Spatially and temporally explicit modeling of conditions for primary production of annuals in dry environments

Tal Svoray\textsuperscript{a,}\textsuperscript{*}, Rakefet Shafran-Nathan\textsuperscript{a}, Zalmen Henkin\textsuperscript{b}, Avi Perevolotsky\textsuperscript{b}

\textsuperscript{a} Department of Geography and Environmental Development, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel
\textsuperscript{b} Department of Agronomy and Natural Resources, Agricultural Research Organization, Volcani Ctr, Bet Dagan 50250, Israel

\textbf{A B S T R A C T}

Geographic information technologies provide powerful tools for spatially explicit modeling of primary production. However, current models are focused on two scales mainly: national/continental and local/plot. Consequently, little is known about the spatio-temporal dynamics of grasslands on the landscape scale. This is a notable gap as researchers, practitioners and decision makers are often interested in ecological and environmental information at the scale of topographic units. We developed here a heuristic model that predicts, on a daily basis, conditions for germination and production of annual vegetation in heterogeneous environments, at a cell resolution of 25 m $\times$ 25 m. The model is based on simulations of hydrological processes, derived from two sources: (I) environmental sub-models including radiation, rock cover and runoff-contributing area and (II) climatic factors including rainfall depth, surface temperature and evaporation rate. Prediction of conditions was strongly correlated with (I) biomass harvest at two sites in Israel: Lehavim—semi-arid ($R^2 \approx 0.76–0.84$, depending on year) and Korazim—Mediterranean ($R^2 \approx 0.66–0.75$) and (II) normalized difference vegetation index (NDVI) data at the two sites—Lehavim ($R^2 = 0.77$, $p < 0.001$) and Korazim ($R^2 = 0.69$, $p < 0.001$). However, the effect of changing conditions on production differed significantly between these two sites. At Lehavim the effects were similar in the early and late phases of the growth season, whereas in Korazim there was a clear difference between the two phases. We attribute the site-specificity of the responses to differences in soil depth and texture. The results show that beyond qualitative assessments, the dynamics of annual grassland production can be quantified and modeled in homogenous topographic units. Therefore, our model can serve as a basis for predictions of ecosystem response to climate change and management regimes. Future developments and applications of the model presented here should include further refinement of the sub-models and model utilization for the study of primary production dynamics in time and space.

\textcopyright 2008 Elsevier B.V. All rights reserved.

1. Introduction

Aboveground net primary production (ANPP) is among the most important indicators of ecosystem capabilities, functioning and resource utilization efficiency (Jobbagy et al., 2002; Cao et al., 2004). Consequently, many ecological studies require reliable quantification of ANPP (Shmida and Burgess, 1988). More specifically, information on spatial and temporal variation in ANPP is essential for applied and scientific purposes in four fields: (I) indication of the status and change in ecosystem
conditions, between disturbance, recovery, and deterioration (Cao et al., 2004); (II) study of carbon storage and the biogeochemical dynamics of terrestrial ecosystems (Polly et al., 2005); (III) improvement of rangeland and livestock productivity (Ungar et al., 1999); and (IV) prediction of the effect of climate change on ecosystems (Coughenour and Chen, 1997).

Existing models that predict ANPP operate mainly on two, very different, spatial scales: the local/plot and the national/continental. Those operating on the plot scale are mostly detailed models of plant-soil processes (e.g., Coughenour and Chen, 1997) that usually involve physiological parameters of the vegetation such as photosynthesis rate and plant growth. These parameters are linked to the dynamics of abiotic factors—nutrient flow, water and temperature. ANPP predictions on large scale are based on physical models (Schimel et al., 1997) but also on satellite remote sensing data (Tracol et al., 2006), mostly NOAA-AVHRR and more recently MODIS, that were used for terrestrial gross and net primary production mapping (Zhao et al., 2005). The remote sensing studies often make use of the normalized difference vegetation index (NDVI) that was later modified for application in environments of sparse vegetation using indices such as soil adjusted vegetation index (SAVI) and others (Liu et al., 2004).

Although they include important information on the factors and processes that determine ANPP variation, plot and regional scale models lack consideration of external effects such as topography (Seligman and VanKeulen, 1989), and little is known about the processes that govern spatio-temporal variability in ANPP on an intermediate spatial scale between the plot and the region. This scale is referred here to the sum of several plots; an area affected by hydraulics of overland flow (Phillips, 1999) and pedogenesis along the catena line from the interfluve to the channel bottom (Conacher and Dalrymple, 1977). The main reason for the lack of studies of ANPP on the scale of topographic units is, most certainly, the difficulty in explicitly quantifying climatic and environmental conditions, as well as ANPP, on this scale. In dry environments, the complexity of the mechanisms that govern the effects of climatic and environmental conditions on soil moisture presents an additional difficulty (Yair and Kossovsky, 2002).

Since ecological phenomena do not occur on any single scale, but reflect variability on a range of spatio-temporal and organizational scales, there is crucial need to study ecosystems across range of scales (Levin, 1992). The research gap in the intermediate scale further advances the need to study with more details the processes involved in ANPP dynamics on the scale of topographic units. This could be done by developing models which account for the strong temporal variability in rainfall and are dynamic in nature (Guisan and Zimmerman, 2000).

Developments in the availability of satellite data on the scale of a few meters, improvement in representation of morphometric factors, and refinement of dynamic rainfall-runoff models (Peters et al., 2003) have all presented new opportunities to study ANPP variation in a spatially and temporally explicit manner (Jørgensen, 2005). However, most of the current studies statistically relate vegetation characteristics to environmental features at a given time step and they are usually temporally static in nature (Guisan and Zimmerman, 2000). Static models are insufficient when predicting ANPP due to the complexity of the two integrated, yet distinct, groups of mechanisms that affect vegetation production. The first group comprises the biological-physiological processes that contribute directly to productivity, starting with germination, continuing through biomass production, and ending with seed production and dispersal (Fischer and Turner, 1978). The second group involves the environmental and climatic factors that determine the effectiveness of the biological processes (Austin, 2002). In drylands, the linkage between the two groups of mechanisms is based on the assumption that soil moisture is the limiting factor for the biological processes (Noy-Meir, 1973). However, the soil moisture balance is the outcome of climatic and hydrological processes that occur at several different scales (Rodriguez-Iturbe et al., 1999) and static models have difficulties to simulate the effect of, e.g., length of dry and wet spells and rainfall frequency and onset, on spatio-temporal variation in ANPP. As one of the characteristics of drylands is the strong temporal variability in rainfall, thus, whereas in wetter environments mean rainfall may be a good approximation and static approach is justified, in dry environments the representation of temporal dynamics can be important.

