The application of remote sensing to study shrub–herbaceous relations at a high spatial resolution

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ABSTRACT

Ecosystems of mixed woody and herbaceous vegetation are under increasing pressure and threat from human activity and global climate changes. Many processes that shape these ecosystems remain poorly understood despite their large geographic extent, the services they provide, and their importance for wildlife and livestock. Some of these processes occur simultaneously on small and large scales; therefore their study requires methodologies that combine high spatial resolution with large spatial extent. In this study, we explored the phenomenon of rings—“circlets”—of relatively dense herbaceous biomass that seem to occur around patches of Sarcopoterium spinosum in the semiarid northern Negev. We developed a novel, non-destructive method to estimate herbaceous biomass at a high spatial resolution, over an area of 1500 m². Steps in the study process included: low-altitude aerial photography, image rectification, delineation of shrub patches, computation of herbaceous biomass in the intershrub area, and analysis of herbaceous biomass as a function of distance from the nearest shrub. Our results confirmed the existence of circlets, and we estimated their width to be approximately 10 cm. Herbaceous biomass at the peak of the green season was approximately 40% greater in the circlet than in the remainder of the intershrub area. Circlets are probably an important feature of the ecosystem; since they covered ca. 20% of the intershrub area, their contribution to primary (herbaceous) production at the ecosystem level, and, in turn, to secondary production, is substantial. We discuss possible mechanisms in the creation of circlets, as well as the possible implications of circlets for range management and improvement.

Keywords: circlets, islands of fertility, motorized parachute, Sarcopoterium spinosum, semiarid rangelands

INTRODUCTION

Ecosystems of mixed woody and herbaceous vegetation cover 15–35% of the world’s terrestrial ecosystems, and they support a large proportion of global biodiversity and much of the world’s livestock production (House et al., 2003). Nevertheless, despite the importance of these ecosystems, our understanding of the processes and dynamics that shape them is poor. Increasing human press-
sure and the climatic changes that appear to be occurring on a global scale in the last decades have intensified the need for better understanding of these ecosystems. Such understanding aims to improve the scientific basis of management that seeks to minimize threats to these systems while, at the same time, enhancing the services they provide.

Most of the terrestrial ecosystems in Israel can be categorized as woody–herbaceous ecosystems; they change along the rainfall gradient from dry savannas in the south to dense Mediterranean woodlands in the north. The present study was conducted in the northern Negev—a transition zone between the arid and the Mediterranean zones. The vegetation in the study area, as in many water-limited ecosystems around the globe, includes distinct patches with higher levels of water availability, organic matter, and essential nutrients, which are often called “islands of fertility” (Aguiar and Sala, 1999).

The woody vegetation patches are scattered in a matrix of relatively bare soil, which is often covered by biogenic crusts (West, 1990), and populated by a diffuse pattern of herbaceous vegetative cover. The woody patches form mainly as a result of positive feedbacks between the vegetative biomass and the resources in the patch (Klausmeier, 1999). A patch begins with the establishment of a shrub seedling, often at microsites with ameliorated conditions such as animal burrows (Jones et al., 1994). The growing shrub slowly accumulates soil, dust particles, and plant litter close to its stem and beneath its spreading canopy. In a process enhanced by positive feedback, the contrast between conditions in the matrix and those in the vicinity of the shrub sharpens, and leads to source–sink relationships between the two patch types. During rain events, raindrops that fall in open spaces—especially those covered by the hydrophilic, biogenic soil crusts—create aboveground water flows that carry with them soil and other particles. When the water arrives at the soil mound under a shrub patch, the flow slows down and much of the water and particles are retained by the porous micro-topography of the mound. This horizontal redistribution adds water to that which falls directly on the shrub canopy, with the result that the shrub and its close surroundings receive a greater supply of moisture than they would if the ecosystem had been homogeneous (Aguiar and Sala, 1999). In addition, seeds, soil, and organic matter are transported to the patch by water, wind, and even animals, and are retained by the physical barrier that the patch presents.

These ameliorated conditions in the woody patch affect not only the shrubs, but also the herbaceous vegetation. Numerous studies on the herbaceous community in patchy landscapes found that annuals in the woody patches were more abundant (Tielbörger and Kadmon, 2000), more successful in production and reproduction (Holzapfel and Mahall, 1999), and more diverse (Wright et al., 2006) than those in the open spaces. These differences have been attributed by both theoretical and empirical studies to the shrubs acting as nurse plants, facilitating herbaceous growth by improving water availability and by protecting the herbaceous plants from solar radiation, high temperatures, and winds (Vetaas, 1992; Gilad et al., 2004).

