Plant Ecology **145:** 243–254, 1999.

Effects of grazing and topography on long-term vegetation changes in a Mediterranean ecosystem in Israel

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Received 22 December 1998; accepted in revised form 21 June 1999

Key words: aerial photographs, gis, landscape ecology, spatial structure, regression model, vegetation dynamics

Abstract

The dynamics of Mediterranean vegetation over 28 years was studied in the Northern Galilee Mountains, Israel, in order to identify and quantify the major factors affecting it at the landscape scale. Image analysis of historical and current aerial photographs was used to produce high resolution digital vegetation maps (pixel size = 30 cm) for an area of 4 km^2 in the Galilee Mountains, northern Israel. GIS tools were used to produce corresponding maps of grazing regime, topographic indices and other relevant environmental factors. The effects of those factors were quantified using a multiple regression analyses. Major changes in the vegetation occurred during the period studied (1964–1992); tree cover increased from 2% in 1964 to 41% in 1992, while herbaceous vegetation cover decreased from 56% in 1964 to 24% in 1992. Grazing, topography and initial vegetation cover were found to significantly affect present vegetation patterns. Both cattle grazing and goat grazing reduced the rate of increase in tree cover, yet even intensive grazing did not halt the process. Grazing affected also the woody-herbaceous vegetation dynamics, reducing the expansion of woody vegetation. Slope, aspect, and the interaction term between these two factors, significantly affected vegetation pattern. Altogether, 56% and 72% of the variability in herbaceous and tree cover, respectively, was explained by the regression models. This study indicates that spatially explicit Mediterranean vegetation dynamics can be predicted with fair accuracy using few biologically important environmental variables.

Introduction

Grazing is an important factor determining patterns of vegetation in Mediterranean ecosystems (Naveh & Whittaker 1979; Davis & Goetz 1990). Quantitative information about grazing effects on vegetation is crucial for planning grazing regimes in order to achieve specific goals such as optimizing resource production for livestock (Noy-Meir & Seligman 1979; Biondini & Manske 1996; Pickup 1996), conserving local biodiversity (e.g., Montalvo et al. 1993), or reducing fire hazards (e.g., Naveh 1977; Perevolotsky & Haimov 1992). Most previous studies of grazing effects on vegetation concentrated on the short-term ($<$10 years) expression of these effects, and on small spatial scales (e.g., Gibson & Brown 1992). Only few studies have addressed the question of grazing impact on long-term vegetation changes at the landscape-scale (Callaway & Davis 1993; Wahren et al. 1994); these studies were limited to a grazing vs. no grazing comparison.

It is generally accepted that in Mediterranean ecosystems, grazing inhibits the development and growth of woody vegetation, and that intensive grazing may reverse the course of succesion in such systems (Joffre et al. 1988; Callaway & Davis 1993; Seligman & Perevolotsky 1994). Yet, several studies have indicated that grazing may play a more complicated role in determining the dynamic relationships between herbaceous and woody vegetation components. For example, grazing may open niches for woody seedling establishment by reducing the biomass of competing herbaceous vegetation (e.g., Mitchell & Kirby 1990; Alon & Kadmon 1996).

Another factor considered important in shaping Mediterranean vegetation pattern is topography. There is a substantial literature that describes vegetation responses to local topographic variation (e.g., Armesto & Martinez 1978; Kirkpatrick & Nunez 1980; Davis & Goetz 1990; Jobbagy et al. 1996). Most of these studies, however, have concentrated on spatial patterns of the vegetation, while studies of topographic effects on temporal changes in the vegetation are still rare (Kadmon & Harari-Kremer in press).

It is widely accepted that in the northern hemisphere, south-facing slopes receive more solar radiation then north-facing slopes and are therefore characterized by lower water availability (e.g., Holland & Steyn 1975). Given the water-limited Mediterranean vegetation, one would expect that rates of vegetation changes in such ecosystems would be influenced by topographic conditions.

The major goal of this study was to evaluate the combined effects of grazing regime and topography on vegetation dynamics, at (relatively) large scales of space and time, and high spatial resolution. A range of grazing intensities, by cattle and by goats, as well as the independent effects of slope, aspect and their interactions – are analyzed, for a mountainous area in the Mediterranean region of Israel. Image analysis of historical and current aerial photographs is used to produce digital vegetation maps. GIS tools are used to produce corresponding maps of grazing regime, topographic indices and other relevant environmental factors. The effects of these factors on vegetation dynamics are analyzed, and the net effect of each factor is quantified.

Methods

Study area

An area of 4 km^2 (400 ha) on the northern slopes of Mt. Meron, Upper Galilee Mountains, Israel (32° N, 35° E) was chosen. The climate is Mediterranean, with dry summer and cool, wet winter. Average annual precipitation is 900 mm, January and July average temperatures are 14 °C and 25 °C, respectively (Markus 1994). The study area is heterogeneous in terms of topography (Figure 1) and vegetation types, but homogenous in its bedrock conditions (brown rendzina on dolomite rocks, Dan et al. 1975). The dominant tree, shrub, and dwarf shrub species are *Quercus calliprinos*, *Calicotome villosa* and *Sarcopoterium spinosum,* respectively (Zohary 1960). The entire area was subject to intensive grazing and tree harvesting until 1948, when the nearby Arab village (Sasa) was abandoned. Grazing has been largely reduced since then, and a process of vegetation recovery has taken place in the region. Starting in the early-sixties, different parts of the area experienced different grazing regimes, in terms of both the type of livestock (goats vs. cattle) and grazing intensity. These regimes were kept relatively constant from 1964 to present.