The complex effect of conditions and resources on space-time variation of ANPP (Guisan and Thuiller, 2005) and the need to use dynamic modeling approach (Burke et al., 1997) arise the necessity for a method that can integrate several functions to better represent the spatio-temporal heterogeneous nature of landscapes. The fuzzy sets approach has been found very successful in modeling entities that involve gradual transitions rather than the use of sharp boundaries (Zhu et al., 1996). This is done by attributing a degree of membership rather than a crisp category to each observation—a grid cell in the GIS (Wagner and Fortin, 2005). Thus, for ANPP prediction, areas of differing conditions can be represented as multivariate surfaces of membership in potential ANPP (Svoray et al., 2007). Fuzzy logic is among the most flexible modeling techniques that was first proposed by Zadeh (1965) and, since then, has been widely used for ecological modeling (for example Svoray et al., 2004). Fuzzy logic provides the ability to model inexact, imprecise and ambiguous entities and relationships between different model components (Burrough et al., 1992). Since the combined effect of the climatic and ecological processes on the production rate of herbaceous vegetation cannot be represented by simple statistical model (Henkin et al., 1998) and since a homogenous patch of annuals production is an indeterminate geographical entity that is not characterized by a sharply defined boundary, fuzzy logic representation was chosen here as the modeling approach.

The aim of this paper is to develop a model that predicts conditions for germination and production of annual vegetation in dry environments. The concept is heuristic and the model uses simulations to improve our understanding of ANPP variation. Such a model that predicts conditions for ANPP, within the detailed landscape scale, makes the basis for future spatial decision support system (SDSS) to manage open areas and mainly rangelands and nature reserves (Leriche et al., 2001; Frank et al., 2002).
2. Methods

2.1. The study sites

The model we developed here was applied and tested in two sites at both ends of a Mediterranean to semiarid climatic gradient.

2.1.1. Korazim site—Mediterranean (ME)

The Korazim site is located within the Kairei Deshei experimental farm (35°35′E; 32°55′N). The topography is hilly with varying rock coverage, ranging from sparse cover of little stones to large boulders (Seligman et al., 1989). The parent rock is basalt and the soils are variants of brown basaltic protogrumosol (Dan et al., 1970). Patches of soil, up to 100-cm deep, are interspersed between rock outcrops; they present a diversity of 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).

2.2. Model assumptions

We assume that areas that accumulate water readily will create productive conditions, whereas those with lower soil moisture will be less productive. Although other sources of stress such as grazing, nutrient availability and fire can affect both germination and production, we assume that annual production is largely controlled by moisture availability, which varies in both space and time. In that sense our model is conceptually similar to previous ones that predict vegetation dynamics through soil moisture modeling (e.g., Paruelo and Sala, 1995; Rodriguez-Iturbe et al., 1999).

It is difficult to quantify the instantaneous soil moisture balance under realistic conditions in heterogeneous environments. To simplify the simulation of this balance, we assume that the vertical variation in soil moisture content is the result of infiltration and evaporation, whereas the horizontal variation results from variations in surface and subsurface runoff (Beven et al., 1995). We further assume that the roots of annual species are located in the upper soil layer and can use available water down to 30–40 cm (Kosmas et al., 2000). The model therefore expresses the horizontal variation in soil moisture in the root zone based on climatic data including: (I) rainfall depth; (II) evaporation rate and (III) soil moisture storage decay. The spatial variation is expressed on the basis of data on (I) topography and soil hydraulic properties; (II) rock cover and (III) radiation flux. In addition to soil water, we also expressed the effect of temperature on both germination and production.

2.3. Model formulation

In our model, the set $A$ represents a group of cells, i.e., real world unit areas of $25 \times 25 \text{m}^2$, with optimal conditions for biomass production of annual herbaceous vegetation:

$$A = \{x, \mu_A(x)\} \text{ for each } x \in X$$

where $X = \{x\}$ is a finite set of cells and $\mu_A(x)$ is the degree of membership held by $X$ in the set $A$. The degree to which a given cell is part of the set $A$ depends on the factors detailed in Section 3.1 and is quantified at values between 0 and 1 by $\mu_A(x)$, known as the membership function (MF). Numerous analytical expressions for MFs have been published including linear, trapezoidal, sigmoid, cosine, etc. (Robinson, 2003). The MFs that we have chosen to express the effect of each environmental and climatic factor on degree of membership of each cell to set $A$ are presented in Table 1. Those analytical functions were already chosen by several authors to describe the effect of the controlling factors on vegetation and the sources are detailed in Table 1. The coefficients of each function are detailed in Table 2. The model uses the MFs to run over an entire season and calculates the score (i.e. the distance from the set $A$) for each cell at each day.

Fig. 1 illustrates the model progress along the growing season. The model begins with the first rainfall event, reads the climatic conditions at this day from the database described.
Table 1 – A summary of the membership functions used in the model