The patchy arrangement of the woody vegetation strongly affects important ecosystem processes and factors such as flows of resources, dispersal units and individuals among patches, nutrient cycling, demographics and biodiversity, productivity, decomposition, water dynamics, and herbivory (Ludwig and Tongway, 1995; Aguiar and Sala, 1999). It also affects the retention and leakage of resources in and from the ecosystem, and thus affects the ecosystem stability and resilience (van de Koppel and Rietkerk, 2004).

While studying the physical structure of herbaceous vegetation around patches of prickly burnet (Sarcopoterium spinosum (L.) Spach.) at the Lehavim research station in the northern Negev, we noticed that, unlike their distribution in more arid zones, the herbs in Lehavim were not frequent under the shrub canopies, but were aggregated around their outer margins in ring-like formations that we called “circlets”.

In addition to theoretical interest in the phenomenon, studying the circlet pattern as a woody–herbaceous vegetation relationship in the context of landscape patchiness might yield important practical understanding. Since livestock production is a major use of this particular ecosystem, as in many semiarid ecosystems around the world, animals consume a large proportion of the vegetation, especially the herbaceous. If a significant proportion of that vegetation is produced in a certain spatial arrangement, understanding of that arrangement might have practical implications for sustainable management of these ecosystems in order to produce more forage while minimizing damage to long-term production potential.

Today, range managers in Israel regard woody plants, especially S. spinosum, as a competitor to the herbaceous vegetation, and use herbicides, fire, and cutting to eradicate the shrubs and thereby to increase herbaceous production, within the general objective of range improvement (Henkin et al., 1998). However, although shrub removal may have achieved this goal in the more humid areas of Israel (Perevolotsky et al., 2001), such practices may not be appropriate in the semiarid region, if herbaceous production is enhanced in the vicinity of
shrubs. Other management practices, which consider shrubs as potential facilitators rather than competitors, should be considered and tested.

The only previous reports of the circlet phenomenon in the scientific literature derive from one area—the Patagonian steppe in Argentina. In a patchy ecosystem similar to that in the present study, Soriano et al. (1994) and Cipriotti and Aguiar (2005) described “rings” of grasses encircling shrubs; they reported on the presence and completeness of rings around shrubs of various sizes, and under several different sheep-grazing regimes. As discussed below, there are several differences between the present phenomenon and that observed in Argentina, not least with regard to precipitation and the composition of the herbaceous population. Nevertheless, comparison between the two environments enables us to gain better understanding of the pattern and its possible implications.

The overall purpose of this study was to determine whether herbaceous circlets are indeed meaningful features of the study area. Specifically, we aimed to examine the spatial relationship between S. spinosum shrubs and the herbaceous biomass in the surrounding intershrub area, and to discuss their contribution to primary production at the ecosystem scale. Because of the high spatial heterogeneity of the landscape, a further aim was to develop a method for evaluating and mapping herbaceous biomass that would be of high resolution and accuracy, yet would enable data from a relatively large area to be gathered and processed. Our approach was to map the spatial distribution of herbaceous biomass across the landscape in relation to distance from the edge of the nearest shrub canopy. We thereby sought to determine from the raw data whether the circlets are a real phenomenon, as well as their size and biomass. Herbaceous plant biomass is very dynamic in time, and in this study we limited the analysis to peak season conditions.

METHODS

The study area

The study was conducted at the Lehavim LTER (Long-Term Ecological Research) station (31°21′52″N, 34°49′46″E) in the northern Negev region. The climate is semiarid, with mean annual precipitation of 300 mm. The terrain is hilly with slopes ranging from 0 to 24°, with a mean of 11°. Average elevation is 370 m asl.

The landscape is highly heterogeneous, comprising a mosaic of shrubs—mainly S. spinosum—intershrub spaces, and exposed rock. The herbaceous vegetation is dominated by annual species (Danin and Orshan, 1990; Osem et al., 2002). Annual seedlings emerge two to four weeks after the first heavy rains, typically between October and December, grow most rapidly in the spring (March and April), and set seed and desiccate at the start of the dry season in May. From January or February to May, the farm is grazed quite heavily by two flocks of 500 sheep and 200 goats, which are released from a central corral for a daily grazing excursion of around 7 h, accompanied by shepherds (Arnon et al., 2005). The flocks return to the corral at the end of the day and remain there overnight.