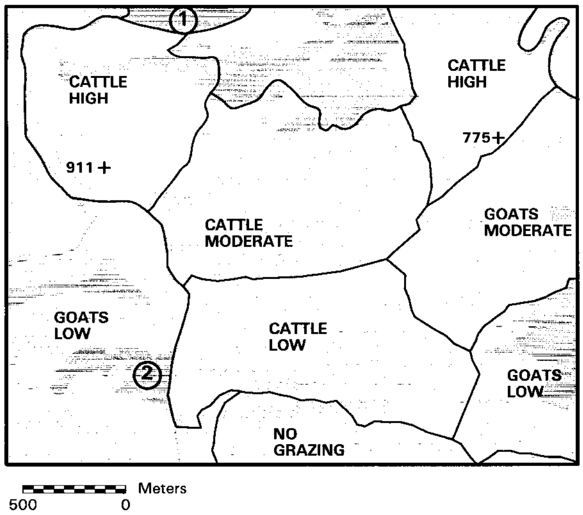

Figure 1. A map of the study area, showing the topography and different grazing regimes. Contour intervals represent 10 m in elevation. Shaded areas are agricultural or villages. 1. Kibutz Sasa. 2. Mt. Meron Field Study Center.

Vegetation maps

The computerized methods we used to produce vegetation maps from pan-chromatic aerial photographs are described in detail by Carmel & Kadmon (1998). The main steps of the procedure are outlined below.

Two aerial photographs of the study area (1964, 1:14 000 and 1992, 1:12 000) were chosen as a basis for the analysis. Diapositives of the photos were scanned at a resolution of 12μ. Using a computerized ortho-rectification process, the radial, tilt, and relief distortion inherent in aerial photos were removed, and the photos were registered to a planimetric coordinate system. Spatial resolution (pixel size) in both photomaps was 30 cm. The combined root mean square (r.m.s.) positional error between the photomaps was 1.13 m. An illumination adjustment process was applied to correct for uneven illumination.

Our approach for classifying the vegetation includes 3 classes based on vegetation height, and is a slight modification of Tomaselli (1977): woody vegetation >2.5 m (‘trees’), woody vegetation <2.5 m, including shrubs, dwarf shrubs, and low trees (‘shrubs’), and herbaceous vegetation, including bare ground (‘herbs’). The vegetation was classified using a ‘neighbor classifier’, that was found to be superior to a standard supervised classification (Carmel & Kadmon 1998). Results were tested against field-based vegetation maps. Overall accuracy of the classification was 89% in the 1992 image and 82% in the 1964 image. Anthropogenic elements (roads, settlements, agricultural areas and pine plantations, which together comprised $<$15% of the study area) were manually digitized on the photos, and excluded from further analyses. Figure 2 portrays the resulting 1964 and 1992 vegetation maps.

The vegetation maps were in raster format, i.e., comprised of grid cells. Accurate assessment of vegetation changes requires that comparisons of vegetation in different points in time are made between grid cells that actually represent the same area (Townshend et al. 1992). To achieve a minimum spatial overlap of 90% between identical grid cells in 1964 and 1992 maps, given an overall Root Mean Square (r.m.s.) positional error of 1.13 m between the two photomaps, we used a cell size of 15×15 m for map comparison. Percentage cover of each vegetation type (‘trees’, ‘shrubs’, and ‘herbs’) in each grid cell was calculated based on the vegetation maps with the 30 cm resolution, using the Arc-Info AML (ESRI 1996). All other digital maps in the database were re-scaled to the same resolution.

Grazing regimes

The study area can be divided into three different units according to its use by livestock (Figure 1):

(1) The central area is used by the cattle of Kibbutz Sasa. Their herd size was kept constant around 150 cows since the mid-sixties. Fences divide this area into plots of three grazing intensities (Figure 1): high (were the cattle stays all year), moderate (were the cattle stays mainly during winter, November–March) and low (were the cattle can be found occasionally). The high, moderate and low intensities correspond to 340, 110, and 30 cattle grazing days per ha per year (CGD/HY, Noy-Meir et al. 1989), respectively.

(2) The west and east parts of the study area were grazed by goat herds from the villages of Hurfeish and Jish, respectively. Quantification of grazing intensity for the area grazed by goats was difficult because several herds used the same area simultaneously, and exact herd sizes were often unknown. Nevertheless, two qualitative levels of goat grazing – moderate and low – were distinguished in the study area; the former represents areas under regular use by the goats, while the latter represents areas that were used only occasionally (Figure 1).

(3) The southern part of the study area experienced almost no grazing during the studied period (1964–1992).

Fire and logging

A single fire event occurred in the area in June 1978. Our study area intersected the edge of that fire, and fire intensity was rather low. Inspection of an aerial photo taken in 1980 showed that the trees in the burnt area were still alive. Fire range was delimited on an aerial photo taken several weeks after the fire, and was digitized into the GIS. A single tree logging event occurred in 1980, around agricultural land. That area was delimited, and omitted from further analysis.

