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The resilience of annual vegetation primary production subjected to different climate change scenarios

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Abstract We examined if climate change in two dry ecosystems—Mediterranean (DME) and Semiarid (SAE)—would cause substantial reduction in the production of annual vegetation. Field measurements and computer simulations were used to examine the following six climate change scenarios: (1) rainfall amount reduction; (2) increases of 10 % in annual evaporation rate and 5 % in annual temperature; (3) increase in magnitude of rainfall events, accompanied by reductions in frequency and seasonal variation; (4) postponement of the beginning of the first rainfall event of the growing season; (5) long dry spells during the growing season; and (6) early ending of the growing season. The results revealed the following outcomes. a) Reduction by 5–35 % in annual rainfall amount did not significantly affect productivity in the DME, but a large (25–35 %) decrease in rainfall would change vegetation productivity in the SAE and lead to a patchier environment. b) Similar results were observed: when temperature and evaporation rate were increased; when the magnitude of rainfall events increased but their frequency decreased; and during a long mid-season dry spell. c) In both ecosystems, changes in the temporal distribution of rainfall, especially at the beginning of the season, caused the largest reduction in productivity, accompanied by increased patchiness. d) Long-term data gathered during the last three decades indicated that both environments exhibited high resilience of productivity under rainfall variability. These results imply that the response of dry ecosystems to climate change is not characterized by a dramatic decrease in productivity. Moreover, these ecosystems are more resilient than expected, and their herbaceous productivity might undergo drastic changes only under more severe scenarios than those currently predicted in the literature.

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1 Introduction

In light of ongoing changes in climate characteristics, the search for imminent ecosystem shifts attracts increasing attention in the scientific literature (e.g., Rustad 2008; Kafle and Bruins 2009; Kèfi et al. 2010). Previous studies showed that global climate change created environmental problems and hazards for species and ecosystems (McCarty 2001). Mediterranean and semiarid ecosystems are expected to be among the most vulnerable, because of their nature as transition zones (Frederick and Major 1997; Schwinning and Sala 2004).

Species biodiversity (Bai et al. 2004), richness (Visser and Both 2005) and composition (Suttle et al. 2007) are considered as indicators for climate change impacts on biological processes, because they are thought to reflect species adaptation to and survival under a wide range of climatic conditions (Bradford et al. 2006). Annual net primary production (ANPP) variations in space and time, however, reflect floral and community responses to fluctuations in weather conditions between and within years (Bradford et al. 2006). This is probably the reason why many studies in dry environments have focused on the response of ecosystem productivity to climatic changes, and especially, to fluctuations in rainfall amount (e.g., Grime et al. 2008; Xu et al. 2009).

Shifts in relationships between climatic variables—especially soil moisture—and productivity relationships are not easily traced, mainly because the responses of biological processes to variation in rainfall and soil moisture are characterized by several temporal and spatial scales (Loik et al. 2004). Between-seasons differences in magnitude and frequency of rainfall events, and in seasonal rainfall amounts and distribution, add to the difficulties in defining threshold values of ecosystem responses to changes in rainfall characteristics (Reynolds et al. 2004). Thus, detection of changes in ecosystem productivity should be established through a long-term study (Heisler-White et al. 2008; Rustad 2008). This is especially true in the case of annual vegetation, which exhibits no carry-over effects from previous seasons, i.e., productivity of each growing season reflects only that specific season’s weather conditions (Schwinning et al. 2004). The impact of changes in climatic conditions on productivity is therefore complex and combines the effects of several driving factors (Lemmens et al. 2006).

Previous studies suggested that in dry regions processes that determine ANPP depend primarily on the rainfall regime, which is characterized by “pulses” and “interpulse periods”. This causes dynamic changes in spatial and temporal soil moisture distributions (Noy-Meir 1973; Snyder and Tartowski 2006) and in the interactions between soil characteristics that control ecosystem functionality (Lauenroth and Bradford 2006). The responses of ecosystems to “pulses” involve several time scales: rainfall events—from minutes to hours; soil moisture—from days to weeks; and vegetation production processes—from days to months (Loik et al. 2004). Therefore, a decline in rainfall amount may not necessarily imply a reduction in ANPP (Wiegand et al. 2004), because of spatio-temporal variations in climatic and environmental conditions (Porporato et al. 2002; Swemmer et al. 2007). For example, it is well known that high temperatures increase evaporation from soil water resources while decreasing the length of the growing season (Trnka et al. 2004). However, low temperatures accompanied by high rainfall amount may also delay production processes, as a result of low evaporation (Notaro 2008), and low evaporation can lead to water ponding, which can not only delay production process, but can even lead to mortality of plants (Ludwig et al. 2005).