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Id</th>
<th>Sym</th>
<th>Type</th>
<th>Membership function (MF)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall amount</td>
<td>C</td>
<td>μRD</td>
<td>Linear positive</td>
<td>( \mu_{\text{RD}} = (x - \alpha)(\beta - \alpha) )</td>
<td>Linear correlation was found between rainfall amounts and vegetation PP (Silvertown et al., 1994)</td>
</tr>
<tr>
<td>Radiation</td>
<td>E</td>
<td>μRAD</td>
<td>Trapezoidal—left open shoulder</td>
<td>( \mu_{\text{RAD}} = \max(\min(1, (\beta - x)/(\beta - \alpha)), 0) )</td>
<td>Shaded areas contribute to linear increase in PP due to reduction in evaporation (Peek et al., 2004)</td>
</tr>
<tr>
<td>Soil water deficit</td>
<td>E</td>
<td>μDEF</td>
<td>Linear negative</td>
<td>( \mu_{\text{DEF}} = (x - \alpha)(\beta - \alpha) )</td>
<td>Linear relationship was observed between available soil moisture and herbaceous PP (Gao et al., 1997)</td>
</tr>
<tr>
<td>Germination temperature</td>
<td>C</td>
<td>μTMPG</td>
<td>Triangle</td>
<td>( \mu_{\text{TMPG}} = \max(\min((x - \alpha)/(\beta - \alpha), (\beta - x)/(\beta - \gamma)), 0) )</td>
<td>Grundy et al. (2000) have reported similar probability function for germination of weeds</td>
</tr>
<tr>
<td>Production temperature</td>
<td>C</td>
<td>μTMPP</td>
<td>Trapezoidal</td>
<td>( \mu_{\text{TMPP}} = \max(\min(1, (x - a)/\gamma), (\beta - x)/(\beta - \delta)), 0) )</td>
<td>Scurlock et al. (2002) have reported similar probability function for germination</td>
</tr>
<tr>
<td>Rock cover</td>
<td>E</td>
<td>μRC</td>
<td>Trapezoidal</td>
<td>( \mu_{\text{RC}} = \max(\min(1, (x - a)/\gamma), (\beta - x)/(\beta - \delta)), 0) )</td>
<td>Rock cover up to 50% increases infiltration while from 80 to 100% it refers mainly to continuous rock coverage which decreases dramatically available soil pockets (Gutman and Seligman, 1985)</td>
</tr>
<tr>
<td>Evaporation</td>
<td>C</td>
<td>μEVP</td>
<td>Trapezoidal—left open shoulder</td>
<td>( \mu_{\text{EVP}} = \max(\min(1, (x - a)/\gamma), (\beta - x)/(\beta - \delta)), 0) )</td>
<td>The study of Dahm et al. (2002) have shown that daily evaporation rate up to 1 mm increased productivity while higher evaporation rate lead to soil drying and increased productivity</td>
</tr>
<tr>
<td>Soil moisture storage decay</td>
<td>C</td>
<td>μRDE</td>
<td>Subtraction</td>
<td>( \mu_{\text{RDE}} = \mu_{\text{RDE}} = \mu_{\text{RD}}<em>{t-1} - \mu</em>{\text{EVP}}_{t-1} )</td>
<td>The subtraction of evaporation from rainfall of the previous day represents the amount of water that remains in the soil from the previous day</td>
</tr>
</tbody>
</table>

Note: \( \alpha \) and \( \beta \), respectively, are the minimum and maximum values of the property; \( \gamma \)-maximum value of the right shoulder of the trapezoidal and maximum value of the triangle, \( \delta \)-maximum value of the left shoulder of the trapezoidal; \( X \), the fuzzy set value from a grid cell or attribute table. These functions are often used in fuzzy logic according the conditions described by Robinson (2003). In the “Id” column, C refers to climatic factor while E is environmental factor. \( \mu_{\text{RDE}} \) determines the rate of decay of stored soil moisture simply by subtracting daily the MF of evaporation from that of rainfall following the end of each rainfall event.

Table 2 – The values assigned as MF boundaries for each factor at each site

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Source</th>
<th>( \alpha )</th>
<th>( \beta )</th>
<th>( \gamma )</th>
<th>( \delta )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AR</td>
<td>ME</td>
<td>AR</td>
<td>ME</td>
</tr>
<tr>
<td>Rainfall amount</td>
<td>Our empirical dataset</td>
<td>min</td>
<td>min</td>
<td>max</td>
<td>max</td>
</tr>
<tr>
<td>Radiation</td>
<td>Our empirical dataset</td>
<td>19.3</td>
<td>19.2</td>
<td>25.1</td>
<td>20.1</td>
</tr>
<tr>
<td>Soil water deficit</td>
<td>Our empirical dataset</td>
<td>0</td>
<td>0</td>
<td>9.4</td>
<td>38.3</td>
</tr>
<tr>
<td>Germination temperature</td>
<td>Grundy et al. (2000)</td>
<td>7.3</td>
<td>7.3</td>
<td>20.5</td>
<td>20.5</td>
</tr>
<tr>
<td>Production temperature</td>
<td>Scurlock et al. (2002)</td>
<td>min</td>
<td>min</td>
<td>14.9</td>
<td>14.9</td>
</tr>
<tr>
<td>Rock cover</td>
<td>Yair and Kossovsky (2002)</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>Evaporation</td>
<td>Our empirical dataset</td>
<td>min</td>
<td>min</td>
<td>max</td>
<td>max</td>
</tr>
</tbody>
</table>
in Eq. (2) \cite{Burrough1992} to calculate the score for germination ($\mu_{Gij}$) in each cell $ij$ at each day $t$:

$$
\mu_{Gij} = \sum_{t=1}^{r} (\lambda_{RD} \mu_{RDt} + \lambda_{RDE} \mu_{RDEt} + \lambda_{RAD} \mu_{RADij} + \lambda_{EVP} \mu_{EVPt} + \lambda_{DEF} \mu_{DEFij} + \lambda_{RC} \mu_{RCij} + \lambda_{TMPG} \mu_{TMPGt})
$$

(2)

where RD is rainfall depth (mm); TMPG is the temperature (°C); EVP is the daily evaporation rate (mm); RAD is the radiation flux (MJ/m²); DEF is soil moisture deficit (m); RC is the rock cover (%) and RDE is the soil moisture storage from last day (mm).

The scores to $\mu_{Gij}$ are calculated on a daily basis (with values between 0 and 1) but the cell is assigned as germinated only after the conditions for germination are fulfilled (i.e., sufficient amount of water accumulates in the soil at day $r$) based on a threshold value. The value was set to 1 based on the assumption that the score 1 represents optimal conditions in terms of water availability \cite{Svoray2004, Svoray2007} and the cell is germinated if the accumulated $\mu_{Gij}$ is equal or larger than 1. The condition is applied using the following rule in

If $\sum_{t=1}^{r} \mu_{Gij} \geq 1$, then cell $ij$ is assigned as germinated,  
else continue logging

(3)

After the cell has germinated, daily production is assigned for each cell based on the following equation:

$$
\mu_{Pij} = \sum_{t=1}^{r} (\lambda_{RD} \mu_{RDt} + \lambda_{RDE} \mu_{RDEt} + \lambda_{RAD} \mu_{RADij} + \lambda_{EVP} \mu_{EVPt} + \lambda_{DEF} \mu_{DEFij} + \lambda_{RC} \mu_{RCij} + \lambda_{TMPG} \mu_{TMPGt})
$$

(4)
where TMPP is the temperature for production. The weights \( \lambda_i \) are of major importance, as their size determines the degree by which each MF contributes to the final set. The weights consequently represent a hierarchy of the variable’s contributions to the JMF and, hence, each variable’s value in the final predictive model. Therefore, the weight determination is an important step for interpretation of the studied phenomenon and for the model realism (Snowling and Kramer, 2001; Vincenzi et al., 2006). We determined the weights in Eqs. (2) and (4) based on the sensitivity analysis procedure described in Section 2.5.3.