The experimental plots

The experimental plots were established in December 2003 on a moderately steep (ca. 16°) northwest-facing slope. A gated perimeter fence, 1.2 m high, was erected around an area of 1500 m² to prevent uncontrolled grazing. Within this area, 20 plots, each measuring 3 × 3 m, and centered on a well-developed shrub patch surrounded by an intershrub area, were selected at random. The plots were randomly allocated to four treatments, comprising the factorial combinations of grazing (yes or no) and removal of the shrub canopy (yes or no). The no-grazing plots were individually fenced.

This paper deals with the “control” treatment, i.e., the plots that were neither cut nor grazed, since our focus is on the central question regarding the existence of herbaceous biomass circlets and the remote sensing methodologies used to address this question. There were four replicate plots for this treatment.

Aerial photography

To obtain aerial photographs of high resolution, we used a motorized parachute that flew at a low altitude of about 40 m, and yielded pixel resolutions of 2.0 to 2.4 cm. Photos were taken around midday, when the sun is closest to the zenith, with a Fuji FinePix 6900 Zoom digital camera.

An aerial photo was taken every three weeks, from the beginning of February to mid-April 2004. In order to analyze shrub–herbaceous relations at the peak of the growing season, we used a photo obtained on 20 March 2004 (Fig. 1).

Image rectification

We geo-referenced the parachute photograph in order to ascribe spatial coordinates to each pixel and thereby enable us to analyze it in a spatial context. For that purpose, we distributed 224 white plastic squares, each measuring 25 × 25 cm, over the study site before the photograph was taken. We then measured the coordinates of each square in an X–Y space, using a laser-based total station, with the northwest corner of the perimeter fence
serving as point 0, 0. We used the ERDAS IMAGINE (Leica Geosystems, Inc.) image-processing software to mark the targets (the plastic squares) as ground control points (GCPs), and to rectify the photo with the affine transformation method.

The root-mean-square distance between the true location of the GCPs and their computed location was 2.6 pixels for the image analyzed in the present study. Multiplication by the pixel resolution of 2.3 cm yields a mean deviation of about 6 cm between a given point in the image, and its location in the real world.

**Calibrating biomass and DN**

The method we developed to estimate herbaceous biomass per unit area is based on the inverse relationship between vegetation cover and amount of biomass on a given surface, and the amount of light reflected from the surface (Dancy et al., 1986). Bare ground presents a relatively homogeneous surface that reflects large proportions of the incident light, and therefore appears bright in an aerial photograph. As the biomass increases, the surface becomes more heterogeneous, and light beams that hit the vegetation are either scattered or absorbed by plant pigments and tissues. As a result, vegetated areas appear darker than bare surfaces (Herwitz et al., 2000).

On the basis of the relationship between the brightness at a certain location in the image and the biomass at the corresponding location in the field, we formulated a calibration function to predict biomass from brightness data. To do so, we used the numerical value assigned to a pixel in a digital format, i.e., the digital number (DN). We used the standard format of RGB (red, green, blue) layers and 8-bit representation of the DN, which ranges from 0 for a completely black pixel to 255 for a completely white one. These three values for each pixel formed the basis for the regression analysis that was used to derive a calibration function.

Before the aerial photograph was taken, 17 inter-shrub patches, each about 0.65 m² in area, were selected in the vicinity of the experimental plots and framed with brightly colored marking tape, so that they could be easily recognized in the aerial photo. These patches were selected to represent the range of biomass levels present in the experimental plots—from nearly bare soil to densely vegetated patches. After the photo was taken, we placed three 10 × 10 cm quadrats in every framed patch, and recorded their distances from the marking tape. We clipped the vegetation inside each quadrat to ground level, dried it for 48 h at 60 °C, and weighed it. We used the ARCGIS software (ESRI, Inc.) and the marking tape to locate the precise position of each patch on the aerial photograph, and delineated three 10 × 10 cm “virtual quadrats” inside it, according to the distance from the marking ribbon measured in the field. We then calculated the mean R, G, and B values of DN for the pixels inside each quadrat. These mean DN values for the R, G, and B layers were used to set up the calibration equation to predict biomass per unit area. The non-negative garrote regression method was employed, which is preferable to the usual least-squares multiple regression when the intention is to derive a prediction equation (Breiman, 1995).

