Rainfall, topography and primary production relationships in a semiarid ecosystem

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ABSTRACT

A series of 15 Satellite Pour l’Observation de la Terra XS images, which were acquired during a single growing season, were used to study the spatial and temporal relationships between topography, rainfall and aboveground net primary production (ANPP) of annuals in a semiarid environment. A digital elevation model was used to locate five physiographic units: interfluve, shoulder, backslope, foot slope, and channel, along the slope catena. ANPP values were then surrogated by the normalized difference vegetation index (NDVI). Four phenological phases were interpreted from the seasonal NDVI profiles: germination, green-up, drying, and senescence. A significant difference between NDVI values of all physiographic units was found, mainly during the green-up phase. NDVI values at peak season were characterized as high meaningfully high NDVI values, due to run-off distribution and a thick soil profile. The seasonal NDVI integral was related positively and linearly to model-derived water availability values for all physiographic units and the NDVI was correlated to multiple-timescale rainfall data and the length of dry spells. The 1-month rainfall data were found to have the highest correlation with the NDVI, indicating lag and cumulative effects of rainfall on production. This implies that the time required for the plants to use the water for production is around a month. It is concluded that studies of ecosystem functioning and capabilities in semiarid environments should consider not only mean annual rainfall amounts, but also the temporal rainfall distribution, mainly on a monthly scale, and the effect of physiographic units. Copyright © 2010 John Wiley & Sons, Ltd.

INTRODUCTION

Aboveground net primary production (ANPP) is one of the most important indicators of ecosystem capabilities, functioning, and resource utilization efficiency (Jobbagy et al., 2002; Cao et al., 2004). In dry environments, water is the limiting factor for vegetation growth (Noy-Meir, 1973; Rodriguez-Iturbe et al., 1999) and rainfall, as the prime water source, is considered to be a critical factor that regulates ecosystem production. As the field of ecohydrology is aimed to improve understanding of processes at the interface between hydrology and ecology, information on the way through which rainfall and surface hydrology affect vegetation production is sought by ecohydrologists studying semiarid areas (Turnbull et al., 2008; Lauenroth and Bradford, 2009).

Previous studies have tried to relate rainfall amount and satellite-derived vegetation production empirically (e.g. Tucker et al., 1991; Paruelo and Lauenroth, 1997; Tucker and Nicholson, 1999; Sannier et al., 2002; Hill and Donald, 2003; Hunt et al., 2003; Chhabra and Dadhwal, 2004; Kogan et al., 2004), mainly by using data acquired from low-to-moderate resolution images of the advanced very high-resolution radiometer (AVHRR), Satellite Pour l’Observation de la Terra (SPOT)-Vegetation, and the moderate resolution imaging spectroradiometer (MODIS) systems (Nagler et al., 2007). With spatial resolution of a few hundred meters to a few kilometres, these systems are characterized by a high temporal resolution of 1 day that enables accurate temporal studies of ANPP along the growing season. Spatially speaking, research with such images provides good understanding of regional and even global phenomena. However, consideration of soil and topographic effects on rainfall—production relationship is limited. As a result, little has been concluded about the effect of hydrological processes on spatial and temporal variabilities in vegetation production, at the landscape scale of physiographic units (Imeson and Prinsen, 2004).

The physiographic unit is a well-established entity in geomorphological studies. Generally, the slope is defined as a three-dimensional body extending from the interfluve to the channel bed (Conacher and Dalrymple, 1977). According to this partition, each point on a slope is allocated to one of nine physiographic units that have distinct pedogenic characteristics, reflecting the influence of soil–water–gravity interrelationships governed by surface forms. Based on the idea of possible links between physiographic units, run-off and sediment flows, and soil formations, Park et al. (2001) developed a method, using a digital elevation model (DEM), to predict six physiographic units: interfluve, shoulder (seepage slope and
convex creep slope), backslope (free face and transportation midslope), footslope (colluvial footslope), toeslope (alluvial toeslope), and channel (channel bed and walls). These units can differ with geological conditions. In a recent paper, Svoray et al. (2008a) distinguished, at the Lehavim Long Term Ecological Research (LTER) site, five physiographic units: interfluve, shoulder, backslope, footslope, and channel (Figure 1). On the scale of physiographic units, the effect of hydrological processes, such as infiltration, percolation, and run-off, on soil water storage is highly complex. Rainfall and surface characteristics can affect the above hydrological processes and therefore, water redistribution in space and time (Beven and Kirkby, 1979). If antecedent soil water conditions do affect vegetation production, rainfall amount per se is not the only characteristic to control vegetation patterns at this scale. The question that arises, therefore, is: to what extent water redistribution between the physiographic units affects production processes? The answer to this question is not trivial (Wilcox et al., 2003) and is beyond the scale of the coarse resolution images.