Holling (1973) defined the resilience of ecological systems as the amount of disturbance that an ecosystem could withstand without changing its spatial patterns, and various studies showed that dry ecosystems have the potential to recover despite severe disturbances (Gunderson 2000). This capability reflects the sensitivity of annual vegetation to changes in soil moisture content, which can vary according to specific rainfall and temperature conditions within a given growing season (Muldavin et al. 2008). The question asked in the present study was whether predicted climate change scenarios would affect the productivity of herbaceous vegetation in a semiarid site, despite its observed stability under seasonal rainfall variations?

Our *aim* in this paper is to explore the responses of annual vegetation to predicted climate change scenarios. We also used long-term ANPP predictions that include varied seasonal conditions, e.g., dry and wet growing seasons, to examine the ability of dry ecosystems to preserve their productive capacity after one or several dry seasons, i.e., their resilience. We further *hypothesized* that annual vegetation in dry environments must be intrinsically adapted to water stress and, therefore, would exhibit only relatively small changes in productivity in response to the predicted climate change scenarios.

2 Materials and methods

2.1 Study sites

The study was conducted in two environments that exemplify the low and high extremes of semi-arid conditions in Israel: a dry Mediterranean environment (DME) and a semi-arid environment (SAE). The DME was represented by the Korazim site (35°35′E; 32°55′N; 80–150 ma.s.l.; average annual rainfall ~500 mm), located north of the Sea of Galilee, in northern Israel. The SAE was represented by Long-Term Ecological Research (LTER) Lehavim, located in the Goral Hills, in the Negev Desert, 11 km north of Be’er Sheva (31°20′N; 34°45′E; 350–500 ma.s.l.; average annual rainfall ~300 mm). Rainfall data for the Korazim site were acquired from the Almagor standard meteorological station, located 3 km south-east of the study area. Temperature and evaporation data were acquired from the Dafna standard meteorological station, located 25 km north of the site (Svoray et al. 2004). The data at the Lehavim site were gathered at the standard meteorological station in the Lahav settlement, 4 km north-east of the study site. Both sites undergo a 5- to 6-month dry period, characterized by high temperatures, every year. At the beginning of the growing season (December-January) production is slow because of the low temperature; it peaks during the warmer months towards the end of the wet season (February-April) (Noy-Meir et al. 1989; Svoray and Karnieli 2011). Growth in spring is rapid, and peak growth, closely followed by seed set, occurs in March-April. In the DME, the herbaceous community is rich, comprising 166 species, of which 74 % are annuals (Sternberg et al. 2000); at the SAE about 130 species, mostly annuals, were found (Osem et al. 2002). Previous studies found that the differences between the two environments in daily variations in soil-water conditions depend not only on the daily weather, but more on soil water storage conditions (Reynolds et al. 2004; Muldavin et al. 2008). At the DME the soil profile is thick (~1–1.5 m) and the soil texture includes more than 50 % clay, which imparts a high water-storage capacity. At the SAE, in contrast, the soil profile is very thin (< 40 cm) and it has a silty-clay texture, which results in a low water storage capacity.

2.2 The hypothetical season and climate change scenarios

Most species in the studied areas are annuals, and the few perennial herbaceous species wither during the dry season (Sternberg et al. 2000). Therefore, spatio-temporal changes in ANPP values are expected to correlate strongly with changes in the contemporaneous distribution patterns of soil moisture (Oesterheld et al. 2001; Reynolds et al. 2004).

Here we used a GIS-based productivity model that operated daily in each 25-m^2 grid cell. The model is based on fuzzy algebra and simulates the effects of solar radiation, hydraulic conductivity, rock coverage, and daily rainfall, evaporation and temperature, on primary production processes of herbaceous vegetation. Additional explanation about the productivity model formulation and the model validation are given in Online Resource 1.