The following calibration equation was obtained by the non-negative garrote regression:

\[ \log(V) = 4.75 - 0.000083 \times R \times G - 0.00025 \times R \times B + 0.00011 \times G \times B \]

where \( V \) = herbaceous biomass (g/m²), and \( R, G, \) and
The tile was excluded from the analysis if the number of exposed rock, there were in the tile. If this number was less than nine (i.e., 50% or less of the pixels in the tile) exposed rock, the tile was treated as an herbaceous tile, and the program computed: (i) the average distance of the herbaceous-type pixels from the nearest pixel defined as shrub; and (ii) the herbaceous biomass of the tile, which it did by applying the calibration equation to the average R, G, and B DN values of these pixels.

The reason for using the 50% threshold was that every pixel affects its neighbors. If there are too many pixels in a tile that are not depicting herbaceous vegetation, they might bias the calibration results for that tile, although their DN values are not included in the calculation itself. Specifically, pixels depicting a shrub or shade might cause their neighboring herbaceous pixels to appear darker. Since such mixed tiles are to be found at the margins of the shrubs, this would have caused those tiles to appear as having more biomass, and the circling to appear even more lush and distinct.

Omitting such mixed tiles near the shrubs did not bias the results regarding the biomass/distance relation in any way, since they were simply regarded as missing data, and were not used in the numerical analyses.

**Image processing**

The distinction between the shrub patches and the background matrix was based on visual interpretation. We used ARCGIS to digitize polygons for each shrub in the four experimental plots of the control (ungrazed, uncut) treatment. Because of an unavoidable shadow of the shrub created by direct sunlight (mainly around the west edge of the shrubs), we marked these shaded areas separately to exclude them from the analysis. Areas of exposed rocks were similarly marked and excluded from the analysis. We overlaid these vector-type layers of shrubs, shadow, and exposed rock onto the photograph, in order to assign a code value to each pixel. Four categories were defined for this purpose: shrub, shadow, rock, and herbaceous, i.e., not shrub, shadow, or rock. Areas of bare or crust-covered soil were still considered “herbaceous”, since they represent the lower extreme of herbaceous biomass. Pixels that fell within the boundaries of a shrub were used for calculating distances of herbaceous pixels from them, but not for calculating biomass. Pixels of shadow or rock areas were omitted from the analyses.

After carrying out these procedures, we exported the picture as a numeric matrix consisting of the following dimensions: X and Y coordinates of the pixel center; a binary code indicating whether the pixel was situated in shrub or intershrub space; replicate number of the experimental plot (1–4); and three DN values, each in the range 0–255, in the red (R), green (G), and blue (B) layers.

**Tiling**

The next step was to downscale the high spatial resolution of the photo (ca. 2.3 cm) to the lower resolution of the clipped samples (10 cm) that were used to calibrate the relationship between DN and biomass.

To do that, we analyzed the data with a purpose-built Matlab program (The MathWorks, Inc.). The program first created tiles of 4 × 4 pixels (equivalent to 9.8 × 9.8 cm) covering the entire surface area of each experimental plot. Since a tile can contain pixels of more than one category, the program then determined how many herbaceous-type pixels, i.e., not shrub, shadow, or exposed rock, there were in the tile. If this number was less than nine (i.e., 50% or less of the pixels in the tile) the tile was excluded from the analysis.

Otherwise the tile was treated as an herbaceous tile, and the program computed: (i) the average distance of the herbaceous-type pixels from the nearest pixel defined as shrub; and (ii) the herbaceous biomass of the tile, which it did by applying the calibration equation to the average R, G, and B DN values of these pixels.

**Statistical analysis**

In order to examine graphically the relationship between biomass and distance from shrub, and to analyze this relationship statistically, the distance variable was discretized and the mean biomass was computed for each distance category within each replicate plot. Several different sizes of distance category were examined, ranging from 1 to 10 cm. The standard error of the biomass estimate for a distance category was based on the four values thus obtained for the four replicate plots. The data set for analysis comprised 1646 records, each representing one tile for which the herbaceous biomass per unit area was computed. The number of records (tiles) from each replicate experimental plot ranged from 356 to 452.

Analysis of variance (ANOVA) was applied to the biomass values obtained at the lowest spatial resolution of 10 cm. The distance category was treated as a categorical variable. The herbaceous biomass for a given distance category within a replicate plot was represented by the mean biomass of all tiles in the plot at that distance. Terms in the model were replicate plot and distance category.

