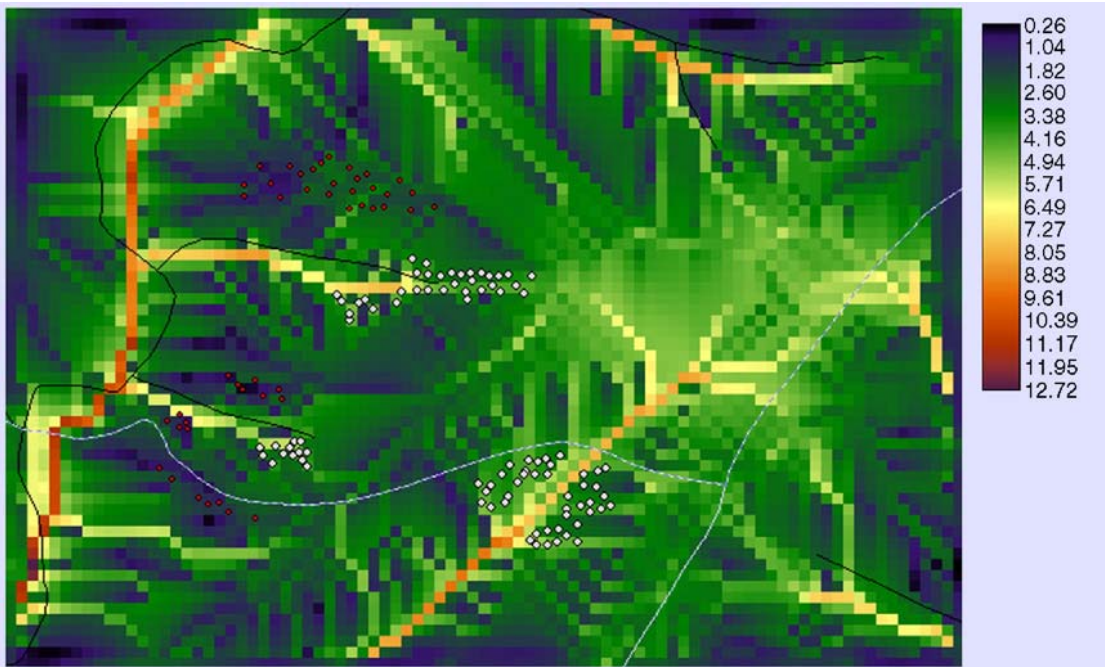
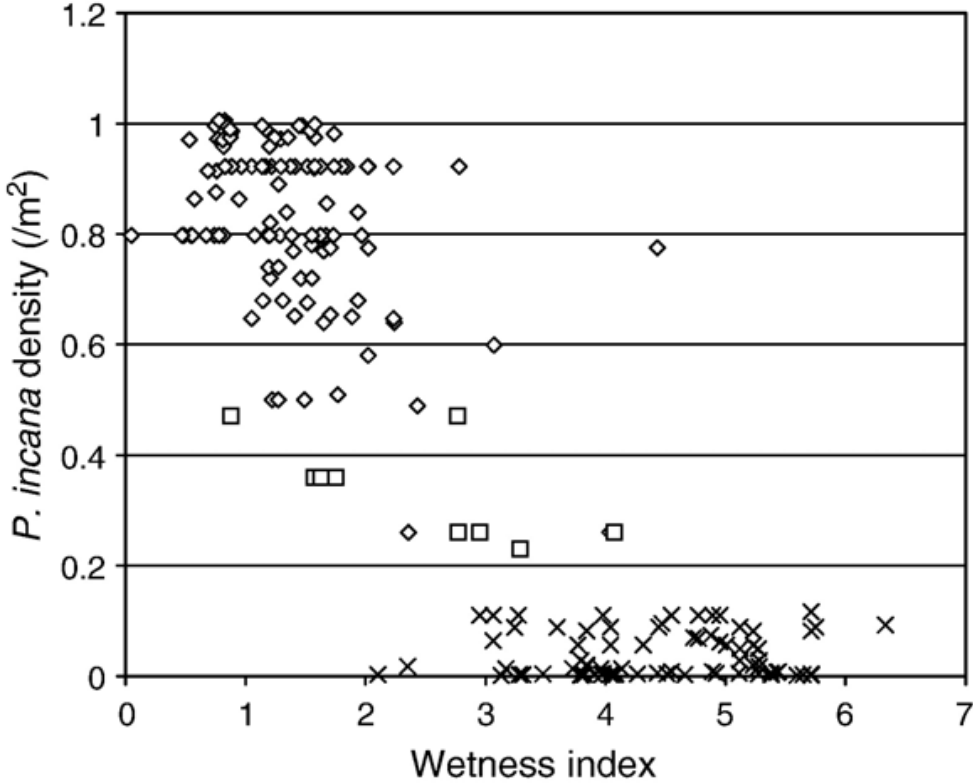