Topography maps

A digital elevation model (DEM, denotes the elevation at each point in the area) was produced in the photo-rectification process. The r.m.s. error of the DEM was 0.75 m (Figure 1 illustrates its contour representation). This DEM was used to derive digital maps of elevation, slope, and aspect for the study area, using Arc-Info algorithms (ESRI 1996). Aspect is represented by angular data (0°–360°), and it was therefore decomposed to its north-south and east-west components (Periera & Itami 1991). The north-south component of aspect is a variable in the range of 0°–180°, where north = 0°, south = 180° and east = west. The east-west component of aspect is a variable in the range of 90°–270°, where east = 90°, west = 270° and north = south.

Statistical analysis

A multiple regression approach was used to analyze the data. Cell-specific vegetation cover was predicted from information on its past vegetation condition, topographic variables and disturbance characteristic.

The database

The digital maps were translated to a database in which each record corresponded to a grid cell in the study area. Preliminary investigations of the spatial structure of the data have revealed that spatial autocorrelation diminishes with distance; for distances of 5 cells (75 m) the autocorrelation values in the residuals

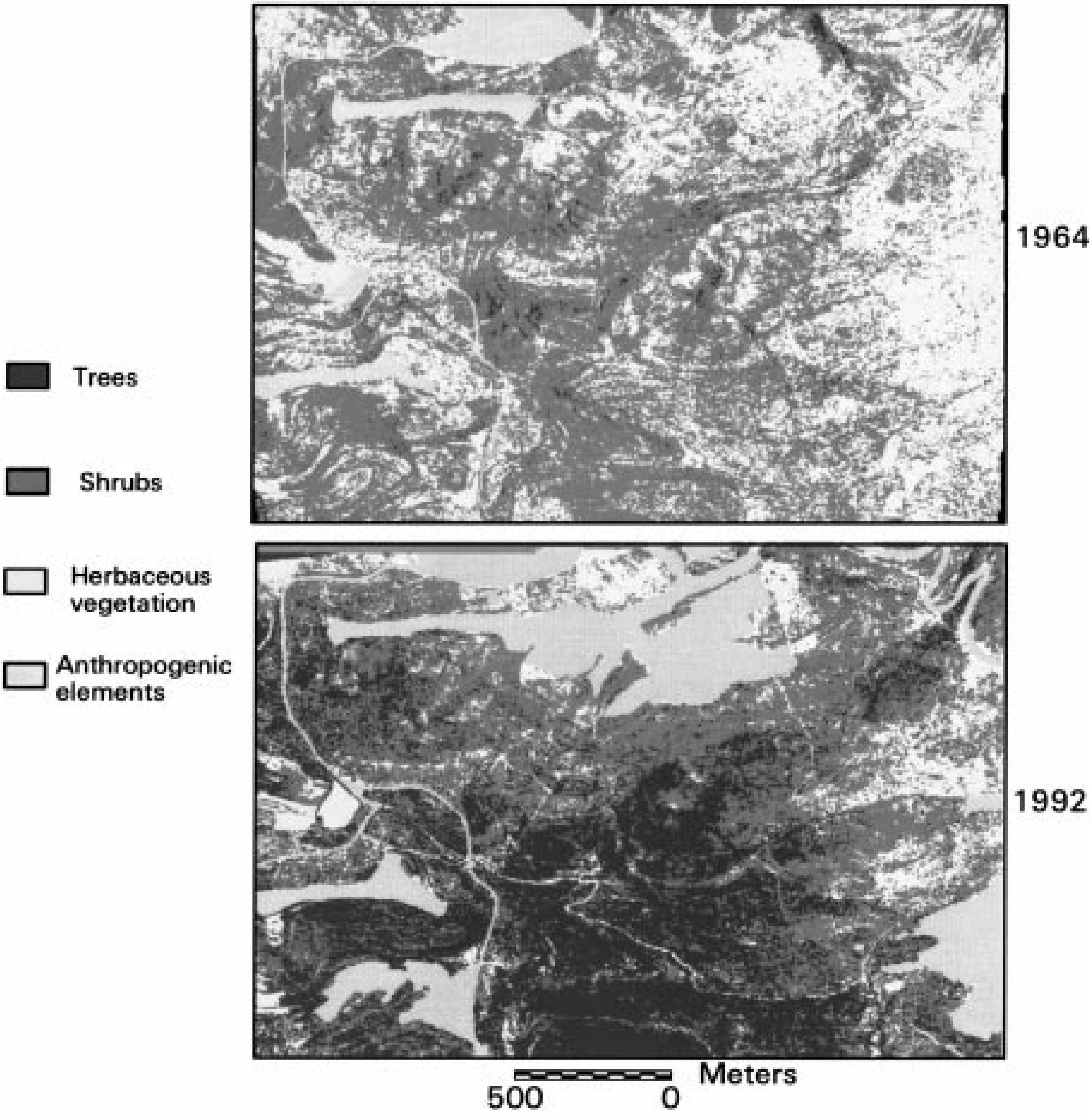

Figure 2. Vegetation maps of the study area in 1964 and 1992, produced using image analysis of aerial photographs. Pixel size is 30 cm. r.m.s. positional error between the two maps is 1.13 m. Modified after Carmel and Kadmon 1998.

of a preliminary model were below 0.1. We therefore employed a systematic sampling scheme (Brown, 1994; Gates et al. 1995), and selected every fifth cell in both row and column directions. This resulted in a sample size of ∼4% of the data ($n = 704$).

The dependent variables

The dependent variables were the 1992 cell-specific percentage cover of trees (TREE92), and the 1992 cell-specific percentage cover of herbaceous vegetation (HERB92). Both variables were arcsin-square-root transformed to stabilize the error variance (Weisberg 1985).