Linear and non-linear regression analysis was applied to the replicate-level averages for the 1-cm category size. This data set comprised 158 records. Analysis of covariance was used for the linear model, with Replicate plot, Distance (as a continuous covariate), and their interaction, in the model. For the non-linear model, we used the first-order decay kinetics equation from the non-linear modeling procedure of the JMP statistical software package (SAS Institute, Inc.). The functional form is:
\[ Y = \theta_1 \exp(-\theta_2 X) + \theta_3 \]

where \( Y \) is the herbaceous biomass, \( X \) is the independent variable (distance from shrub), and \( \theta_1-3 \) are fitted parameters. The number of tiles within replicate and distance category was used as a weighting factor in both the linear and non-linear models.

**RESULTS**

**Biomass distribution in relation to distance from shrubs**

Figure 2 illustrates (for visual impression only) how circlets appear around *S. spinosum* shrubs. It shows the phenomenon in the field—more luscious vegetation close to the shrubs (2a)—and its quantitative representation as biomass (shown here as discrete levels) following image processing and implementation of the calibration equation (2b).

Figure 3 shows the relationship between the mean biomass per unit area in a tile and distance from the shrub, for a range of distance category sizes. Although all the category sizes show a clear trend of declining biomass with increasing distance from the shrub, the pattern obtained at the finer spatial resolution (smaller category sizes) suggests that there is a much stronger...
In the analysis of variance of herbaceous biomass based on 10-cm distance categories, the effect of distance category was highly significant ($p < 0.0001$), and the biomass in the distance category closest to the shrub (0–10 cm) was significantly greater than that in the other distance categories, according to the Tukey–Kramer test. Biomass in the 0–10 cm category (59.4 g/m$^2$) was 38% greater than the average biomass in the more distant categories.

In the analysis of covariance model for biomass as a function of distance from shrub, the overall $F$-statistic was highly significant ($p < 0.001$). The effect of distance from the shrub edge was highly significant ($p < 0.001$) and the coefficient was negative, indicating a decline in biomass with increasing distance. Both the intercept and the slope of the linear function differed significantly among the replicate plots.

The non-linear regression analysis yielded a function that better fit the shape of the decline in biomass with increasing distance from the shrub. The parameter values that were obtained for $\theta_1$, $\theta_2$, and $\theta_3$ were 32.6, 0.074, and 37.9, respectively. Figure 4 shows this function together with the global means for biomass according to distance category.

**DISCUSSION**

**Circlets—herbaceous biomass in relation to distance from shrub**

Our study confirms the existence of a spatial relationship between *S. spinosum* shrubs and the herbaceous biomass in the surrounding intershrub area. Herbaceous biomass was greatest close to the edge of the shrub canopy, and declined with increasing distance from it.

Although the decline in herbaceous biomass with increasing distance from the shrub was not a sharply angled step function, there was a band, approximately 10 cm in width, that contained relatively dense vegetation, and which we refer to as an herbaceous circlet.

The higher biomass in the circlet could be achieved in several ways: (a) larger individuals; (b) more individuals, i.e., higher densities; and (c) larger species. Our study did not address the demographic or physical characteristics of the herbaceous communities in the circlet, in the open spaces, and under the shrub canopy. However, other studies at the same site (Osem et al., 2007) and in a nearby, dryer site (Wright et al., 2006) have found significant differences between the areas under the canopies of shrub species (including *S. spinosum*) and the intershrub areas, in terms of the size of individuals of various herbaceous species, plant density, and species composition. Any of these differences, alone or in combination, may prevail in the circlet, which is a transition zone between the open and under-canopy patch types.

One of the questions raised by the circlet phenomenon is: Why is it found in the semiarid zone of Israel, and not in the arid zone? As mentioned before, many studies of patchy landscapes in arid zones of Israel and throughout the world have reported that annuals are more abundant under the canopies of shrubs than in the open patches. Is there a connection between the differences in precipitation and differences in the ecological relationship between shrubs and herbs which, in turn, is manifested as a change in the spatial relationship between the two life forms?

One possible explanation stems from the stress-gradient hypothesis, which predicts that as abiotic stress decreases, the relationship between neighboring plants will shift from facilitation to competition (Lortie and Callaway, 2006). According to this scenario, plants in Lehavim receive more precipitation than those in more southerly locations, and compete with one another for resources. Thus, a facilitative effect of the shrub on herbs beneath its canopy turns into competition—either relatively passive (competition for water, light, and nutrients), or more aggressive (e.g., allelopathy). This increase in competition causes the area in which the shrub exerts a positive net effect on herbs to shift from...
under the shrub canopy to its outer margins. However, this explanation does not fit the ring patterns observed by Soriano et al. (1994) in Argentina; the mean annual precipitation in their study area was only 142 mm.