The model is used to cover an area of approximately 5 × 5 km² and the cell size is 25 × 25 m². The time-step is 1-day, and the modeling period extends from the beginning to the end of the wet season, i.e., approximately 180 days, depending on specific year conditions. The model is implemented in MATLAB 7.0.4.

### 2.4. Environmental factors sub-models

The environmental sub-models were applied on a GIS database using ARCGIS 9.2 and later were used as a data input to the MFs in Table 1.

#### 2.4.1. Soil moisture deficit (DEF)

Water infiltration into the soil, and its accumulation along the soil profile, largely depend on the upslope contributing area, the local slope and the soil hydraulic conductivity (Barling et al., 1994). Several models predict rainfall-infiltration-runoff processes explicitly, and we have chosen the TOPMODEL (Beven et al., 1995) to calculate the dynamics of soil moisture deficit, i.e., the potential for water accumulation in a given cell after rainfall events. The steady-state assumptions of the TOPMODEL and a further assumption that the form of the exponentially declining transmissivity profile is spatially constant, led to the following relationship between mean catchment deficit (\( \bar{S} \)) and local soil moisture deficit (\( S_{ij} \)) (Peters et al., 2003):

\[
\frac{\bar{S} - S_{ij}}{m} = \ln \left( \frac{\sigma_j}{\tan \beta_{ij}} \right) - \left[ \ln(T_{ij}) - \ln(T_0) \right] \tag{5}
\]

We have calculated the mean catchment deficit (\( \bar{S} \)) by estimating the difference between saturated soil moisture content and mean gravimetric soil moisture content, both measured by us in the field (n = 24 for each site). The upslope contributing area (\( \omega \)) and the local slope angle (\( \beta \)) were obtained from Hall and Cleeve (1990) DEM on a cell basis using the TauDEM procedures (Tarboton, 1997). The shaping parameter (\( m \)) for the form of exponential decline in conductivity with depth was extracted according to Beven (1984), from a regression model between field measurements of soil texture that were converted to hydraulic conductivity by using the equations of Clapp and Hornberger (1978), and soil depth measurements (Krumedjinski et al., 1988). The mean values of the topographic index (\( \lambda \)) were calculated for the two sites separately (n = 80,810 cells in ME and n = 38,792 cells in AR). The saturated hydraulic conductivity (\( T_{ij} \)) and the mean saturated hydraulic conductivity (\( T_e \)) were calculated from our soil texture data along the soil profile. The outcome \( S_{ij} \) is the soil moisture deficit (cm) that was calculated over the entire study area to each of the four physiographic units—interfluve, shoulder, backslope, and footslope along the slope catena. The units were identified by using the process-based terrain characterization model (Park et al., 2001) and the DEM (Hall and Cleeve, 1990). Within these units, similar hydrological, geomorphological, and pedological processes occur and, therefore, the units are assumed to have similar catchment responses. Note that runoff mechanisms differ between the two sites: in ME, we assumed runoff continuity and therefore simulated the water as accumulating towards footslope; whereas in AR we designated the interfluve and backslope as sources, and the shoulder and footslope were assigned as sinks (based on Yair and Kossovsky (2002) and Svoray et al., 2008). \( S_{ij} \) therefore expresses in our model the potential of the given cell to accumulate water by infiltration and it is expected that cells assigned with higher \( S_{ij} \) values will have higher potential to accumulate water and therefore will be more productive.

#### 2.4.2. Rock cover computation (RC)

Apart from topography and soil characteristics, runoff and infiltration processes are also much affected by surface coverage. Rocks and stones are among the most important factors that increase the infiltration rate of water into the soil (Poensen and Lavee, 1994); they may form a micro-environment within their surroundings that provides enhanced conditions for vegetation growth (Schlesinger et al., 1996). Nevertheless, only a few spatially explicit models of vegetation production include the effects of rock coverage. Here, we added to the model the effect of rock coverage through mapping rock cover in the 25 × 25 m² cells of the study sites. First, the supervised maximum likelihood classification (MLC), that has already proved useful in mapping soil and vegetation in semiarid and Mediterranean areas (Svoray and Carmel, 2005), was applied to sort three classes: soil/herbaceous vegetation, shrubs, and bare rock. The data sources were orthophotos from 31 December 2004 with sub-meter resolution. 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 photograph followed by field observations. As a second step, a 25 × 25 m² grid that covers the entire study area was overlapped with the classification layer by using a spatial joining operation to calculate the rock cover percentages in the grid cells, according to the ratios between the areas covered by the rock classes and the overall area of the cell. The outcome is a layer that represents the rock cover percentages in each of the 25 × 25 m² cells. In the model we assume that rock cover from 0 up to 50% increases infiltration while from 80 to 100% it refers mainly to continuous rock coverage which decreases available soil pockets (Gutman and Seligman, 1985).

#### 2.4.3. The radiation (RAD) model

Solar radiation flux in a given area affects evapo-transpiration rates. In the northern hemisphere, South-facing slopes are commonly less humid than those oriented to the north, east or west (Oliphant et al., 2003). Because it has been found that this variation affects the characteristics of plants (e.g., Nevo, 1997), the slope aspect is often used as a surrogate factor to represent radiation conditions. A more comprehensive way to predict
variation in radiation flux is by including in the simulation of the slope aspect the effects of sun position, ground elevation, surface gradient (slope), and shadowing effects as determined by the positions of neighboring pixels (Dubayah and Rich, 1995). We used such a model (Kumar et al., 1997) to calculate the shortwave radiation on a spatially and temporally explicit basis; this model uses the latitude of the study sites, the starting date of the observations, and the above-mentioned DEM, to calculate the slope gradient and orientation, and hill shade. We predicted the spatial variation of shortwave radiation incident on the two study areas, on a daily basis, and then calculated a mean value for the entire season. We assumed that this mean value in (MJ/m²) units represents the spatial variation in radiation over the entire season. By using the RAD factor we intend to express the spatial variation in solar radiation flux while temporal variations due to cloud cover are excluded. The temporal variation in evaporation is expressed through the factor EVP which is acquired from meteorological station data.