Since inter-annual climate variability is usually not included in studies on the effect of climate change on vegetation productivity (Daly et al. 2000; Notaro 2008) our model can explore the effects of rainfall characteristics that are usually disregarded. This is especially important because rainfall distribution and amount in our sites exhibit high inter-annual variability, so that simulations of daily climatic conditions based on a 'typical' season, i.e., an actual season deemed to exhibit representative seasonal average conditions, could be misleading. A 'hypothetical season', i.e., a set of climatic condition randomly selected from local historical data, was therefore designed, and the climate-change scenarios were applied to it.

These scenarios were based on manipulations of actual data of rainfall (mm), evaporation depth (mm) and air temperature (°C), and were applied to a database of long-term daily climatic data for each season (October through April). This procedure covered 30 seasons (1978–2008) at the SAE site and 21 seasons (1986–2008, excluding 1990–1992) at the DME site.

At the SAE site an average of 50 rainy days per season was recorded, of which 65 % were effective storms, in which daily rainfall exceeded 10 mm. At the DME site an average of 53 rainy days per year was recorded, of which 74 % were effective for ANPP processes. These results agree with those of Noy-Meir (1973), who suggested that the SAE environment was characterized by an average of 50 rainy days per season. In our present study, the daily values of evaporation and temperature were selected randomly from lower and upper values recorded for rainy and rain-free days in each month in actual years. The start of the rainy season was set at about mid-October in all scenarios, except for the one in which it was postponed to the latest date recorded in the last three decades in each environment. The exact date of season start was randomly selected from among the season-opening dates recorded over 30 and 21 years at the SAE site and the DME site, respectively. The end of the season was set at 18 days after the last rainfall event (Svoray et al. 2008).

The present analysis is based on two assumptions: 1) temperature, evaporation and rainfall are interrelated, and their effects on ANPP cannot be examined separately; and 2) annual plants are not affected by year-to-year carry-over of resources. The literature offers a large number of possible climate-change scenarios (Weltzin et al. 2003), and the following were selected from the most recent literature on predicted climate change in the Eastern Mediterranean Basin (see also Table in Online Resource 2).

1. Reduction in total annual rainfall—A gradual reduction of 5–35 % in annual rainfall was applied, with a decrease of 5 % at each iteration (Ben-Gai et al. 1998; Romero et al. 1998; Ragab and Prudhomme 2002; Dore 2005). Rainfall reductions were applied on a monthly basis, irrespective of whether rainy days were effective or ineffective. This scenario is referred to as **rainfall**.
2. An increase of 10 % in annual evaporation and a parallel increase of 5 % in annual average temperature. This scenario was predicted to occur by 2100 (Dayan and Koch 1999). In parallel to these changes in temperature and evaporation, seasonal rainfall was reduced gradually by 20–35 % from the seasonal average, by 5 % at each of four iterations. Referred to as **tmp_evop**.

3. Yosef et al. (2009) predicted an increase in the number of extreme rainfall events, accompanied by a reduction in the total number of events. In this scenario, the frequency of rainfall events was reduced and the number of effective events was increased by an order of magnitude. Seasonal rainfall was reduced by 20–35 % from the average annual rainfall, by 5 % at each iteration. This is referred to as **frequency-magnitude**.
4. Long-term changes in the temporal distribution of rainfall events were predicted to affect mostly the beginning and end of the growing season, at both the DME and the SAE sites (Steinberger and Gazit-Yaari 1996; Yosef et al. 2009). This scenario was applied in three alternative variants: a) the growing season starts at the latest date of the season's first recorded rainfall event in the last 30 years in the SAE (12th December) and in the last 21 years in the DME (17th December). This is referred to as **season-begin**; b) the season includes the longest recorded mid-season dry spell—42 days in the SAE and 39 days in the DME. This is referred to as **mid-season**; c) the season ends at the earliest date recorded at each site during the recent decades—25th February in the DME and 14th March in the SAE. This is referred to as **end-season**. In each of these three scenarios annual rainfall was also reduced by 20–35 %, in steps of 5 % at each iteration. The reduced numbers of effective and ineffective events were scattered randomly through the season, and new threshold values of rainfall, evaporation and temperature were set according to the aforementioned principles.