According to the pulse-reserves hypothesis (Noy-Meir, 1973) there are ‘effective’ rainfall events that are more important than others for vegetation growth—those that stimulate plant growth, rather than the total, i.e. the accumulated amount of rainfall in a given season. This model applies mainly to grasslands, but it ignores the effects of soil water conditions and rooting systems (Reynolds et al., 2004). Another paradigm that relates rainfall to vegetation in arid areas is the Walter two-layer hypothesis (Walter, 1971), which predicts that seasonal rainfall characteristics determine large-scale patterns in community composition. To a large extent, composition is determined by soil water conditions, and the coexistence of herbaceous vegetation and shrubs occurs due to the difference in their rooting systems. The main dilemma between the two hypotheses is the importance of antecedent soil water to ecosystem productivity. So far, the two hypotheses were found to be imperfect when confronted with field observations, so there is still a need to better understand the mechanism through which rainfall characteristics and/or antecedent soil moisture conditions affect ANPP variation in the slopes of semiarid areas (Ogle and Reynolds, 2004).

The aim of this paper is to explore the effect of physiographic units and rainfall intervals on spatial and temporal dynamics of normalized difference vegetation index (NDVI) (as a surrogate for ANPP) at a semiarid environment. We use 15 high-resolution multispectral images from the growing season 2002–2003 and ask the following two questions: (i) Do physiographic units affect spatial variation in NDVI? (ii) What is the time lag of vegetation response to rainfall on this scale?

We hypothesize that (i) water distribution through topography substantially influence ANPP variation. Wetter physiographic units are expected to be more productive, whereas physiographic units with poor water availability will show lower NDVI values. And (ii) because soil moisture conditions are assumed to affect production, we assume that biomass growth response to rainfall will not be immediate and that dry spells will have a relatively low effect on NDVI.

**METHODOLOGY**

**Study site**

The LTER site at Lehavim (31°20′N, 34°45′E) is located in the Northern Negev area in Israel, with an average rainfall of 270 mm per annum, falling in the winter. The mean annual temperature measured at the site is 20.5°C, with a maximum and minimum of 27.5 and 12.5°C, respectively (data obtained from the Meteorological Survey of Israel). The terrain is hilly and the area is divided by an east–west ephemeral stream. The dominant rock formations are Eocene limestone and chalk with patches of calcrete. The soils are brown lithosols combined with arid brown loess. The vegetation is characterized by scattered dwarf shrubs and patches of herbaceous vegetation, mostly annual, interspersed between rocks and the dwarf shrubs (Ungar et al., 1999). The dwarf-shrub community shows diffuse vegetation and the herbaceous vegetation appears shortly after the first rains and persists as green forage for 3–4 months. The herbaceous vegetation is highly diverse, comprising mostly annual species that form 56% of the regional flora (Danin and Orshan, 1990). Osem et al. (2002) reported on 130 annual species at Lehavim, of which 15 species contribute 85% of the total average abundance and aboveground biomass of the annuals. The predominant functional groups are grasses (46% of total abundance and 51% of aboveground biomass) and legumes (9 and 21%, respectively).

**Experiment design and sampling**

This research is part of a long-term study of dynamics in vegetation production at the Lehavim LTER site. Field data and data from water availability modelling were acquired from previous studies (Svoray et al., 2008b).

Experimental design and sampling in the current research use satellite data in the five physiographic units, each

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**Figure 1.** The slope cross-section with the pedogeomorphic units along the catena.
is dominated by annual herbaceous vegetation. The model by Park et al. (2001) and a contour-based DEM, with 25 and 10 m vertical and horizontal resolutions, respectively (Hall et al., 1993), were used for mapping five physiographic units: interfluve, shoulder, backslope, footslope, and channel over the entire Lehavim area.