2.4.4. Soil moisture decay (RDE)

Moisture in the upper soil layer can decrease between rainfall pulses to a level that can affect productivity (Noy-Meir, 1973). The loss of water from the upper soil layer may be caused by both infiltrations to lower layers and evaporation to the atmosphere. However, measurements of soil moisture (Hillel, 1959) in semiarid areas show that due to rainfall and surface characteristics, soil moisture below the 30-cm layer is very low. We therefore assume that during dry spells most of the water loss from the upper 30 cm layer, in the study areas, occurs due to evaporation. To express the effect of dry spells and the possibility for soil moisture loss from the upper soil layer by evaporation, the MF of evaporation from the previous day ($\mu_{EVP, t-1}$) was subtracted from the MF of rainfall of the previous day ($\mu_{RD, t-1}$). This expression represents the relative amount of water that remains in the soil from the previous day.

2.4.5. Climate data (RD, EVP, TMP)

Daily data of rainfall depth (mm), evaporation (mm) from standard pans, and surface temperature (°C) for all three seasons (2002–2005) were acquired from two standard meteorological stations located near the study sites: Rosh Pina station located 5 km north of the ME site, and the meteorological station of the Lehavim LTER located at the center of the AR site. For the use of our model, the daily data of the three factors was stored in three 1D arrays, one for each factor.

2.5. Model tests

2.5.1. Validation data

Measuring ANPP directly over wide regions is a complex task (Pieper, 1988). Therefore, we used temporal measurements of biomass as a surrogate, a procedure that was justified because this study was focused on annuals (Ungar et al., 1999). The total dry biomass (kg/m²) was measured in randomly selected plots during six field campaigns in the course of three growing seasons (2002–2005). Each season was divided into two phases: early phase (early February) and late phase (mid-April) which represented moderate and peak growth conditions, respectively. The specific dates of these phases depend on the temporal distribution of rainfall events, and may differ, sometimes significantly, from year to year. We selected February and April for generalization purposes. Each harvested plot extended over at least 75 × 75 m² (a 3 × 3 cells kernel window in the model) and represented a specific topographic site in terms of uniformity of environmental and botanical characteristics. The plots were delineated on the GIS to enable geometric correspondence with model predictions. The harvest-calibration method was used, with 10 samples per plot (Tadmor et al., 1975). Grazing activities were excluded from the plots, to avoid disturbance of the measured vegetation production.

In addition, two multi-spectral, 4-m resolution, IKONOS images were available for validation. The ME image was acquired on 21 March 2004 and the AR one on 3 March 2005. To facilitate the accurate analysis of the satellite signal, the IKONOS four spectral bands were calibrated against reflectance units according to the empirical line technique (Smith and Milton, 1999). File coordinates of the two images were transformed to the Israel Grid, on the basis of more than 50 differential GPS (DGPS) measurements, through a first-order transformation (RMS < 1 pixel), and the image pixels were re-sampled by means of the nearest-neighbor technique. After preprocessing, the NDVI values were calculated. NDVI

<table>
<thead>
<tr>
<th></th>
<th>Interfluve</th>
<th>Shoulder</th>
<th>Backslope</th>
<th>Footslope</th>
</tr>
</thead>
<tbody>
<tr>
<td>AR</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Shoulder</td>
<td>0</td>
<td>80</td>
<td>15</td>
<td>0</td>
</tr>
<tr>
<td>Backslope</td>
<td>0</td>
<td>10</td>
<td>75</td>
<td>5</td>
</tr>
<tr>
<td>Footslope</td>
<td>0</td>
<td>10</td>
<td>10</td>
<td>95</td>
</tr>
<tr>
<td>n = 20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME</td>
<td>100</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Shoulder</td>
<td>0</td>
<td>80</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Backslope</td>
<td>0</td>
<td>20</td>
<td>85</td>
<td>5</td>
</tr>
<tr>
<td>Footslope</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>95</td>
</tr>
<tr>
<td>n = 9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The validation data was gathered in the field in randomly distributed plots.
has been used as a surrogate of biomass production by other authors (e.g., Paruelo et al. (1997)), who found good correlations between these two factors in grassland ecosystems. That is because NDVI is sensitive to green biomass, not to the woody components that in many ecosystems form the largest biomass contributor. Thus, the use of NDVI to predict biomass is especially appropriate for herbaceous vegetation. We compared NDVI and biomass of annuals in several plots in our study area, and found that the values were strongly correlated (Arredondo et al., 2007), and the regression line was: Biomass = 1.93 + 0.78 NDVI (r² = 0.81, p < 0.001).

2.5.2. Statistical tests
Tests of the model were based on regression analysis applied between the mean $\mu_{Pij}$ scores and its harvested biomass of the respective sampling plots. To enable exact comparison between field and model data, we accumulated the $\mu_{Pij}$ scores from the day of germination until the day of harvest during each year. Similarly, to add validation plots, we regressed the corresponding $\mu_{Pij}$ scores against biomass data extracted from NDVI calculated from the IKONOS images. We assume that final $\mu_{Pij}$ score expressed soil moisture and temperature conditions in each cell and, therefore, that it significantly affect the production process. Since we studied annual herbaceous vegetation, we expected soil moisture and temperature dynamics to be rapidly expressed in biomass harvests and NDVI values. To test if the relationships between predicted soil moisture and measured biomass differed between the two seasonal phases, in the two sites, during the 3 years of observation, we performed an analysis of covariance, with the JMP software package, version 5.1 (SAS Institute Inc., Cary, NC). We hypothesized that the two sites differed in the responses of their ANPP to seasonal changes in conditions, i.e., that AR would exhibit similar ANPP-conditions relationships in the two phases of the season, whereas ME would exhibit a significant difference between the two phases.