2.3 What is considered a change in ANPP?

First, we look at the change at X, Y axes, which is the area size that was covered at each scenario by annual vegetation. Changes in covered area size of ANPP were established by zonal tabulate area calculation (ArcGIS 9.3.1). The ANPP values in the raster cells were classified into productive groups separated by 50- and 100-gm^{-2} intervals at the SAE and the DME site, respectively. Then, the appearance and disappearance of productive groups as a result of climate change scenarios were examined. We also examined the changes in values recorded along the Z axis, i.e., in the value of biomass amount that reflect the height and density of the plants in the same area. For this purpose we used the long-term ANPP data to define the lower and upper boundaries of ANPP in the two environments. We divided the ANPP values of each environment into three groups—low, medium and high productivity. At the SAE, the ranges were 20–100, 100–170 and 170–240 gm^{-2}, respectively; at the DME they were 200–500, 500–650 and 650–860 gm^{-2}, respectively. Since each group had upper and lower boundaries, each scenario outcome, i.e., ANPP values—each averaged over thousands of grid cells was assigned to one of these groups. The Results of each scenario (average ANPP that represents thousand of cells) against the long-term ANPP values are listed at Online Resource 3.

2.4 Detection of ecosystem resilience

The differences between ANPP values in successive seasons may indicate the existence or non-existence of a trend in ANPP. Between-seasons differences in modeled ANPP were computed with Eq. 1.

$$\Delta \mathrm{ANPP} = \mathrm{ANPPseason}_{t} - \mathrm{ANPPseason}_{t-1} \tag{1}$$

In which $ANPP_t$ represents model predictions for season t, and $ANPP_{t-1}$ are the corresponding values for the previous year (Fig. 1a). Long-term model predictions of ANPP were used to examine whether a decline in ANPP was followed by a recovery of the productivity in subsequent years, or by a degradation process. In the present paper, ΔANPP represents the change in the values of thousands of grid cells on the curve. We examined how close to one another are the means of two normally distributed populations of ANPP values from two separate years. The criterion for a substantial change was that the value of ΔANPP differed from zero by at least ± one standard deviation (Jensen 1996; Volcani et al. 2005). This approach enabled us to distinguish between changed and unchanged grid cells and also to determine the magnitude and the direction of changes. Thus, positive or negative changes were considered to have occurred when ΔANPP differed from the average threshold value by more than ±1 SD; the size of the difference, expressed in SDs, and its sign were regarded as the magnitude and direction of change. A sequence of years with increasing negative changes, without a trend towards recovery, would be considered indicative of ecosystem degradation or of a decline in ecosystem resilience (Fig. 1b).

3 Results

3.1 Impact of predicted climate change on PP

Reduction in annual rainfall by 5–35 % (**rainfall** scenario) did not significantly reduce ANPP in the DME (Fig. 2a), and the average simulated ANPP values—at 720.2–760.9 gm^{-2}—remained

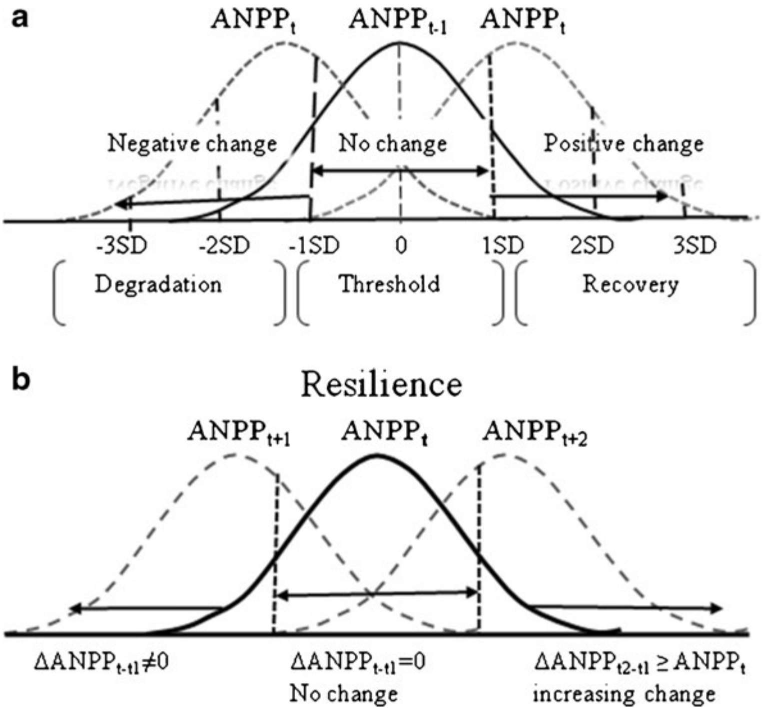

Fig. 1 Schematic illustration of ecosystem resilience change-detection approach used in the study