Fig. 13. Wetness index surface derived from one of the DEM windows of the same size as the digital camera images. Red and white dots overlaid are *P. incana* and grass/no *P. incana* clusters respectively. A road and main river vector files digitised from an orthophoto map are superimposed. (For interpretation of the reference to colour in this figure legend, the reader is referred to the web version of this article.)

It can thus be said unequivocally that, in the area, disturbed lands in the form of mainly abandonment, particularly on steep south-facing slopes, are highly susceptible to invasion by *P. incana*.



x No *P. incana*/Low density ◇ High density *P. incana* □ Moderate density *P. incana*

Fig. 14. Scatterplot depicting the relationship between the WI and *P. incana* density

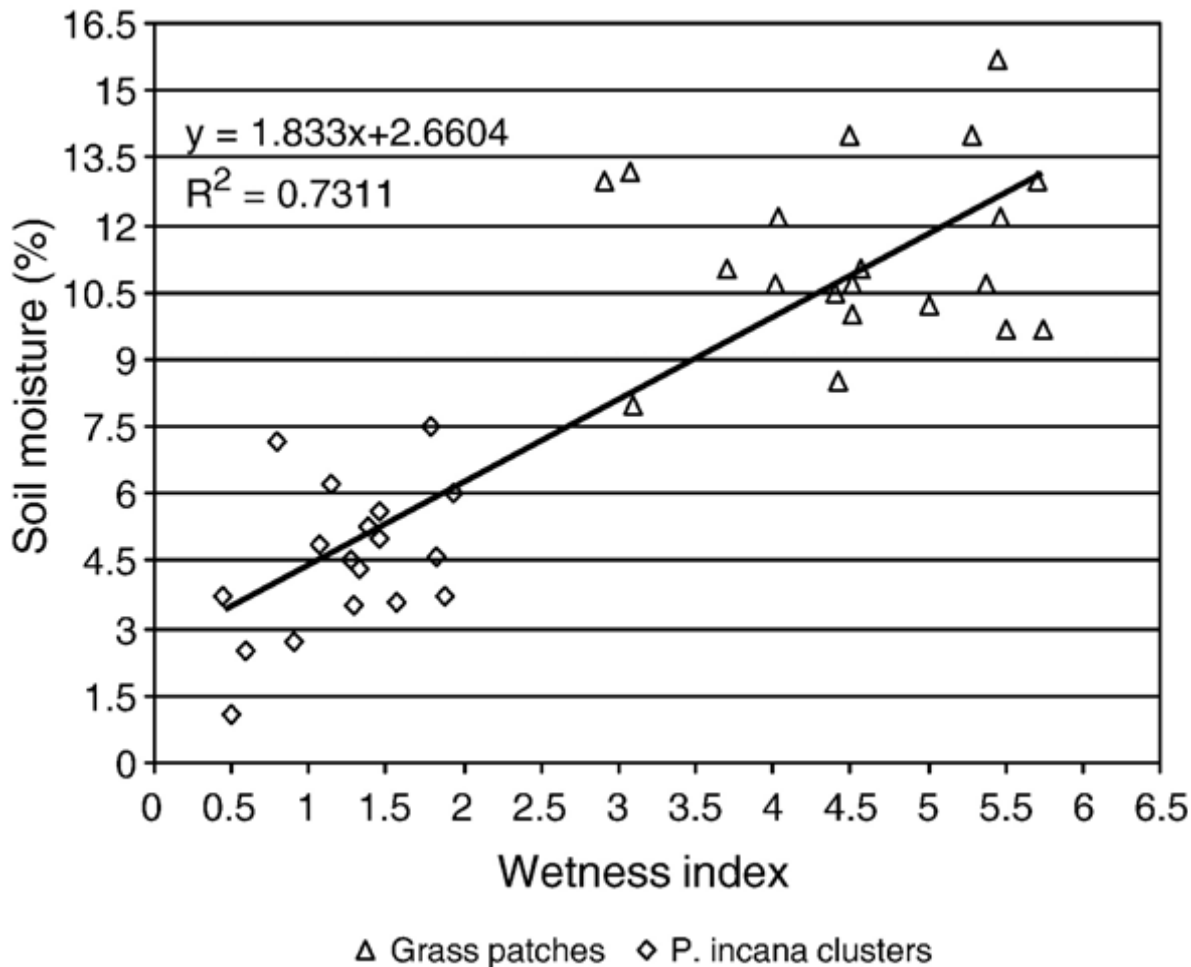
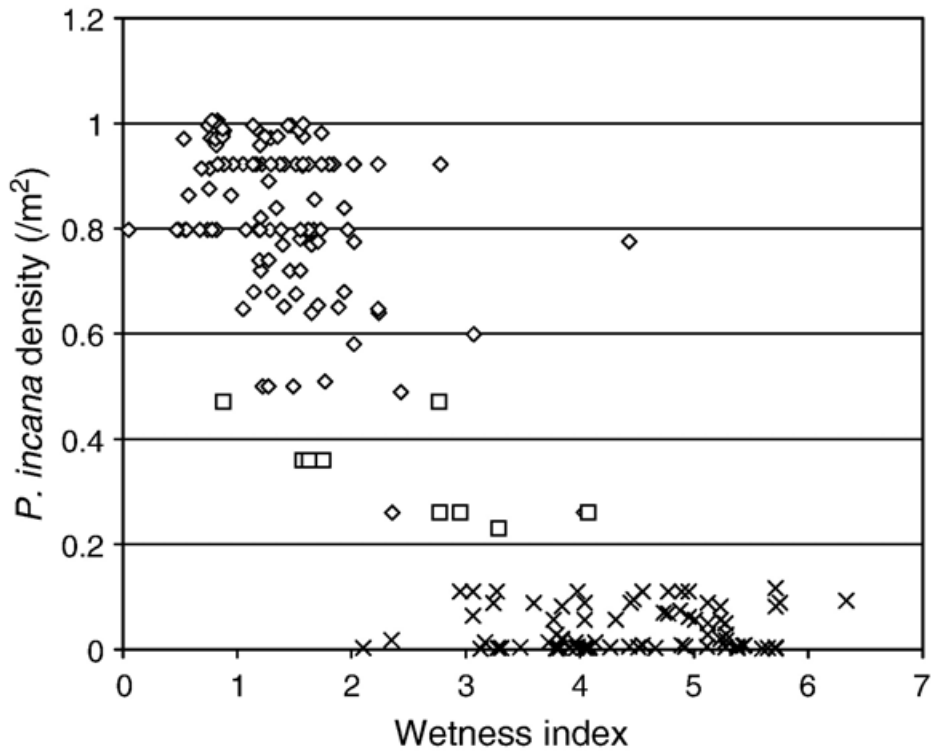


Fig. 15. The relationship between the Topographic Wetness Index and soil moisture (%).