For each of the five physiographic units, five replica plots, each located in different slope in the watershed, were selected to represent the intra-unit variation due to characteristics such as solar radiation flux, rock and stone cover, and soil properties. Each of the 25 replica plots is composed of several DEM cells (9 < n < 35). Replica site selection was performed randomly in the areas dominated by herbaceous vegetation (stratified random sampling), using the ARCGIS random function. The suitability of the Park et al. (2001) model for the Lehavim site was tested against field data (n = 22 observations per unit), using confusion matrices that yielded an overall accuracy of >75%.

Satellite data

Fifteen SPOT XS images, at 20 m spatial resolution, were acquired at different dates throughout the growing season of 2002–2003. For the radiometric correction, digital numbers (DN) were converted to radiance $L$ (W m$^{-2}$ sr$^{-1}$ µm$^{-1}$) using Equation (1):

$$L = \frac{DN}{a} + b$$

(1)

where $a$ and $b$ are the gain and offset calibration coefficients, respectively. In the SPOT data, the offset is always equal to 0 and thus, only the gain, which depends on the system and changes with time, was obtained for each band from the image header file. For atmospheric correction, the second simulation of satellite signal in the solar spectrum (6S) software (Vermote et al., 1997) was used. Sun and satellite geometry parameters were acquired from the header file. Values of aerosol optical thickness (AOT) at 550 nm and water vapour content were obtained from a sunphotometer located at the Jacob Blaustein Institutes for Desert Research of Ben-Gurion University of the Negev (Sede Boker AERONET site). The ozone content was derived from the total ozone mapping spectrometer (TOMS) sensor aboard the Nimbus-7 spacecraft. Final product of the atmospheric correction procedure was an image in reflectance ($\rho$) values.

The geometric correction procedure was carried out with the ERDAS IMAGINE software. As a first step, one image was registered to a 1:50 000 digital map, using ground control points (GCP), in the New Israeli Grid projection, with a root-mean-square error (RMSE) of less than one pixel. The first corrected image was used as the reference for the other images by image-to-image correction techniques (with RMSE < 0.5). Following the pre-processing procedures, NDVI values were calculated, using the following equation:

$$NDVI = \frac{\rho_{B3} - \rho_{B2}}{\rho_{B3} + \rho_{B2}}$$

(2)

where the subscripts represent the SPOT band 3 (near infrared) and band 2 (red), respectively. In the next stage, each of the 15 NDVI layers was overlapped with the 25 physiographic units and statistics were calculated for each.

NDVI is used here as a surrogate for vegetation production, because the relationship between the two is well established both theoretically and empirically (Pettorelli et al., 2005). NDVI has shown consistent correlation with vegetation biomass and has been found useful for the study of regional patterns in primary production in, e.g. North American shrub lands and grasslands (Paruelo et al., 1995; Paruelo and Lauenroth, 1997). The relationship between rainfall and NDVI of prairie and croplands in the Great Plains of Kansas was successfully studied in a biweekly analysis between 1989 and 1997 (Wang et al., 2003) and in Sahelian Africa (Tucker and Nicholson, 1999). Although other vegetation indices were developed, NDVI has had, and will continue to have, a key role in future research of ecosystem dynamics. It is a useful tool to couple climate and vegetation distribution (Pettorelli et al., 2005). In the studied area, a strong linear correlation ($R^2 = 0.8$, $N = 22$, $P < 0.05$) was observed between NDVI and biomass harvests. We have also tried to use different soil adjusted vegetation indices but NDVI gave the best predictive results.

Vegetation cover

In this study, we focus on the response to water availability of herbaceous vegetation only and therefore, we selected the 25 replica plots on slopes that are entirely dominated by herbaceous vegetation. The spatial mixture between shrubs and grasses in the studied area can be on the scale of the sub-meter. Also, several assemblages of plant species can produce a similar NDVI value and temporal trend (Nagendra, 2001). It is therefore difficult to differentiate between species with the 20 m SPOT data. For that reason, we used very high-resolution aerial photography to map surface covers and to select slopes and physiographic units that are dominated by annual herbaceous vegetation. The supervised maximum likelihood classification (MLC), which already proved useful in mapping soil and vegetation in a nearby study site (Svoray et al., 2007), was applied to identify three classes: herbaceous vegetation, shrubs, and bare soil. The data were obtained from an RGB Orthophoto, with sub-meter resolution, produced on 31 December 2004.