2.5.3. Sensitivity analysis
In general, model output can be affected by changes in model input (Snowling and Kramer, 2001) and in parameters weight (Vincenzi et al., 2006). Therefore it is of interest to determine the best fit weight to each of our model parameters. We applied a sensitivity analysis procedure to determine the weight of each of the seven climatic and environmental factors in predicting ANPP (Eqs. (2) and (4)). This was done based on Monte Carlo simulation approach as described in the following five steps: (I) based on previous research (Svoray et al., 2004, 2007) a relatively wide range of variation $\lambda_{\text{min}} - \lambda_{\text{max}}$ was determined to each of the seven weights $\lambda_i$. Then a truncated distribution function beta within the range $\lambda_{\text{min}} - \lambda_{\text{max}}$ was established to each parameter (Vincenzi et al., 2006). (II) A random value from the probability distribution function of each factor was selected, and (III) the vector of seven random weights was used to calculate the ANPP model using Eqs. (2) and (4) from the first rainfall event until the date representing the end of two growing seasons: 2003/4 and 2004/5. At step (IV), model predictions were regressed against biomass harvests in all field plots (see Section 3.4 for details on sampling and measurement procedures) while $R$ and $p$ values of each regression line were documented for the next step. Steps 2–4 were repeated 4000 times (1000 iterations per site × two sites × 2 years), while each iteration has resulted in a vector containing the value of the seven weights. The number of thousand iterations is higher than the minimal number of iterations for testing the effect of each weight (Crosetto and Tarantola, 2001). At step (V), the 4000 records of model output (including the seven weights and...
R- and p-value of the regression lines were ranked according their p-value and model outputs with weight combination that show significant relationship (p < 0.05) between the model prediction and the biomass harvests were averaged and standard deviation and confidence interval of $\alpha = 0.05$ were computed. The sensitivity analysis was carried out with MATLAB 7.0.4.

### 3. Results

Overall, the results of the environmental sub-models were satisfactory. The identification of the physiographic units was tested in the field and the total accuracy is 88% for AR and 90% for ME with the confusion matrix presented in Table 3. The MLC classification accuracy was also satisfactory for all surface covers with total accuracy 96% for AR and 97% for ME; for details see the confusion matrix in Table 4. The radiation model predictions were also tested against actual field measurements and were found to have good agreement with the validation data (Table 5).

Table 6 summarizes the statistics of the climatic and environmental parameters measured in the study sites, during the 3 years of observation. Substantial difference was found in (I) climatic conditions between the days of observation and (II) environmental conditions between the different areas observed. For example, maximum daily rainfall is 38 and 66 mm in AR and ME, respectively. Daily temperature can vary between 6 and 27°C in both sites and rock coverage can be as high as 50 and 100% in AR and ME, respectively. However despite the differences in conditions, the range of values in all parameters is at the same scale.

Previous research in the surroundings of the study sites (Svoray et al., 2004, 2007) showed that the factors in Table 1 are not interrelated, and that none of these factors dominates the other factors in their influence on annuals ANPP. Furthermore, simple multiple regression models were proved insufficient in correlating these factors with ANPP. In the

### Table 7 – The results of regression models for the relationship between soil moisture conditions and biomass harvests

<table>
<thead>
<tr>
<th></th>
<th>Winter</th>
<th></th>
<th>Spring</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>ME</td>
<td></td>
<td>ME</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2002–2003</td>
<td>0.75</td>
<td>&lt;0.001</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003–2004</td>
<td>0.74</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>AR</td>
<td></td>
<td>2004–2005</td>
<td>0.75</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002–2003</td>
<td>No Data</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003–2004</td>
<td>0.72</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004–2005</td>
<td>0.83</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

The $a$ values are the regression slope coefficients and the $b$ values are the intercepts.

### Table 8 – The statistics of the $\lambda$ values that yielded significant relationship and minimal deviation between biomass harvests and model outputs for the seven factors using Eqs. (2) and (4)

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th></th>
<th>2005</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$n = 48$</td>
<td>$p &lt; 0.05$</td>
<td>$0.61 &lt; R &lt; 0.77$</td>
<td>$\bar{\lambda}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AR</td>
<td>RD</td>
<td>0.25</td>
<td>0.13</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>EVP</td>
<td>0.17</td>
<td>0.11</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>RC</td>
<td>0.15</td>
<td>0.09</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>RAD</td>
<td>0.10</td>
<td>0.08</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>S$_{ij}$</td>
<td>0.16</td>
<td>0.12</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>RDE</td>
<td>0.10</td>
<td>0.11</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>TMP</td>
<td>0.09</td>
<td>0.11</td>
<td>0.03</td>
</tr>
<tr>
<td>ME</td>
<td>RD</td>
<td>0.24</td>
<td>0.14</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>EVP</td>
<td>0.19</td>
<td>0.12</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>RC</td>
<td>0.14</td>
<td>0.09</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>RAD</td>
<td>0.11</td>
<td>0.08</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>S$_{ij}$</td>
<td>0.19</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>RDE</td>
<td>0.08</td>
<td>0.08</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>TMP</td>
<td>0.08</td>
<td>0.08</td>
<td>0.01</td>
</tr>
</tbody>
</table>

The weights are normalized between 0 and 1 and the CI refers to the confidence interval.
Fig. 2 – Model predictions of germination in AR in the course of the growing season of 2003–2004. The colors show the number of days, after the first rainfall event, until each cell germinated.

Fig. 3 – Model predictions of conditions for annuals production in ME and AR at different phenological phases in the course of the growing season of 2003–2004.
present study, however, we have found two lines of evidence that our model predictions were correlated with annual ANPP. First, regression analyses (Table 7) indicate strong correlation between simulated production conditions ($\mu_{ij}^{\text{t}}$) and actual biomass measurements, over the three studied years, during the two phenological phases (winter and spring), in both ME ($R^2 = 0.66–0.75$) and AR ($R^2 = 0.76–0.84$). The relationships in both ME and AR were exponential and can be attributed to the sensitive response of annual vegetation production to spatial variation in soil moisture conditions ($\mu_{ij}^{\text{t}}$), and to the relative importance of soil moisture to each plant community, in semiarid sites. Previous studies in AR revealed that, hydrological sink areas such as footslopes and wadi shoulders supported significantly higher biomass production than source areas (Ungar et al., 1999). Second line of evidence is the regression analysis between $\mu_{ij}^{\text{t}}$ and the biomass estimated from the IKONOS images that showed also strong correlations in both ME ($R^2 = 0.69, p < 0.0001$) and AR ($R^2 = 0.77, p < 0.0001$).