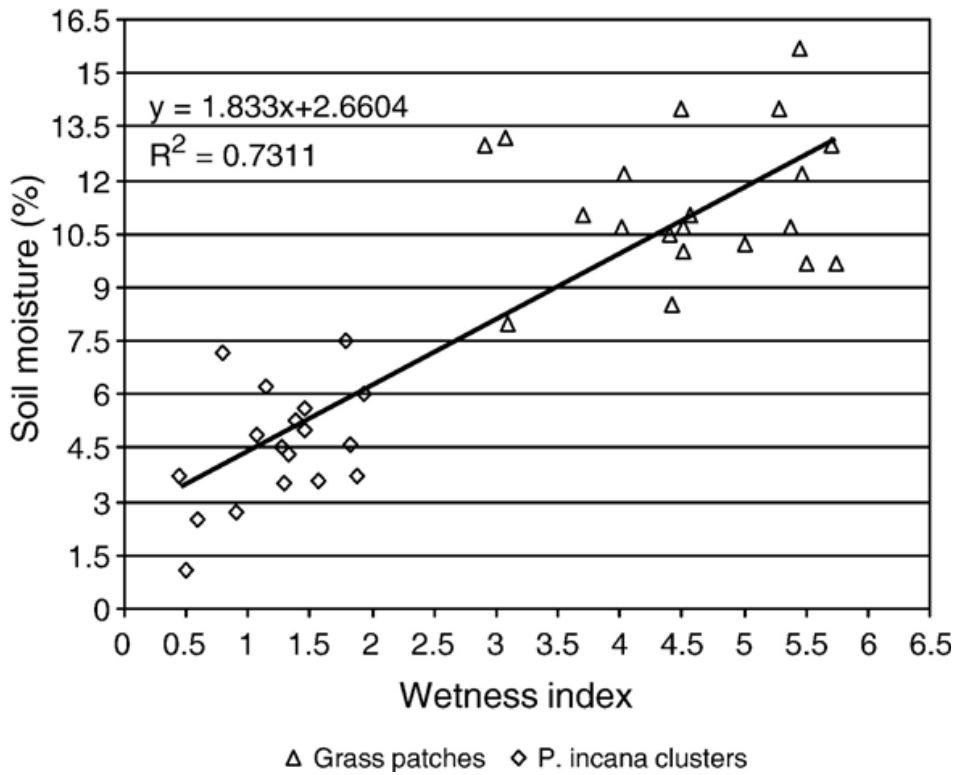
4.4. Local topographic control on *P. incana* spatial distribution and density

The implications of the local topography for particularly moisture distribution, which in turn influences the pattern of *P. incana* invasion and the persistence of some grass species were examined by deriving the Wetness Index. Fig. 13 is a WI image derived from one of the DEM windows. Having carried out extensive soil moisture surveys in the area depicted, the WI image is deemed a fair representation of the local wetness conditions. Whereas *P. incana* clusters are noticed to occupy low WI convexities, the reverse is true of the high WI concavities bordering drainage lines, where grass patches persist. This relationship was explored further by comparing the WI images generated from all 10 DEM windows of the same size as the digital camera images with *P. incana* density maps prepared for each image. Thirty point features were digitised on each of the WI images. Hillslope units with visibly low WI values on the one hand and high ones on the other were targeted. Obvious riparian areas were excluded. The points were rasterised and values files were extracted from the image masks. The same points were overlaid on the respective *P. incana* density maps and the density values of the polygons in which the points lay were recorded. Fig. 14 is a scatterplot of the wetness values and *P. incana* density. A clear pattern is discernible from the Scatterplot, with high *P. incana* density (0.5–1/m²) associated with low WI values, concentrated between 0.2 and 2. The reverse is true of the low density or 'no *P. incana*' areas, with WI values concentrated between 2 and 6.5. It can thus be said that the topographically controlled wetness as a surrogate for soil moisture variability has a strong influence on the spatial distribution of *P. incana* and that it is a strong indicator of the environments conducive for its invasion. Fig. 15 illustrates a strong spatial relationship ($R^2 = 0.73$) between the WI and soil moisture (%) based on selected field sites. A clear divide between soil moisture and Wetness Index values for grass and *P. incana* patches is readily noticeable. This confirms that *P. incana* occupies dry areas as opposed to grass whose remanent patches persist in the wetter concavities and hollows.



x No *P. incana*/Low density ◇ High density *P. incana* □ Moderate density *P. incana*

Fig. 14. Scatterplot depicting the relationship between the WI and *P. incana* density.