Table 1. List of potential predictors for the regression model. Square terms of the predictors and interaction terms between them were also tested for inclusion in the model.

Group	Variable	Measurement
1964 Vegetation conditions	TREE64	Proportion of trees in each grid cell in 1964
	SHRUB64	Proportion of shrubs in each grid cell in 1964
	HERB64	Proportion of herbaceous vegetation in each grid cell in 1964
Topographic variables	ASPECT-NS	North-south linear component of aspect angle (0°-180° scale, where N=0°, S=180° and E=W)
	ASPECT-EW	East-west linear component of aspect angel (90°-270° scale where E=90°, W=270° and N=S)
	SLOPE	Slope inclination
	Z	Elevation in m above sea level
Disturbance characteristics	LOWCATTLE	Value 1 for cells in areas with low cattle grazing regime, 0 for all other cells
	MODCATTLE	1 – moderate cattle grazing, 0 – other
	HIGHCATTLE	1 – high cattle grazing, 0 – other
	LOWGOAT	1 – low goats grazing, 0 – other
	MODGOAT	1 – moderate goats grazing, 0 – other
	FIRE	1 – inside the fire range, 0 – other

Model predictors

The potential predictors for the regression models were classified into three groups (Table 1): 1964 vegetation conditions, topographic variables and disturbance characteristics (grazing and fire). Dummy variables were created to represent the disturbance categorical data; for example, the variable LOWCATTLE accepted value of 1 for cells in plots with low intensity of cattle grazing and 0 in all other cells. Similarly, the variable FIRE accepted value of 1 for cells inside the actual range of the 1978 fire event and 0 for cells outside that range. Environmental variables may be related to vegetation non-linearly. We therefore fitted the square of each variable, as well as the variable itself, into the regression model (Gates et al. 1995). All possible combinations of first order interactions between the selected variables were also tested for inclusion in the final model. A forward stepwise selection procedure was used to select a set of predictors for the model.

One problem associated with spatially structured data, is that a predictor may be chosen for a regression model because it shares a common spatial structure with the dependent variable, regardless of causality (Legendre & Fortin 1989). To account for this possibility, the selected predictors were also subjected to the following procedure: A regression model was constructed, with TREE92 as the dependent variable. Easting, northing, their higher polynomials and their interaction terms up to a third order (x^2, xy, y^2, x^2y, y^2x, x^3, y^3) were included as covariates (Legendre 1993). A regression model including these spatial terms would partial out much of the large-scale spatial pattern in the data (Legendre 1993). Next, the residuals of that model were used as the dependent variable in a new regression model, where the predictors selected previously (using the stepwise procedure described above) were the independent variables. A significant effect of a predictor on these residuals is much less likely to be an artifact of spatial pattern. Only predictors that had a significant effect on the residuals were used in the final model for tree cover. A similar procedure was carried out for the herbaceous cover (HERB92).

Model assessment

Model fit was characterized using R^2. A validation data set was constructed, using the remaining 96% of the data, which were not used in model building. Parameters derived from the regression analyses were used to predict percentage cover of trees and herbaceous vegetation for each grid cell of the validation data set. The shrub cover was estimated as the remaining proportion. The correlation between actual and predicted cell-specific percentage cover of trees, shrubs and herbs was calculated to assess the fit of the models to the validation data set. Plots of the studentized residuals against predictions and against predictors confirmed compliance with model assumptions. The error independence assumption was inspected via maps of distribution of residuals in the study area, produced using the 'Grid' module of Arc-Info (ESRI 1996).

Results

Tree cover in the study area increased from 2% to 41%, and herbaceous vegetation cover decreased from 56% to 24% between 1964 and 1992. However, the vegetation changes that took place in the study area were not uniform; some areas have undergone rapid changes while other areas remained almost unchanged (Figure 2).

The increase in tree cover was negatively correlated with grazing intensity, while the change in herbaceous cover did not show any clear pattern with respect to grazing intensity (Figure 3). The increase in trees was clearly related to aspect; a sinusoidal pattern was found, with south-east facing slopes having the lowest rates of increase in tree cover, and north-west slopes having the highest values of change in tree cover (Figure 4a). The opposite pattern was found for the change in herbaceous vegetation (Figure 4b). The change in tree cover was positively related to slope, while no trend was found for the change in herbaceous vegetation (Figure 5). The change in tree cover showed non-linear relations when plotted against 1964 herbaceous cover (Figure 6). The change in herbaceous cover decreased monotonically with 1964 herbaceous cover, with a slight deviation where 1964 cover was >95% (Figure 6).

The regression model results indicated that both tree- and herbaceous cover were influenced by past vegetation conditions, topography and grazing (Table 2). Slightly different sets of predictors were selected for the two models (Table 2). All variables selected using the stepwise procedure were also significant after partialling out the large scale spatial structure (as described in the methods). The models for trees and herbaceous vegetation had an adjusted R^2 of 0.72 and 0.56, respectively.

In the tree cover model, all regression coefficients of grazing were negative, and coefficients of high grazing intensities were higher than those representing low grazing intensities. In contrast, in the herbaceous vegetation model all grazing coefficients were positive. This indicates that higher grazing intensity resulted in larger herbaceous cover and lower tree cover. This latter pattern was not detected in the univariate analysis (Figure 3b); it was revealed only when the effects of initial vegetation cover and topography were accounted for in a multiple regression.