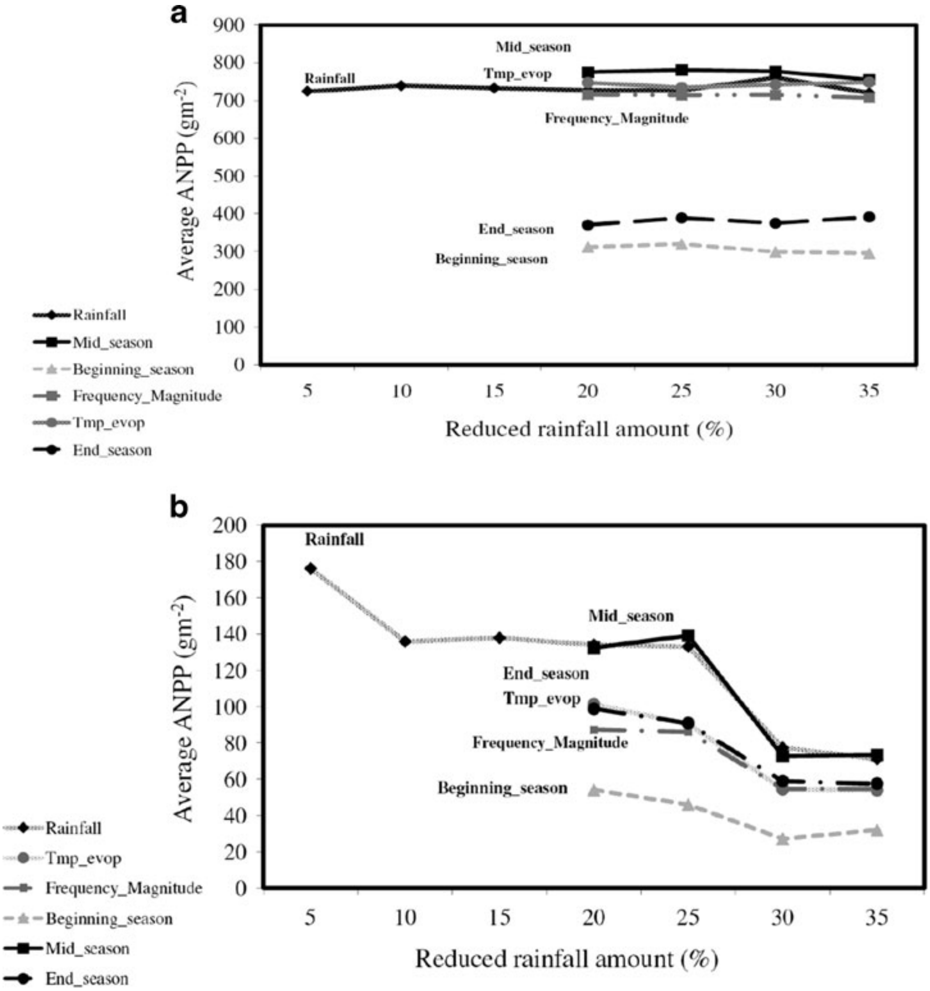

Fig. 2 The effect of simulated rainfall reduction (5–35 %) on average ANPP under each scenario, at SAE (**a**) and DME (2B)

in the high-productivity range. Groups that represent of high-productivity biomass (> 600 gm^{-2}) covered 70 % of the site in all cases (Fig. 2a). However, the response in the SAE differed, and when annual rainfall was reduced by 5–10 %, a reduction of 23 % in ANPP (from 176 to 135.8 gm^{-2}) was predicted (Fig. 2b). Nevertheless, these ANPP values are still within the long-term medium-production range. When rainfall was reduced by 30 %, ANPP declined from 133 to 77.2 gm^{-2}—a drop from the long-term medium-productivity range to the long-term low-productivity range—and the percentage of productive groups (i.e., patches) in the whole area of the SAE was transformed as annual rainfall diminished. The least productive group (0–50 gm^{-2}) occupied only 4 % of the site when annual rainfall was reduced by 5 %, but when rainfall was reduced by 35 % this group covered 70 % of the area (Fig. 2b).