The training sets were derived using data collected in the field while, to validate image classification, accuracy assessment was carried out using visual interpretation of aerial photographs, followed by field observations. An accuracy assessment of the classification was carried out using a visual interpretation of the orthophoto on a sample of 200 pixels per class and field observations; accuracy was tabulated in a confusion matrix (a table within each predicted class is plotted against the observed class and the number of items within each is compared). Overall
classification accuracy was >85%. As a second step, the zonal layer of the 25 replica plots was overlapped with the classification layer, using a spatial joining operation to calculate shrub and herbaceous vegetation percentages in the grid cells, according to the ratios between the areas covered by these classes and the overall area of each plot. The outcome is a layer that represents the shrub and herbaceous vegetation cover percentages in each of the plots.

Statistical analysis

To test if a significant variation exists between NDVI values recorded in the physiographic units at any date of observation, we used analysis of variance (ANOVA). As the samples were obtained from predefined plots, we added the plot factor to the statistical model in a nested manner. The plot factor allows the effect of the unique characteristics of the plots on the dependent variable to be tested. Note that in this operation, we do not try to explore the effect of the plots on the dependent variable, but try to assure that they do not act as a source of error.

To test the effect of rainfall on NDVI values recorded in the physiographic units at any date of observation, a stepwise regression model was applied, in which the dependent variable is NDVI and the independent variables are defined as follows: Day, the amount of rainfall a day before the image acquisition; Three, the amount of rainfall in the 3 days before the measurement; Week, the amount of rainfall in the week before the measurement; Month, the amount of rainfall in the month before the measurement; Total, the amount of rainfall since the last measurement (satellite data acquisition); Totsum, the amount of rainfall in the entire season until the day of measurement; and, finally, Number, the number of days without rainfall since the last measurement. The analysis was implemented using the statistical analysis system (SAS) package.

RESULTS

Overall rainfall in the 2002–2003 rainy season was 196 mm, which is 66% of the mean annual rainfall measured at the Lehavim LTER site during the 18 seasons between 1987 and 2005 with maximum = 528, minimum = 140, and standard deviation = 94.47. The dominance of annual herbaceous vegetation, ~50–60% cover, and the low shrub cover, <5%, on the studied research plots are shown in Table I. In accordance, bare soil (soils not covered by vegetation throughout the season) areas were similar between the plots—~35–45%. Despite the relatively low amount of rainfall, NDVI values measured were typical of semiarid areas, as observed in previous studies (Svoray and Shoshany, 2004) in wetter years—for example, the footslope and the channel, which are typical of NDVI values from humid areas.

Figure 2 shows that the 196 mm dropped in this season was distributed over seven events of effective rainfall (≥10 mm, based on Noy-Meir, 1973) and, in addition, there were two consecutive rainfall events (#2ab in Figure 2) after event #2 of ~7 mm each, which, due to the low evaporation rate in winter, can be considered as an effective event. Accumulated effective rainfall depth in this growing season was 109 mm, whereas the other 87 mm was distributed in very small events.

The minimum NDVI values in Figure 2 represent areas covered with bare stony soils or rock coverage with no vegetation all year long. As expected, these areas show very low NDVI values with small variation, if any, between the dates of observation along the growing season. It is important to note that these areas are not covered by biological crusts as previous studies have shown that biological crusts increase NDVI values at the beginning of the winter (Karnieli, 2003). The minimum NDVI time series is therefore a relatively flat line near zero NDVI. This value is even lower than the NDVI ~0.15 shown by senescent vegetation during the summer (the four dates of observation in May and June, Figure 2). The curve of maximum NDVI values represents the most productive habitats on each date and, apparently, they follow the curve of mean values.

The curve of mean NDVI of Lehavim LTER site is similar to other curves of NDVI measured on clear days in the Negev (Karnieli, 2003) and in other places in the world (Pettorelli et al., 2005). A detection of life history trait with NDVI shows that NDVI increases from germination to the peak of greening-up and then decreases to the lowest value, in our case, towards early May–mid June. Senescence was found to occur faster than greening-up with rate of increase in NDVI during the winter: \[ y = 0.0025x - 95.249, \quad R^2 = 0.92; \]
and rate of decrease towards summer: \[ y = -0.0033x + 123.88, \quad R^2 = 0.94 \]
where \( y \) is the NDVI and \( x \) is the rainfall amount. The germination process occurs