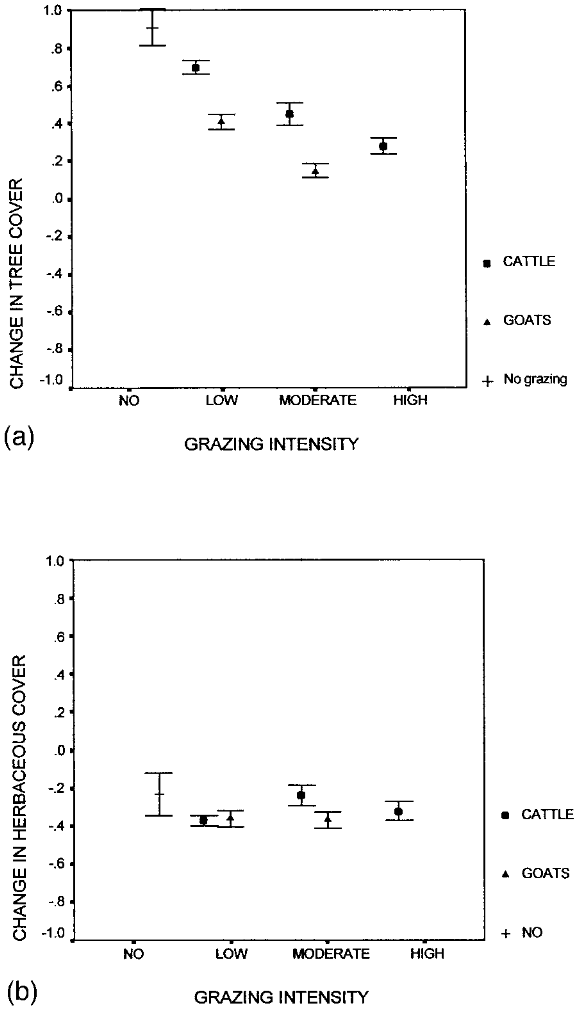

Figure 3. Change in cover of (a) trees and (b) herbaceous vegetation, between 1964 and 1992, as a function of grazing intensity (mean ± standard error). Change was calculated as (1992 cover) − (1964 cover).

The regression results further indicated an increase in tree cover from south- to north-facing slopes, and from- east to west-facing slopes. Herbaceous vegetation cover also related significantly to aspect angle, but in the opposite direction. Tree cover increased, while herbaceous cover decreased with slope inclination. Note that the latter pattern was not detected in the univariate analysis (Figure 5); it was revealed

Table 2. Predictors included in the final regression models. The dependent variables are cell specific percentage cover of trees and herbaceous vegetation, respectively.

Group	Variable	Regression coefficients in the trees model	Regression coefficients in the herbaceous vegetation model
	Constant	1.027 ***	0.372***
1964 Vegetation conditions	HERB64	−0.423**	NS
	$(HERB64)^2$	−0.310*	0.531***
Topographic variables	ASPECT-NS	−1.426E-03***	2.220E-03***
	ASPECT-EW	3.146E-03***	−1.082E-03***
	SLOPE	0.883*	−0.574**
	ASPECT-NS∗SLOPE	−4.123E-03***	NS
Disturbance characteristics	MODCATTLE	−0.356***	8.952E-02***
	HIGHCATTLE	−0.533***	0.117***
	LOWGOAT	−0.296***	9.745E-02***
	MODGOAT	−0.356***	0.222***

Significance level for each predictor is indicated by * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$.

only when multiple regression was used. In the tree model, the interaction between slope angle and the north-south component of aspect angle was also statistically significant. The effects of fire and elevation were not significant in both models. Analysis of the effects of topography on initial vegetation cover (in 1964) revealed no significant effect of slope or aspect on neither trees nor herbaceous vegetation cover in 1964.

The validation data-set was used to calculate correlation coefficients between actual and predicted cell-specific vegetation cover; these coefficients were 0.813, 0.616 and 0.720 for the tree-, shrub-, and herbaceous cover, respectively. Maps of the differences between actual and predicted cover of trees and the herbaceous vegetation show that certain patchiness exists in the distribution of errors (Figure 7).

Discussion

A major goal of our study was to assess long-term effects of grazing on vegetation dynamics. We found that grazing significantly inhibited vegetation succession. It inhibited both the transition from herbaceous to woody vegetation, and from non-tree vegetation to trees. It should be noted, however, that even in plots with relatively intense grazing, either by cattle or by goats, vegetation recovery was not halted.

Results from previous studies suggest that grazing may have simultaneous and contradicting effects on the dynamics between herbaceous and woody vegetation components. By browsing shrubs and trees, livestock can inhibit their growth (e.g., Seligman & Perevolotsky 1994; Tsiourlis 1998). In contrast, grazing may create niches for woody seedling establishment, by trampling and/or reducing the biomass of competing herbaceous vegetation (Miles & Kinnaird 1979; Vinther 1983; Mitchell & Kirby 1990; Alon & Kadmon 1996, Y. Shaharabani unpubl. data). Such an effect may lead to an increase in woody vegetation cover. We assume that the long-term effect of grazing on the dynamics of herbaceous and woody components reflects the net effect of these counteracting processes. In our study area, the net effect of grazing – by both cattle and goats was to inhibit woody vegetation recovery. The increase in woody vegetation recovery with decreasing grazing intensity is consistent with previous studies of Mediterranean vegetation dynamics, that found intensive grazing to decrease woody vegetation cover and increase herbaceous cover (McBride & Heady 1968; Joffre et al. 1988; Johnson & Fitzhugh 1990; Callaway & Davis 1993; Tsiourlis 1998; Tsiourlis et al. 1998; Giourga et al. 1998).