The sensitivity analysis results (Table 8) show that the size of all seven parameter weights that yield the significant relationship and minimal deviation between biomass harvests and model outputs is consistent in both sites and both years. In general the parameter weights can be ordered as follows: rainfall depth (RD) was found to have the highest weight (with 0.24 as the mean value for the two sites and 2 years) while the soil water deficit ($S_n$) and the evaporation (EVP) both with mean value of 0.18 are the second highest weights. These three factors were found to have the strongest effect on annuals ANPP. The next factors include the rock cover (RC) with 0.15 and hillshade radiation (RAD) with 0.11. The effect of the soil water balance from the previous days (RDE) with mean value of 0.09 and the daily temperature (TMP) with 0.08 were found to be of the lowest weight.

Because the actual production generally matched the model predictions, an analysis can be applied to both study sites on a seasonal basis. Fig. 2 shows the model predictions of germination day (in days after first rain) in AR during the 2003–2004 season. The results show that the cells of the study area vary in the conditions they provide for germination and, consequently, they germinate on different days. However, 12 days after the first rain, the entire study area had germinated, and areas of relatively late germination were mostly located in the divides (interfluves) or were subjected to intensive radiation. The areas at the upper left corner of Fig. 2 are lower and therefore enjoyed greater accumulation of water flow, which also affected their production rate. Fig. 3 shows model predictions of the conditions for ANPP in ME and AR for the growing season of 2003–2004; it shows that until December, cumulative conditions for production were relatively poor, and that only from late January onwards did such conditions become significantly more favorable for vegetation development. At this point, the difference between the two sites is clearly indicated by the greater spatial variation in AR than in ME. Early in the season, i.e., in February, moderate conditions for growth ($\mu_{ij}^{\text{t}} \sim 0.5$) dominated in ME, whereas in AR such conditions were still limited to hot spots, and large parts of the area had accumulated relatively low scores ($\mu_{ij}^{\text{t}} \sim 0.25$). The “end of March” layers of Fig. 3 indicate that, at this time, almost all of ME exhibited very high conditions scores ($\mu_{ij}^{\text{t}} \sim 0.7$) whereas AR exhibited a much more heterogeneous landscape with areas/patches showing scores ranging from $\mu_{ij}^{\text{t}} = 0.15$ to $\mu_{ij}^{\text{t}} = 0.6$. The daily dynamics of our model is illustrated in Fig. 4, which shows the variation in $\mu_{ij}^{\text{t}}$ in a relatively high-quality topographic unit (0.35–0.75, depending on the day) in AR, and the daily rainfall in the site. Comparison of the two

<table>
<thead>
<tr>
<th>Year</th>
<th>Phase</th>
<th>AR</th>
<th>ME</th>
<th>p</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002–2003</td>
<td>Early</td>
<td>117</td>
<td>596</td>
<td>0.2643</td>
<td>0.0599</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>299</td>
<td>754</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003–2004</td>
<td>Early</td>
<td>245</td>
<td>627</td>
<td>0.1373</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>269</td>
<td>665</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004–2005</td>
<td>Early</td>
<td>210</td>
<td>353</td>
<td>0.1532</td>
<td>0.0115</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>261</td>
<td>381</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note that in ME there is no significant difference between the two phases whereas in AR there is.
... and Newman, 2005), and modeling this interaction is especially now in the center of attention in dryland ecology (Wilcox 4. Discussion

plots in Fig. 4 shows that increased because of the effect of rainfall events, and subsequently decreased because of the effects of evaporation. The effect of daily temperature variations is also significant and is shown clearly in Fig. 4 in the days without rain. On days of drying out during long dry spells, changes in were strongly affected by the drying process, as expressed in .

The results of the GLM analysis indicate that during the 3 years of observation, the relationships between soil moisture and biomass were significantly similar in AR (0.14 < p < 0.26, Table 9), whereas in ME there was a significant difference between the regression lines for the early and the late phases of the season (0.001 < p < 0.06, Table 9). This was despite the fact that in ME the rainfall in the winter of 2005 was half that in the winters of 2003 and 2004. This result may imply that in AR, the effect soil of conditions on productivity is temporally dynamic whereas in ME there is a seasonal variation in the impact of soil moisture.

4. Discussion

The interaction between hydrological and ecological processes is now in the center of attention in dryland ecology (Wilcox and Newman, 2005), and modeling this interaction is especially important for better understanding of the composition, productivity and distribution of the vegetation associations of the desert fringe. A spatio-temporally explicit model that predicts cause and effect scenarios could contribute to ecological studies but, hitherto, spatially and temporally explicit models were viewed by ecologists with skepticism, because they are highly complex and were suspected of being unrealistic (Schieggl et al., 2005). The model presented here differs from previous studies in three respects: (I) it takes into account spatial variations in rock coverage—an important factor with regard to soil moisture in semiarid areas (Poens and Laevée, 1994); (II) it considers the effects of hydrological sinks and sources with regard to the spatially realistic prediction of water deficit conditions on slope sub-units—an important factor in runoff generation on semiarid slopes (Yair and Kossovsky, 1998) and (III) it combines actual rainfall and temperature data with topographic, soil and rock-cover data to accurately simulate the temporal variations in the conditions for germination and production, and to account for the effects of rainfall pulses (Noy-Meir, 1973). Our model also contributes to existing published ANPP models, in its focus on the slope as the most relevant scale.

In dry environments, ANPP is hypothesized to be greater in sites with improved and stable soil moisture conditions: seedling establishment, and plant development and survival are higher in moist areas. Svoray et al. (2004) showed that there is a positive and significant relationship between site conditions and annual vegetative ANPP. However, their model was static and did not include the effects of rainfall onset, dry and wet spells and temperatures variation on conditions for production. Other models are empirical (Epstein and Lauenorth, 1997), based on field data (Polly et al., 2005) or remotely sensed data (Svoray and Shoshany, 2003). The empirical models may be of high agreement with field measurements (R², 0.45–0.81, depending on location and year; Shafran-Natan, 2006) but are usually site-specific. An advantage of our model over remote-sensing models (e.g., Bénié et al. (2005)) is the use of higher resolution, mainly in time but also in space, than that available in the most frequently used satellite images. In addition, our model is free from the notoriously disturbing effect of clouds, which seriously limits the use of satellite data during the winter.