The scenario **tmp_evop** also did not cause any substantial change in spatial patterns of productivity in the DME, where it remained in the range of 748.4–734.3 gm^{-2} (Figs. 2a and

3a), which is within the long-term high-productivity range. However, at the SAE site, **tmp_evop** caused a decrease in average ANPP to 53.9–101.3 gm^{-2}, leading to a drop to the low-productivity group, and 60–80 % of the site, with productivity of 0–50 gm^{-2}, was covered by the lowest group (Fig. 3b). This extreme reduction in ANPP occurred only when the annual rainfall was reduced by 25–35 % (Fig. 2b).

In the **frequency-magnitude** scenario, a reduction of rainfall amount did not cause any change in average ANPP, which remained at 706.9–715 gm^{-2}. Under all simulations under the **frequency-magnitude** scenario with 25–35 % rainfall reduction the ANPP values were within the long-term high-production range (Fig. 2a). This scenario also did not elicit a large change in the area occupied by the predicted ANPP groups in the DME site (Figs. 2a and 3a). In the SAE, however, a 30–35 % reduction in rainfall led to a drop in average ANPP to 54.7–87.1 gm^{-2} (Fig. 2b) and to a change in the areas occupied by the respective productivity groups: that covered by the least productive group (0–50 gm^{-2}) rose from 60 % when annual rainfall was reduced by 20 %, to 80 % of the area when annual rainfall was reduced by 35 % (Fig. 3b).