<table>
<thead>
<tr>
<th>Physiographic unit</th>
<th>Channel</th>
<th>Footslope</th>
<th>Backslope</th>
<th>Shoulder</th>
<th>Interfluve</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbaceous vegetation</td>
<td>51</td>
<td>61</td>
<td>59</td>
<td>58</td>
<td>64</td>
</tr>
<tr>
<td>Shrub</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Bare soil</td>
<td>44</td>
<td>35</td>
<td>38</td>
<td>39</td>
<td>34</td>
</tr>
<tr>
<td>Total cover in unit</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

The data are based on remotely sensed data classified with maximum likelihood with >90% accuracy. In all units, shrub cover <5%; herbaceous vegetation cover ~50–60%; and bare soil (soils not covered by vegetation throughout the season) ~35–45%.
underground and therefore NDVI in this period is still lowest. Then vegetation starts to grow aboveground (green-up) where NDVI increases up to the peak, and during the drying phase, there is a decrease in NDVI down to the senescence phase with low NDVI at the end of the season.

The mean NDVI curve also shows that vegetation response to rainfall is not immediate and it reflects the life history traits of time to germination. Thus, nearly a month after the first effective rainfall event, which occurred on 31 October 2002, the observed NDVI was still very low until mid-December, when the first increase of NDVI was observed (15 December 2002), with no effective precedent rainfall event during the days before the rise. The increase in NDVI continued until mid-January, with no effective rainfall event during that period. There was continuous growth in February, but in March and April, despite five effective rainfall events, NDVI did not increase but remained flat and even started to decrease. In April, despite the contribution of one more effective event (event #7), NDVI continued to decrease. Apparently, the amount of rainfall in event #7 was not used by the vegetation for production.

Mean NDVI values of the five physiographic units and rainfall data for the growing season of 2002–2003 are presented in Figure 3. The four phases are also distinguished in all units and show a similar trend. The first phase—germination—occurred between 15 November and 6 December 2002, where mean NDVI values of all physiographic units were very low for both dates of observation and were similar to those usually observed in dry vegetation surfaces (Svoray and Shoshany, 2004). The second phase—green-up—was observed between 19 December 2002 and 19 March 2003, reflecting a pronounced increase in NDVI values, up to the peak on 19 March 2003. In the third phase—drying—between 3 April 2003 and mid-May, there was a significant decrease in NDVI values, representing the drying phase in the semiarid vegetation. The fourth and last phase—senescence—occurred between mid-May and mid-June (this is the last date of observation, as the summer dry season without vegetation growth is well established by this date). There was thus, a return to the dry phase with low NDVI values.

The spatial variability within the site is shown in Figure 4, where, in the green phase, the channels and footslopes are considerably greener than the interfluves and the backslopes/shoulders. Based on the research plots, on all observation dates, there is a significant statistical difference between the NDVI values measured for the footslope, the channel, the interfluve, and the shoulder/backslope (Table II). This implies the fact that one can detect subtleties of NDVI responses across a local terrain suggests a capacity for high precision analysis of large landscapes. The difference between the physiographic units seems to increase with increasing NDVI values, although it is important to note that $F$-values are relatively low during the first phase and increase dramatically during the second phase; they then drop again in the drying phase. As was shown earlier, there is a lag in the response of production to rainfall supply that can be due to the germination lag and lack of detection of small plants as they grow. The fact that no differentiation by landform is observed until later may suggest this.

This is also shown in the results of the stepwise regression. The variable Month (rainfall amount in the month prior to the image acquisition) explains the NDVI with highest Pearson correlation coefficients (Table III). These findings are almost identical in all physiographic units, thus further enhancing the validity of this statistical model. Variables such as 3 days, the length of dry spell, and the total amount of rainfall until the date of measurement were insignificant in explaining NDVI, but terms such as weekly rainfall and the amount of rainfall
Figure 3. ANPP of the five physiographic units at the Lehavim LTER site, estimated by the NDVI. Each data point represents the average value for the date of measurement for five plots, each covering an area of a few tens of SPOT XS pixels.

Figure 4. The sequence of 15 SPOT XS-based NDVI images running from top to bottom and from left to right. The colour plates are unified to represent the NDVI range from NDVI = 0 (brown) to NDVI = 0.8 (green). The images clearly show the seasonal growth, the four phases, and the spatial variability within the site, where the channels and footslopes are considerably greener than the interfluves and the backslopes/shoulders.
from the last satellite measurement, were found more influential and near significant, although with a lower coefficient of determination than that of the monthly rainfall.