Goats browsing is known to inhibit tree growth (Perevolotsky & Haimov 1992). Our findings, that increase in tree cover at the landscape-scale, over several decades, is inversely related to goat grazing intensity, support this view. Moreover, it was found that cattle grazing leads to a similar (although weaker) result. It is often thought that cattle do not browse shrubs and trees, while goats do (Stuth 1990). However, in

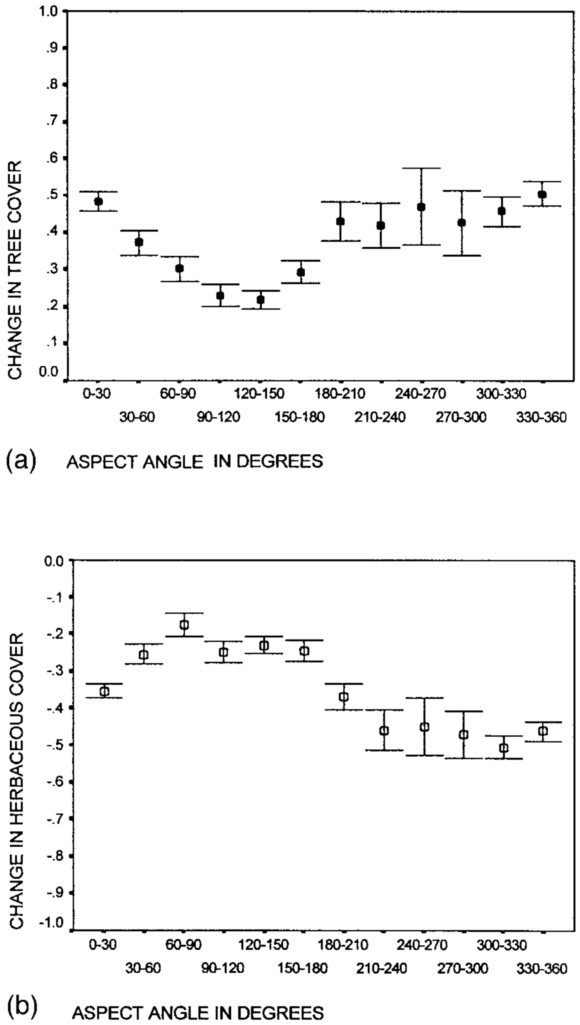

Figure 4. Change in cover of (a) trees and (b) herbaceous vegetation between 1964 and 1992, for different ranges of aspect angles (mean ± standard error).

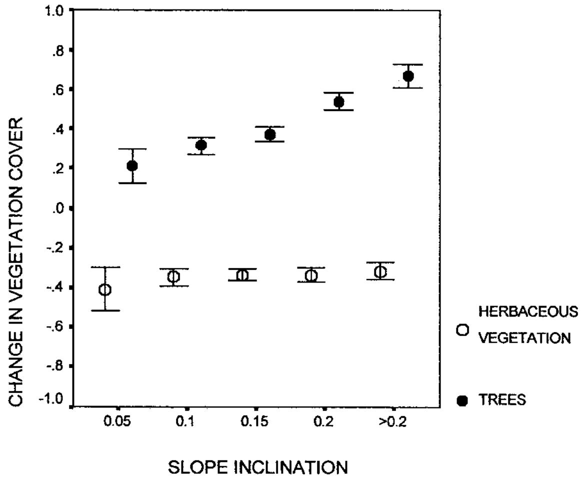

Figure 5. Change in cover of trees and herbaceous vegetation between 1964 and 1992, for different slope inclinations.

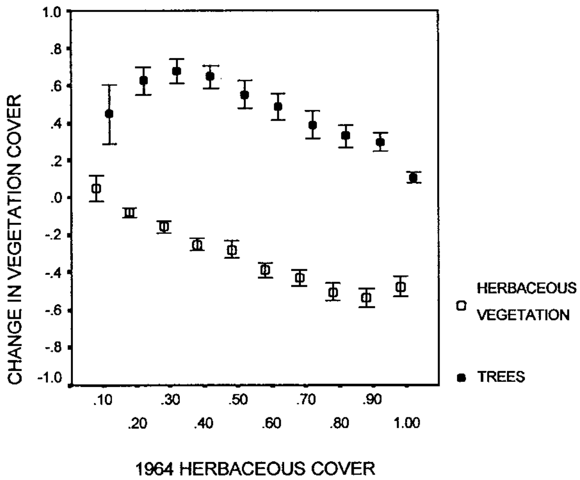

Figure 6. Change in the cover of trees and herbaceous vegetation as a function of 1964 herbaceous vegetation cover (mean ± standard error).

the study area, as well as in other Mediterranean areas, cattle were found to feed on woody vegetation – often the young branches of trees and shrubs (Gutman et al. 1990). This is to be expected, especially in early summer, when there is a shortage in herbaceous vegetation, and woody vegetation is still palatable (A. Perevolotsky pers. comm.). The effects of goats grazing vs. cattle grazing on vegetation recovery could not be compared, since the intensity of goat grazing (in terms of goats per unit area per unit time) could not be quantified in this study.