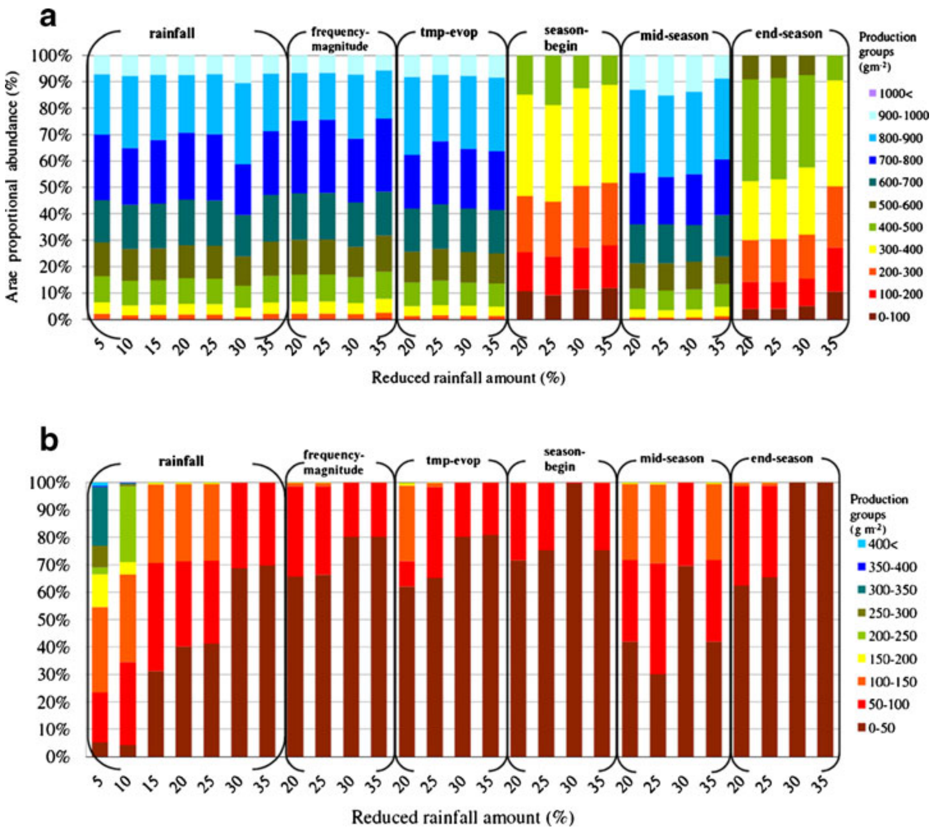

Fig. 3 The effect of annual rainfall reduction (%; secondary X axis) on ANPP cover (% area; Y axis) under each scenario, in the SAE (**a**) and in the DME (**b**). ANPP values of each environment were divided into groups at every 100 gm^{-2} in the DME and every 50 gm-2 in the SAE (legend). One hundred percent area size represents 50 km^2 in the DME (**a**) and 25 km^2 in the SAE (**b**)

The **season-begin** scenario had the greatest effect on average ANPP, and changes in the ecosystem patterns were observed in both environments. In the DME, ANPP values were reduced to the long-term lowest range, at 295.1–319.5 gm^{-2} in all cases, by rainfall reductions ranging from 20 % to 35 % (Fig. 2a). This scenario resulted in the lowest ANPP values that were predicted in this environment: some 80 % of the site was covered by medium-productivity groups (100–500 gm^{-2}; Fig. 3a) as a result of rainfall reductions of 20–35 %. In the SAE, average ANPP also showed the largest decline by 27–31.9 gm^{-2} (Fig. 2b) resulting from rainfall reduction of 30–35 %, and the lowest-productivity group (0–50 gm^{-2}) covered 70–100 % of the study site (Fig. 3b).

Surprisingly, the **mid_season** scenario increased average ANPP in the DME—to 754.9–780.8 gm^{-2}—and thereby raised it to the long-term highest-productivity range. As in most other scenarios, there was almost no change in average ANPP values under this scenario, and no substantial change in vegetation coverage of the various productivity groups was detected (Figs. 2a and 3a). In the SAE, annual rainfall reduction by 20 to 25 % caused a shift from long-term medium productivity—132.4–139.1 gm^{-2} (Fig. 2b)—under a reduction of annual rainfall by 20 % to 25 %, to the long-term low-productivity range—72.6–73.2 gm^{-2}—under a reduction of annual rainfall by 30 to 35 %. Thus, long rainy spells combined with reduction of 30–35 % in total annual rainfall led to a change in ecosystem productivity, but changes in cover of productive areas were only moderate: 30–70 % of the study site was covered by the medium-productivity groups (100–200 gm^{-2}; Fig. 3b).

When the rainy season was simulated to end at an earlier date (**end_season** scenario), ANPP predictions in both environments showed low average values, in the long-term low-productivity range. These values were higher than those predicted for the **season-begin** scenario. At the DME (Fig. 2a), the ANPP was in the range of 370–390.9 gm^{-2}, which implies a fall to the medium-productivity group (100–600 gm^{-2}) in 90 % of the site; at the SAE (Fig. 2b) ANPP was in the 54.4–97.8 gm^{-2} range. Both environments also exhibited a reduction in vegetation cover, which implies a patchier spatial pattern. At the DME 15–100 % of the vegetated coverage was in the production range of 200–600 gm^{-2}, and at the SAE 95–100 % of the site was covered by the lowest productive groups (0–100 gm^{-2}; Fig. 3b).

3.2 Long-term ΔANPP as an indicator of ecosystem resilience

Several change-detection analyses were applied to determine if a decline in ANPP after one or several dry seasons would initiate a process of ecosystem recovery or degradation (Volcani et al. 2005). We calculated the difference ($\Delta ANPP_{t,t-1}$) between the seasonal ANPP predictions for any given year (t) and those for the previous year (t-1); this encompassed 44,421 cells in the SAE and 80,089 cells in the DME. The difference, in standard deviations, between any $\Delta ANPP_{t,t-1}$ and the average $\Delta ANPP_{t,t-1}$ value (i.e., the percentage of grid cells in the entire grid layer that belong to this group) represents the magnitude of change between the seasons. The average ΔANPP of the whole study area indicated whether the direction of the process was positive or negative. Furthermore, the percentage of the grid cells whose ANPP value changed between successive years was also calculated and the percentage of "no-change" grid cells indicated how persistent was the ANPP in the ecosystem. The percentage of grid cells that changed by more than ±1 SD indicated how much the ANPP changed from the previous year. Student's *t*-test was used to assess the significance of the differences in the distribution of ANPP values between any season and the previous season.