△ Grass patches ◇ *P. incana* clusters

Fig. 15. The relationship between the Topographic Wetness Index and soil moisture (%).

5. Discussion

The threshold slope angle and aspect for *P. incana* occurrence have been identified by means of a logistic regression model. However, the model assumes neither a linear nor a causal relationship. It has also been established that the steeper the slope angle, the greater the density of *P. incana*, with categories above 10° having the greatest density. Slopes with a southerly orientation were identified as having a greater *P. incana* density than the other slope directions. The relationship between slope angle and *P. incana* invasion can be explained in terms of processes that operate on slopes. These are manifest in the interaction between surface and sub-surface water flux and redistribution, with slope gradient as the controlling factor. Steep slopes have lower runoff thresholds, thinner soils, reduced soil moisture storage and consequent sparse vegetation (Kirkby et al., 2002). The 'Walther model' and its implications for competition between grass and shrubs will therefore play itself out. The model articulates that soil depth and different moisture dependencies determine the competitive advantage between grasses and shrubs or bushes. Deeprooted shrubs like *P. incana* will gain a quicker competitive advantage and eventual replacement of grass species, particularly in thin moisture-constrained soils, for instance, topographic convexities.

The development of 'resource islands' as articulated by Reynolds et al. (1999) is another coping mechanism developed by shrubs that facilitates replacement. In disturbed environments, for instance abandoned lands, individual shrubs develop litter zones beneath them, where nutrient cycling is confined. Whereas bare crusted inter-shrub zones become resource poor, owing to overland flow generation and soil erosion, shrub tussocks which progressively coalesce enhance interception and stemflow, confining infiltration of nutrient-enriched rainfall directly beneath the shrubs Reynolds et al. (1999). Such shrub-induced alterations to ecosystem processes, particularly surface water flux augment the replacement of grass species.

The role of aspect in *P. incana* invasion is subtle and can be better appreciated when viewed in combination with land use and slope angle. The abandonment of land on steep, mostly south-facing slopes predisposed it to resource fluctuation, impairment of soil biophysical properties and erosion, creating an enabling environment for *P. incana* invasion. The fundamental control that slope aspect has on the spatial variability of soil moisture explains why southfacing slopes were the most farmed. The slopes are supposedly shadier than the sunny north-facing ones and, given the geographical location of the study area, in close proximity to the east coast, the dominant south east onshore moist winds make the slopes moister and thus more suitable for farming. This influence is manifest on the regional scale rather than at the local hillslope scale, where local topographical configuration is the main underpinning of soil moisture redistribution.

Besides the role of slope angle and aspect, another pertinent question to be answered is: What makes abandoned lands so susceptible *P. incana* invasion? In the present study, drought, soil physical properties and disturbance in the form of land abandonment are envisaged to have interacted to cause a shift in water availability beyond the uptake threshold for grass species. The persistence of bare abandoned plots as discerned from the 1975 aerial photographs is most likely to have been perpetuated by drought periods (see Fig. 5). As evidenced by the characteristics of the soil samples in Table 1 above, the soils of the area are highly susceptible to crusting subsequent to disturbance related age-long hardening. The latter process explained by Gerits et al. (1990) as resulting from earlier disturbance of particle-toparticle bonds, must have been one of the effects that drought had on the bare soils of abandoned plots. Impaired soil surface conditions are seen to have reduced infiltration capacity, promoted runoff and reduced soil moisture beyond the rooting depth of grass species. Thus, a combination of disturbance, drought and age-long hardening of the soil surface may have created less competitive conditions for grass species. Coupled with stripping away of the humic layer on the characteristically steep slopes when the wet season set in, abandoned lands were rendered highly vulnerable to blanket invasion by *P. incana*.