Noy-Meir (1998) addresses the question of the optimal grazing intensity recommended to minimize loss of floristic diversity in Mediterranean grasslands. He notes that a moderate grazing intensity is likely to maintain more species than either heavy grazing or zero grazing; yet, if any single grazing-intensity is applied uniformly throughout the landscape, a slow loss of species which are narrowly adapted to extreme conditions of zero grazing or heavy grazing, is likely to occur. Noy-Meir (1998) concludes that an optimal management strategy for conserving regional biodiversity in grasslands would therefore include diversification of grazing intensity over the landscape. Our study indicates that this conclusion may be similarly valid for Mediterranean woodland-scrub systems. The complex nature of our study area, where proportions of shrubs, trees and herbaceous vegetation vary across the landscape, was shown to be partly a result of the spatial diversity in grazing intensity. Such habitat complexity is likely to contain larger biodiversity than a more uniform distribution of vegetation formations, that would have resulted from a homogeneous grazing regime.

In the present study there were only one or two plots for each combination of grazing type and intensity. Therefore, the data are, to some degree, pseudoreplications (Hurlbert 1984). The nature of long-term, landscape-scale studies precludes replications in the way they are constructed in classical experimentation (Hargrove & Pickering 1992). However, this should not prevent ecological interpretations, especially where patterns and processes have been well documented (Hurlbert 1984; Carpenter 1990; Belsky 1992; Hargrove & Pickering 1992; Stewart-Oaten et al. 1992; Wahren et al. 1994). In this study, the effects of grazing were adjusted to other spatially heterogeneous factors, such as topography, by the use of multiple regression. In addition, an attempt was made to partial out the large-scale spatial structure of the data, by including easting, northing, and their higher polynomials in a preliminary regression analysis. Grazing was found to have a significant effect on the residuals of that regression. We therefore believe that our approach overcomes at least some of the problems associated with pseudoreplications and autocorrelation in landscape-scale studies.

Based on calculations of solar radiation, Holland & Steyn (1975) suggested that topographic effects on vegetation should be most pronounced in mid-latitudes (30°–60°). Several studies have shown that vegetation structure is more mesic on north-facing vs. south-facing slopes in Mediterranean type ecosystems (e.g., Armesto & Martinez 1978; Callaway & Davis 1993). This study examined topographic effects on vegetation dynamics, analyzing slope angle and aspect angle independently, as constant variables. It shows that vegetation dynamics is strongly affected by topography. We were able to characterize the pattern in which vegetation changes relate to aspect angle; Sinusoidal pattern was found, with north-west slopes having the largest rates of change and east and south-east – the smallest. Regression results showed that both linear components of aspect angle had significant effects on vegetation, corresponding to two gradients, a north-south and a west-east gradients. The former gradient is consistent with the common view of relations between solar radiation and vegetation. A possible explanation of the latter gradient lies in the local differences in wind-driven rainfall that is intercepted on sloping ground. As prevailing winds during rainfall come from the west and south-west, west-facing slopes characteristically receive more rainfall than east-facing slopes (Arazi et al. 1997; Sharon & Arazi 1997).

Topography had no significant effect on 'initial vegetation', in 1964. We assume that this is an outcome of the intensive disturbance regime prior to 1948, that left the entire area almost completely bare; at that point, both north-facing and south facing slopes were devoid of woody vegetation.

Several studies have converted slope and aspect to various indices of radiation or moisture, in an attempt to make them more biologically relevant and less location-specific (Kirkpatrick & Nunez 1980; Austin et al. 1984; Callaway & Davis 1993; Jobbagy et al. 1996; Pinder et al. 1997). However, as Pinder et al. (1997) noted, if vegetation does not respond similarly to gradients in slope and aspect – then keeping them separately would be preferred on any single index. Results of this study show that each topographic factor (aspect and slope) had an effect of its own on vegetation dynamics, while there was also a significant effect of the interaction between both factors. These effects could not be fully explained by solar radiation alone.

Elevation was found to affect vegetation structure in previous studies (e.g., Pinder et al. 1997), probably because of the correlation between elevation and climatic factors. At the scale of our study area, given the relatively small differences in elevation, the insignificance of elevation was expected. Similarly, the insignificance of fire should be attributed to the specific circumstances of our study, where only a single weak fire-event occurred during the period studied.

The maps of differences between actual and estimated vegetation cover revealed several patches of model errors. The interpretation of residual patterns from a comparison of observed and predicted vegetation maps may be complicated because differences can originate both from mapping errors and from inadequacies of the model (Davis & Goetz 1990). However, we found that some of the residual patterns were, in fact, interpretable, based on our knowledge of the studied region. Inspecting Figure 7, we identified some of the errors as mapping errors. Other errors were identified as small patches of marl, 10–100 m^2, that were scattered in the study area. Some of the remaining errors may point to latent environmental factors that are responsible for some of the spatial heterogeneity in the observed dynamics. Based