Table IV shows the slope of the regression lines between the beginning of the green-up and the peak, representing the rate of green-up; and between the peak and the dry season, representing the rate of senescence. The results show that, similar to the average profile reported earlier, the rate of senescence is faster than the rate of green-up, for all physiographic units. In addition (well illustrated in Figure 3), the speeds of increase and decrease rise with the productivity of the physiographic unit. In the case of green-up, the coefficient of determination also rises with the productivity of the unit.

During the green-up phase, there is a significant statistical difference between the NDVI values measured for the physiographic units. Yet, on several dates, the shoulder cannot be distinguished from the backslope, although these two can be distinguished from the other units. The difference between the physiographic units is well demonstrated using the seasonal NDVI integral (calculated on the basis of the trapezoidal rule) that varies between the five units as follows: Channel 0-21, Footslope 0-18, Backslope 0-16, Shoulder 0-16, and Interfluve 0-14. The difference between the units is in their water availability conditions and this is probably the reason for the difference in NDVI. Figure 5 shows a positive correlation between the seasonal NDVI of the different physiographic units and the water availability conditions mapped for these physiographic units (Svoray et al., 2008a).

**DISCUSSION**

The use of satellite remote sensing for studying rainfall–productivity relationship has revealed so far new evidence for the physiographic units.

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**Table II.** P-values and F-values of the difference between NDVI values in the different physiographic units.

<table>
<thead>
<tr>
<th>Date</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 November 2002</td>
<td>25.73</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6 December 2002</td>
<td>23.43</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>15 December 2002</td>
<td>25.82</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>30 December 2002</td>
<td>43.34</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>10 January 2003</td>
<td>36.89</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>1 February 2003</td>
<td>67.66</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>8 March 2003</td>
<td>59.55</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>17 March 2003</td>
<td>65.79</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>3 April 2003</td>
<td>60.09</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>17 April 2003</td>
<td>67.04</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>29 April 2003</td>
<td>24.65</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>8 May 2003</td>
<td>18.88</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>13 May 2003</td>
<td>15.18</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>11 June 2003</td>
<td>16.40</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>21 June 2003</td>
<td>15.53</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

This difference increases with increasing NDVI values; F-values are relatively low at the dry phase and increase dramatically during the green-up phase; they then drop again in the senescence phase.

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**Table III.** Pearson correlation coefficients and P-values for the stepwise regression of the effect of rainfall on NDVI of the five physiographic units at the Lehavim LTER site.

<table>
<thead>
<tr>
<th>Physiographic unit</th>
<th>Channel</th>
<th>Footslope</th>
<th>Backslope</th>
<th>Shoulder</th>
<th>Interfluve</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td>R</td>
<td>P</td>
<td>R</td>
<td>P</td>
<td>R</td>
</tr>
<tr>
<td>Three</td>
<td>0.04</td>
<td>0.8818</td>
<td>−0.03</td>
<td>0.9241</td>
<td>0.001</td>
</tr>
<tr>
<td>Week</td>
<td>0.55</td>
<td>0.0511</td>
<td>0.52</td>
<td>0.0666</td>
<td>0.52</td>
</tr>
<tr>
<td>Month</td>
<td>0.89</td>
<td>0.0001</td>
<td>0.88</td>
<td>0.0002</td>
<td>0.87</td>
</tr>
<tr>
<td>Total</td>
<td>0.78</td>
<td>0.0018</td>
<td>0.74</td>
<td>0.0039</td>
<td>0.69</td>
</tr>
<tr>
<td>Totsum</td>
<td>0.19</td>
<td>0.5145</td>
<td>−0.07</td>
<td>0.9805</td>
<td>−0.06</td>
</tr>
<tr>
<td>Number</td>
<td>0.20</td>
<td>0.5046</td>
<td>0.06</td>
<td>0.8296</td>
<td>−0.02</td>
</tr>
</tbody>
</table>