Despite the similar patterns, there is a major and potentially crucial difference between the composition of the rings reported by Soriano et al. (1994) and Cipriotti et al. (2005), and the circlet formation reported here. In the Lehavim area, the circlets consist of annual species and are, therefore, formed every year by new individuals that reoccupy bare spaces around the shrubs, which had been cleared by summer grazing of livestock and wind erosion.

In the Patagonian steppe, on the other hand, the rings are composed mainly of three species of tussock grasses—perennials that do not go through a dormant phase. It has been shown that once established, perennial grasses in the Patagonian steppe compete strongly for soil water (Aguiar et al., 1992). Therefore, the ring formations reported from the Patagonian steppe seem to be the result of continuous, year-round processes that persist for many years, whereas the circlets of the northern Negev are formed by seasonal processes, whose dynamics might change from year to year.

The implications of circlets

From analysis of the aerial picture of the study site (Fig. 1) we estimated the relative cover of shrubs, circlets, and the remainder of the inter-shrub area, on the assumption that there was a circlet 10 cm in width around each shrub. This analysis yielded 30, 13, and 57% cover for shrubs, circlets, and the remainder of the inter-shrub, respectively. Thus, the circlets constitute 19% of the inter-shrub area.

If the biomass density in the circlet is approximately 40% greater than that at greater distances from the shrub, the herbaceous production in circlets constitutes 26% of the total herbaceous production of the ecosystem. It is noteworthy that Soriano et al. (1994) also found that grass rings made a high contribution to production (44%) relative to their cover (18%).

In addition to their contribution to primary production at the ecosystem level, circlets might have implications for the dynamics of the herbaceous community. Germination, establishment, and seed-set by herbaceous vegetation are more difficult in the open spaces. This may be due to biotic factors such as seed predation (West, 1990), inhibition of germination and growth by the well-developed crusts (Zaady et al., 1997), and grazing by herbivores (Osem et al., 2007), or abiotic factors such as relative lack of water and nutrients (Schlesinger and Pilmanis, 1998; Gilad et al., 2004), and greater exposure to radiation and wind (Vetaas, 1992). Therefore, the survival and seed-set of some species may occur primarily in the circlets, and the circlets may serve as a seed source for the open patches, especially in dry years. Thus, although the individual circlet covers a relatively small area it may have an effect on larger scales, up to the ecosystem scale, because of its special features.

Cipriotti et al. (2005) inferred, by examining patches under different sheep grazing pressures (intense, light, and none), that the rings did not form because the shrubs protected their adjacent neighbors from herbivores. Our results agree with this inference: the study plots we monitored were all protected from grazing, and circlets still appeared in those plots. Of course, this does not exclude long-term processes, which might be affected by herbivore activity such as trampling and soil compaction.

Methodology

The method we developed to study the spatial distribution of herbaceous production proved to be an efficient tool in that it was non-destructive, enabled estimation over a large and continuous area, and achieved a high spatial resolution. Once mastered, it is also fairly easy to employ since it does not require special equipment, other than the means to take aerial pictures at a low altitude. Current options include motorized parachutes (as used in this study), unmanned aerial vehicles (Hardin and Jackson, 2005), and tethered balloons (e.g., www.skyballoons.co.il). Further development of the method may include using images in the near-infrared light range, which is highly correlated with vegetative biomass (Everitt et al., 1989).

Despite its advantages, the method we developed has two major shortcomings, which stem from the fact that the shrubs are objects with a height dimension. This inevitably results in some proportion of the area surrounding the shrub being blocked from view by the shrub canopy, or falling in its shadow. Such areas remain unmapped and, in the latter case, are difficult to exclude automatically from the analyses and require manual processing of the images.

Open questions

Our present findings raise several questions for future studies. What are the underlying factors that increased production in the circlet (e.g., different species, larger individuals, more individuals)? Do sections of the circlet differ according to their position relative to the shrub (upslope, downslope, or parallel)? How do the properties of circlets respond to seasonal rainfall? What is the ecogeographical extent of the circlet phenomenon? Answers to these questions will contribute to better understanding and management of patchy landscapes.
CONCLUSIONS

We conclude that circlets of enhanced herbaceous biomass do, in fact, develop around shrubs of *Sarcopoterium spinosum* in the northern Negev region of Israel. Circlets contribute a larger proportion of primary production than their proportional cover, and thus probably affect secondary production too. It appears that grazing is not the main force that shapes this spatial phenomenon, but rather that the regulation of resource (especially water) availability by shrubs creates favorable conditions for herbaceous annuals to establish and mature.

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REFERENCES