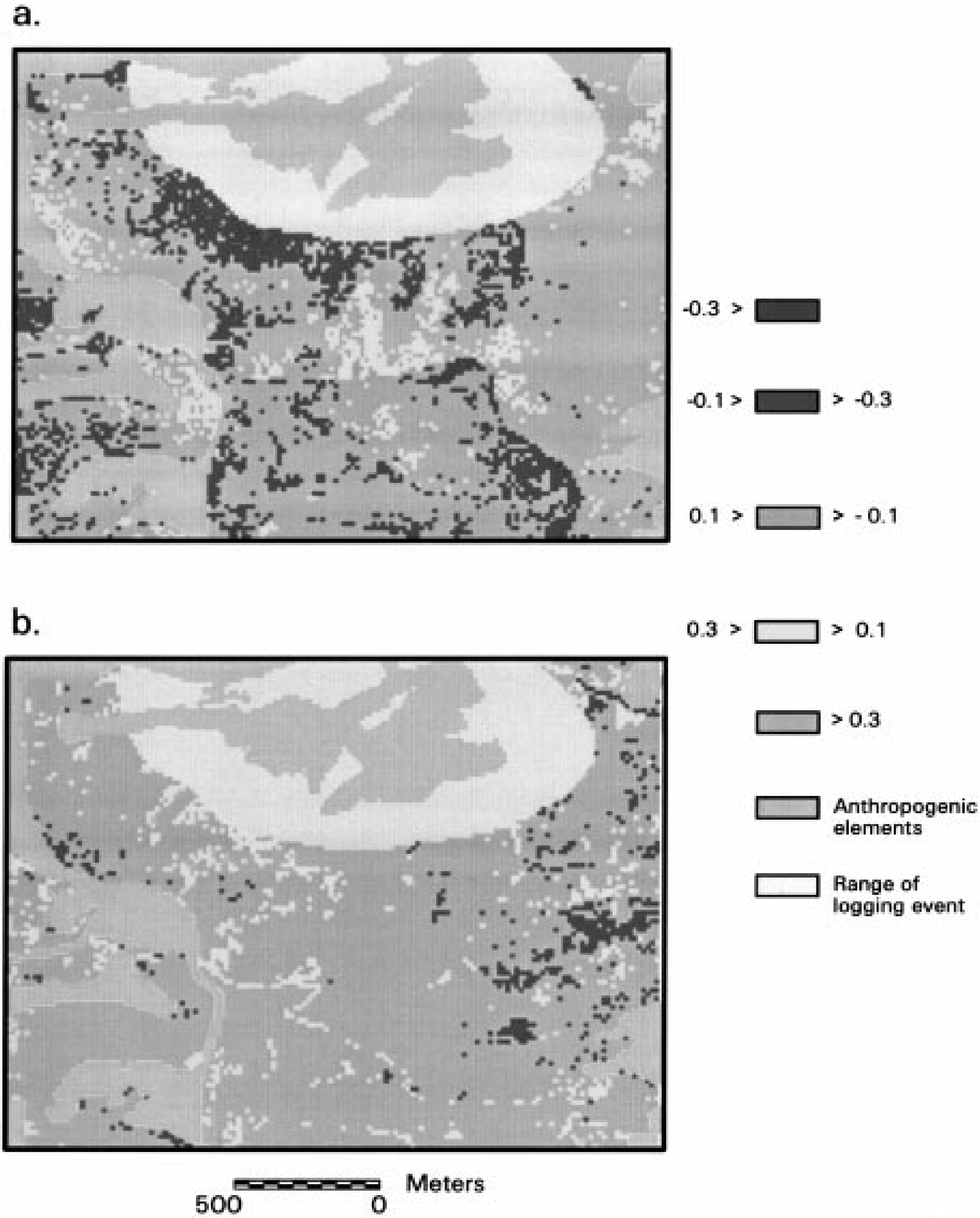

Figure 7. Differences between actual and predicted vegetation cover, for (a) trees and (b) herbaceous vegetation. Differences were calculated as [(actual cover) – (predicted cover)]. Anthropogenic elements include settlements, roads and agricultural areas. Range of logging event indicates areas of natural vegetation that were subject to a limited tree harvesting in 1980. Both types were excluded from all analyses. Modified and reproduced with permission from Opulus Press Uppsala, J. Veg. Sci. 9: 445–454.

on our familiarity with the area, we suggest three potential latent variables: small scale differences in soil type, local differences in grazing intensity that were not accounted for by the grazing plots, and other local, undocumented disturbances. These factors are almost impossible to map at the scale and resolution of our database. In spite of these limitations, our results indicate that landscape-scale vegetation dynamics can be fairly well modeled, using few biologically important variables.

Conclusions

The use of image analysis of aerial photographs enabled us to map current and historical vegetation of a relatively large area at a high resolution and high spatial accuracy. It was found that rapid succession processes occurred in the study area during the last 30 years. Efforts were made to document the history of various disturbance agents during the period studied, which culminated in maps of the range and extent of grazing, logging, fire, and topography. These attributes of the database, namely, high resolution, high spatial accuracy and extensive documentation of disturbance history, enabled us to assess long-term effects of grazing and topography on vegetation dynamics, disentangling them from other environmental factors. We found that grazing by both goats and cattle inhibited the establishment of woody vegetation and tree growth; yet, these processes were not halted even under relatively intense grazing. Slope and aspect strongly affected the rate of vegetation change, with the largest rates of change occurring on North-West facing slopes.

Acknowledgements

Special thanks to Ronit Nirel for her help in the statistical analysis. Adi Ben-Nun provided technical support with the GIS system. This study was funded by the JNF and was supported by the GIS center of the Hebrew University of Jerusalem. Michael Weinberger of the JNF Forest Department, Menachem Assaf of the Nature Reserve Authority, Yak Metek and Luciano Assin of Kibbutz Sasa provided valuable help in documenting disturbance history of the area. Avi Perevolotsky, Madhur Anand, Curtis Flather and Shimrit Lahav-Ginot provided valuable comments on a previous version of the manuscript.

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