The analysis is based on NDVI data from the 15 dates of observation and the 25 replicas of physiographic units. The rainfall data used are presented in Figure 1. Total, the amount of rainfall since last measurement; Three, the amount of rainfall 3 days before the measurement; Week, the amount of rainfall in the week before the current measurement; Month, the amount of rainfall in the month before the measurement; Totsum, the amount of rainfall in the entire season until the day of measurement; Number, the number of days without rainfall since the last measurement. The bold variables are significant.
regarding spatio-temporal variation in ANPP in semiarid ecosystems. However, these observations raise several questions regarding the nonstationary spatial relationship between rainfall characteristics and vegetation productivity (Foody, 2003). With the record of four decades of satellite data, with a resolution of tens of meters, the mapping of highly varying patterns of vegetation productivity on the landscape scale and using the derived information in ecosystem studies are becoming feasible (Cohen and Goward, 2004). Here, the use of 15 SPOT images with 20 m resolution, from a single growing season, allowed us to study the effect of rainfall on NDVI in 5 physiographic units at the Lehavim LTER site, during a relatively dry season. To the best of our knowledge, this is the first attempt to use such an intensive seasonal time series on this scale of observation; the procedure allowed us to test the effect of topography and of accumulated soil moisture on the production of annuals in four phenological phases.

Our results show that the physiographic unit does affect the spatial variation in the NDVI of herbaceous vegetation on the landscape scale. Theoretically, the variability in NDVI observed between the physiographic units may be related to natural and man-made disturbance regimes (Paruelo and Lauenroth, 1997; Sala et al., 1997), but studies of grazing habits at the Lehavim LTER site have shown that grazing pressure is not biased by physiographic units (Svoray et al., 2009). Also, studies in other areas have shown that fire spread is unlikely to be limited by sub-slope distances (Carmel et al., 2009). In the absence of nonuniform disturbances, the spatio-temporal variation in productivity is expected to be governed by the limiting resource in arid regions, i.e. water. We assume an equal distribution or only minor variation of rainfall over the entire watershed, with no substantial variation between the physiographic units (Svoray et al., 2007). Thus, this suggests that the difference in NDVI values between the units can be mainly attributed to the variation in available soil water, due to redistribution processes. According to this assumption, it is expected that plants in the lower physiographic units, i.e. the footslope and the channel, should respond well to improved water and soil conditions and, therefore, should be more productive.

On the annual scale, the dependence of productivity on water redistribution processes was shown in the strong correlation between the modelled soil water in the unit and its seasonal NDVI accumulation (seasonal NDVI integral). The footslope and channel units allowed the production of more biomass than the interfluve and shoulder/backslope units, which, with poor water availability, showed lower NDVI values. The importance of these results lies in the complex rainfall—run-off—plant relationships in semiarid regions (Rodriguez-Iturbe et al., 1999). Due to the complex response of different surfaces to rainfall characteristics (Yair and Kossovsky, 2002), which is not yet fully understood, it is unclear to what extent water is actually redistributed in space after rainfall events and if so, how the plants’ water consumption and biomass production are affected. The difference between the productivity of the physiographic units found here strengthens the assumption that the water is redistributed and also strengthens the hypothesized importance of antecedent soil moisture conditions to the response of vegetation production to rainfall events (Ogle and Reynolds, 2004).

Furthermore, when we increase temporal resolution up to the single-event scale, the results show that NDVI response to rainfall is not immediate and that dry spells have a relatively low effect on NDVI. Note that intermediate times lag—week-to-month—was found in the response of NDVI to rainfall pulses in the physiographic units. The fact that the NDVI did not respond immediately to an effective rainfall event, nor was it largely affected by the length of the dry spells, implies that water that accumulates along the growing season in the soil, is being used by the plants in accordance with their physiological state (Kigel, 1995). In other words, the seeds do not germinate until a sufficient amount of water accumulates in the soil (Gutterman, 1994) and then germinate and grow in accordance with the available water in the soil reservoir.

Obviously, effective rainfall events are important as the main source of water supply. Indeed, in the current case, it is most likely that the large event in early February did affect germination and the beginning of greening-up. However, apparently, the very small events and the water stored in the soil until mid-January—the next effective rainfall event—were sufficient to allow the rapid growth in all units during this period. This reinforces the importance of the physiological processes in the vegetation growth that are probably determining.

Figure 5. Variation in the annual NDVI integral at the Lehavim LTER site. The water availability was estimated for every physiographic unit, based on the Svoray et al. (2008b) water availability model. The model is spatially and temporally explicit and was calculated with fuzzy algebra based on rainfall, temperature, evaporation conditions for the corresponding period and based on topographic, soil, and radiation conditions of the specific plots. The predicted water availability conditions are in normalized units between 0 and 1. The best fit was obtained with a linear model: Each data point represents the average value for the date of measurement for five plots, each cover an area of a few tens of SPOT XS pixels over the 15 dates of observation.
the relatively slow rate of greening-up during the winter and the rapid rate of drying in the end. The fact that the length of the dry spell did not affect significantly NDVI values also implies that under the conditions of this year, even in the dry period, NDVI still increases if there is enough soil water that is available to the plant.