The overriding control of local topography on *P. incana* spatial distribution is rooted in soil moisture variability and is demonstrated by the Topographic Wetness Index, which is based on the local topographic heterogeneity. The strong correlation between the WI and field moisture values, illustrated by Fig. 15, confirms the reliability of the index as a tool to predict slope configuration induced moisture variability. *P. incana* is associated with low WI values as opposed to grass, demonstrating that their moisture dependencies are largely controlled by the local topographical variations. The WI, however, may not fully explain soil moisture variability and hence *P. incana* distribution. Heterogeneity may exist even within the same topographic unit due to varying soil properties, underlying bedrock and outcrops of bedrock, causing the conductivity profile to vary greatly (Asserup and Eklöf, 2000). The steady state assumption inherent to the WI does not consider such small-scale variations.

The *P. incana* distribution scenario is compounded by land disturbance cycles, particularly on abandoned land, which will have altered soil moisture conditions. Gully erosion in particular targets deep soils in hollows or concave lower slope elements, which are supposedly topographically high wetness areas. This will induce "inverted topographic wetness conditions" by drying out potentially high wetness areas. This explains the recommendation by Anderson and Burt (1990) that topographic Wetness Index methods may not be appropriate for slope sections that are gullied or where soil piping is well developed.

The focus of rehabilitation efforts on degraded abandoned hillslopes should be on trapping of sediment and litter, and moisture retention on the inter-patch bare areas. This is achievable by laying piles of brush oriented along contours to trap and store the limited soil resources (Tongway and Ludwig, 1993). Restoration of patches on bare slopes using brush piles of 10 m³ has been achieved by Tongway and Ludwig (1996). Cognisance should, however, be taken of the local topographic configuration when laying structures to trap sediment as it governs water redistribution on hillslopes. Moisture deficiency has been identified as the main underpinning in the competition between grass species and *P. incana*. Trapped sediments will restore the two-level moisture conditions conducive for grass to re-establish itself. Once grass is re-established in the hitherto crusted bare areas, *P. incana* tussocks could then be systematically cleared and replaced by more sediment traps to encourage grass growth. The success of such an exercise would necessitate grazing control, such that animals are kept out of the areas where rehabilitation is underway.

6. Conclusion

The use of high resolution imagery in conjunction with a Digital Elevation Model has enhanced our understanding of the influence of topographic variations on the spatial distribution of *P. incana*. At the catchment scale, slope angle and aspect significantly influence the shrub's absence or presence. The probability for *P. incana* occurrence increases with slope steepness and the southerly slope orientation. Whereas the influence of the former on *P. incana* occurrence is manifest in the interaction with surface and sub-surface water redistribution, the bearing of the latter is indirect, as it is explained in terms of the greater land disturbance due to cultivation on the south-facing slopes than the other slope directions.

The interaction between land disturbance, slope angle and aspect to promote *P. incana* invasion is borne out by the high density of the shrub on abandoned land located mostly on steep south-facing slopes. Against the background of the timing of land use changes and climatic fluctuations that prevailed in the study area, the combined role of land abandonment and stochastic climatic fluctuations like drought and the attendant age-long hardening of soils may have enhanced the invasibility of the abandoned lands. At the hillslope scale, the spatial relationship between vegetation type and the topographically driven Wetness Index confirms that the soil moisture dependencies of the invader and grass species are largely determined by local topographic variations. Implicit in the topographically controlled soil moisture variability is the two-layer moisture theory as illustrated by the Walther model. Soil depth variations between convexities and concavities demonstrate the coupling between local topographic variations and soil depth, which in turn draws the line in the competition between shrubs and grasses. Rehabilitation of run-out hillslopes should focus on moisture and sediment retention by way of laying run-on structures in the inter-patch areas.

Acknowledgements

The authors wish to acknowledge research grants from the National Research Foundation (NRF) and South Africa–Netherlands Research Programme on Alternatives in Development (SANPAD), which funded fieldwork and the imagery.

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