Our results show that conditions for ANPP of annual vegetation can be simulated realistically and that model predictions agree well with ground and satellite biomass measurements (Table 7). The relatively high agreement proves that fuzzy rule-based model can be successfully used to study ecosystem responses to variations in temperature and rainfall. The unexplained variation observed here can be attributed to two major sources. The first is uncertainty in sub-model predictions and the consequent error propagation within the GIS database. The second comprised parameters that were not considered in our model such as nutrient – mainly nitrogen and phosphorus – availability (Augustine, 2003); the plant-community structure (Osem et al., 2002); ecological interactions within the plant community (Mouquet et al., 2004) and seed dispersal, which we considered to be spatially homogeneous. The biotic parts could be added to the model in future work as here we were focused mainly on modeling the climatic and environmental conditions for annuals ANPP.

The results of the sensitivity analysis imply that rainfall depth is the most important factor to cause variation in ANPP. But, the difference between its weight and that of other factors we tested is relatively small while the combined effect of rainfall depth and evaporation rate is very similar to the combined effect of topography (including runoff model and radiation) and rock cover. This means that spatial-environmental variation in soil moisture is of similar importance to climatic conditions in causing ANPP variation. The importance of temperature, however, was found less significant than that of water availability although other studies (e.g., Henkin et al. (1998)) showed that cold days could decrease productivity. The reason is probably the fact that our regression results reflect the productivity two phenological phases while in this time scale other conditions compensate on the delay caused by a cold day. Similarly the effect of drying between rain pulses was found to have lower significance.

The difference in the date of germination between the sites, shown in Fig. 2, is reasonable and our field observations clearly show similar results. Similarly to the model predictions, field observations also show that nearly 2 weeks after the first effective rainfall event the entire study area has germinated. Yet, despite the fact that in a relatively short duration the entire study area germinates there is a large difference in spatio-temporal variation in ANPP between the two ecosystems as shown in Fig. 4 and further quantified in Table 9. The difference can be attributed to differences in phenological phases of annuals in the two ecosystems which can be explained by differences in the environmental infrastructure. Gutman and Seligman (1979) indicated the following phases in the growing season of annuals in ME: germination, which occurs after the first rainfall event; slow production during December and January, because of low temperatures; the appearance of fully established vegetation towards February; continuation...
of production until April. In May, when moisture decreases significantly, the annuals dry and wither, and most of the seeds are dispersed (Sternberg et al., 2000). In contrast, in AR, production begins also shortly after the first rains, but the life-cycle of most plants is very short, so that by March most of them has matured and dispersed their seeds. In AR the annuals are under continuous water stress conditions (Danin and Orshan, 1990) while in the Mediterranean site the provision of rainfall is more stable. The difference between the two sites is enhanced by differences in their soil characteristics and especially hydraulic conductivity and soil depth. With regard to hydraulic conductivity—the soil in ME contains more clay (50%) whereas that in AR is dominated by silt and sand particles, which enhance infiltration, but also increase water loss through evaporation and percolation. With regard to soil depth—the average soil profile is deeper than 2 m in ME, compared with 30–40 cm in AR. These two soil characteristics are expressed in our model through the soil-deficit (DEF) sub-model, and we therefore assume that in ME water accumulates during rainfall events in December and January as stored soil moisture that will be used, if needed, by the annual vegetation during the warmer season (February–April). Thus, in ME, in the later phase of the season, annuals can benefit also from the soil moisture storage while in AR, because of the shallow depth and high hydraulic conductivity of the soil, water does not accumulate after rainfall events and is not available for the annual plants later in the growing season. Consequently, we observed that in AR there was no significant difference in the dependency of ANPP on water availability between the first and the second phases of the season.

5. Conclusions

We developed here a spatially and temporally explicit model to predict conditions for aboveground net primary production of annual herbaceous vegetation from climatic data and environmental sub-models. The model was applied to two study sites in a climatic gradient during 3 years of observation. The variation of climatic and environmental conditions experienced offers an opportunity to test the model against ground and satellite measurements.

ANPP predictions were strongly correlated with actual biomass harvests in both sites, however, the coefficient of determination were higher in the semiarid site than in the Mediterranean site. Despite expected noise, due to mixed pixels, predicted conditions were also in agreement with NDVI data from IKONOS images. This might be due to the fact that satellite data reflect the biomass amounts in the entire plot area, including the effects of rocks that reduce the total predicted biomass and were expressed in our model while harvests involve extrapolation of biomass data from small quadrats to large areas.

Rainfall depth is indeed the most important factor to cause variation in ANPP but the difference between its weight and that of other factors is not large and the combined weight of rainfall depth and evaporation rate is similar to the combined weight of topography (including runoff model and radiation) and rock cover. This means that variation in soil moisture due to water redistribution is of similar importance to climatic conditions in causing ANPP variation. The weights of temperature and soil drying rate were less significant.

The resulted model outputs show variation in both time and space in conditions in both Mediterranean and semiarid areas while they confirm that the semiarid area is more heterogeneous in nature, in both time and space, and that the differences in phenological phases between the two sites can be simulated. Daily simulations of our model show that conditions for ANPP increase due to the effect of rainfall events, and subsequently decrease because of the effects of evaporation. The effect of daily temperature variations is also significant and is shown mainly in dry days. On days of drying out during long dry spells, changes in conditions were affected by the drying process. Our results further reflect the differences in soil hydraulic conductivity and depth between the two sites while in the semiarid site, in the two phenological phases, production was under water stress but in the Mediterranean site annuals are less dependent on rainfall amount and distribution in the later phase of the season, as they benefit from the soil moisture storage.

The model presented here is relatively simple and can be applied using available image processing and GIS software, a fact which increases the feasibility of its use by researchers and practitioners. Future developments and applications of this model should further refine the sub-models, but should also include further analysis that will involve delimitation of ANPP dynamics in time and space, and assessment of the effect of stress scenarios on the ANPP of annual vegetation.

Acknowledgments

This research was supported by The Israel Science Foundation (grant No. 692/06). We thank the Geological Survey of Israel for providing us the DEM and prof. Joel Dan for the Soil map. We thank Itzhak Benenson for useful comments on an earlier version of the manuscript, Noam Seligman for fruitful discussions, and two anonymous reviewers for useful comments and thorough review. We also acknowledge the help of Eugene David Ungar with the GLM analysis and Raffi Yonathan, Dani Barkai, Hagit Barlam, Amit Dolev and Yehuda Yehuda for their help with the field work.

References