In general, the increase in NDVI may occur due to an increase in plant size (mainly height in the case of annuals) or due to an increase in the number of individuals or by a change in the dominant species or species composition (Paruelo et al., 1997). We therefore assume that the channel and the footslope, with a large contributing area and thick soil profile, are dominated by species with high growth rates, due to the lower water stress. For the poorer physiographic units, the dominance of species with relatively low growth rates acts as a likely constraint on the response of ANPP to accumulating rainfall.

This phenomenon was also observed at the Lehavim LTER site by Osem et al. (2002), who found that harvested dry biomass at peak season on the slopes was typical of semiarid ecosystems with 10–200 g m\(^{-2}\) and on channel shoulders (up to 700 g m\(^{-2}\)), a value that reaches the range of subhumid grassland ecosystems. Osem et al. (2002) also found that productivity in the studied area rises with richness in the variety of species. Increase in species richness may increase drought resistance, through variation in root structure and leaf area that affect photosynthesis and growth rates. But, the large growth rate may result in an increase in competition for other resources, such as nitrogen and phosphorus. According to previous studies, it is indeed expected that nutrient limitation would increase relative to the rise in water availability (Menge et al., 2009).

Understanding spatial variations in production as a function of physiography is essential as there are significant differences in production across the landscape that affects our estimations. An accurate monitoring system will help to indicate the status and change in ecosystem conditions between disturbance, recovery and deterioration (Cao et al., 2004); to predict carbon storage and the bio-geochemical dynamics of terrestrial ecosystems (Polly et al., 2005); to improve rangeland and livestock productivity, as understanding changes in NDVI across the slope catena may improve estimates of carrying capacity over extensive rangeland areas in dry hilly ecosystems (Ungar et al., 1999); and to predict the effect of climate change on ecosystems (Coughenour and Chen, 1997).

The results showed here also call attention to the need to study the sink–source effect on semiarid ecosystems at multiple scales. For example, the effect of NDVI variation in physiographic units on the analysis of NDVI data from coarse resolution spaceborne systems (i.e. NOAA–AVHRR) in hilly and mountainous areas should be addressed. Generalizing different physiographic units, in a lower resolution analysis, may lead to an unbalanced estimation of the ecosystem functioning, due to the nonlinear effect that small ‘hotspot’ areas of high NDVI values, such as a channel and its banks, may have on the mean value from a given area (Karnieli et al., 1996) and therefore may mislead interpretation of the analysis of mean values.

Future progress in working with such a detailed time series of satellite data on the landscape scale could be achieved through coupling these observations with heuristic rainfall-production models (e.g. Ogle and Reynolds, 2004; Svoray et al., 2008b) that explicitly formalize, in time and space, how different functional types respond to rainfall events through the use of rainfall thresholds and plant strategies. Such a coupling will allow better understanding of the effect of rainfall events and of soil moisture storage on ecosystem productivity in semiarid zones and eventually allow us to scale up production responses to the landscape level.

CONCLUSIONS

Our study shows that NDVI temporal profiles over the Lehavim LTER site and the different physiographic units can be explained by the four phenological phases of semiarid annual vegetation. It reinforces the value of using NDVI data in conjunction with topographic data to study vegetation conditions in the heterogeneity that occurs across landscapes. Furthermore, our results strengthen the hypothesized importance of antecedent soil moisture conditions to the response of ecosystem productivity to rainfall events. More specifically, our results show that

1. The NDVI differ significantly in value between the interfluve, slope shoulder and backslope (two units that appeared indistinguishable), footslope and the channel. However, all of these showed a similar trend, with a moderate increase in growth, but much sharper decline during the drying phase.
2. There is relatively late response of vegetation to rainfall events. Monthly rainfall was much more significant in explaining NDVI than daily rainfall, total rainfall, and the length of dry spells. Ecosystem health monitoring and study should therefore consider not only mean rainfall, but also long-term effects of rainfall events and physiographic units.

This evidence regarding the constraints on NDVI magnitude by physiographic units allows better understanding of ecosystem responses to stress, as well as better generalization from plot to regional scale. Such generalization can be misleading, due to the neglect of surface hydrological processes at these scales.

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