The results for both environments showed that most of the growing seasons did not exhibit the same ANPP pattern as the previous season: only six growing seasons out of 21 at the DME (Table 1B) and three out of 30 at the SAE (Table 1A) showed non-significant changes in the $\Delta ANPP_{t,t-1}$values. Moreover, the percentages of grid cells in the entire $\Delta ANPP_{t,t-1}$ grid layers that showed no change were 0–69 % in both the SAE and the DME. In the SAE, within-year change in ANPP indicated continuous recovery over 16 seasons, and continuous degradation over 12 seasons, five of the latter in recent years. In the DME, recovery was observed during 10 seasons, and degradation during nine seasons.

In the SAE site, the largest negative change (negative steps of six SDs) occurred between 2001 and 2002, whereas in the DME the largest negative changes (negative steps of more than eight SDs from the threshold value) occurred between 1994 and 1995 and between 2001 and 2002. In the SAE the largest positive change—more than 7 SDs from the threshold value—was observed between 2006 and 2007, whereas in the DME the largest positive change—by more than eight negative SDs steps—from the threshold value occurred between 2000 and 2001.

4 Discussion

Ecosystems dominated by annual plants are subject to a continuous threat of water stress (Rees et al. 2001). Therefore, the survival and productivity of annual vegetation under conditions of frequent dry seasons depend on the ability of the ecosystem to recover after a drought period (Cox and Allen 2008). Climate changes are expected to induce persistent water stress and promote degradation processes. However, the results of our analyses did not reveal a clear decline in ANPP in the two studied ecosystems. These results indicate that over the last three decades droughts did not initiate a lasting degradation process in either environment. In other words, ecosystem resilience—the capacity to retain productive potential in spite of stress or disturbance—was not damaged by frequent droughts.

The high resilience of the ecosystems is expressed in the maintenance of ANPP level, in most cases, within the ranges of values that were previously recorded in the two environments under inter-seasonal climatic fluctuations. Nevertheless, the results of the climate change scenarios show reductions in ANPP: to the low- and medium-productivity groups under all scenarios in the SAE; to the low-productivity group under the **end_season** and **season-begin** scenarios in the DME. These ANPP reductions may reflect changes in spatial distributions of water resources and in prevalence of adequate germination conditions across the landscape.

Reduction in long-term ANPP because of low soil moisture availability leads to patchy distribution of water resources over the landscape (van de Koppel et al. 2002). Results of the **rainfall** scenario in the DME showed that changes in seasonal rainfall by 5–35 % did not cause substantial change in predicted ANPP. Moreover, there were almost no differences among four scenarios—**rainfall**, **tmp-evop**, **mid-season**, and **frequency-magnitude**—in average ANPP values and in coverage of productivity levels. Comparison of observed long-term ANPP values with the predicted ANPP values obtained under these four scenarios identified years with high ANPP values. These results show that, although available soil moisture was the main limiting factor for biological processes in dry environments (Noy-Meir 1973), there was only a limited response of ANPP to changes in total rainfall amount within the range predicted by climate change scenarios (Porporato et al. 2002; Huxman et al. 2004). Therefore, we may conclude that in these two dry environments, ANPP patterns are determined mostly by the length of the growing season and not by rainfall amount *per se*. The length of the growing season is determined by the number of days from the first effective rainfall event until 2–3 weeks after the final rainfall event and by soil-moisture storage capacity

Table 1 Detection of long-term change in ANPP, the magnitude of differences between current-season ANPP and previous-season ANPP, as determined by the number (percentage) of grid cells that fits the SD category. The SD and average ΔANPP values were calculated from the distribution of ΔANPP values, and showed the directions of ΔANPP differences. Positive SD at each SD category (percentage of grid cells) indicates recovery of the primary production process; negative ΔANPP SD indicates degradation. Student's *T*-test was used to determine the significance of differences between current-season and previous-season ANPP distributions – not significant (NS); $P<0.05$ *; $P<0.001$ **; $P<0.0001$ *** – in the SAE (Table 1A) and in the DME (Table 1B)

Current year	Previous year	Degradatio - increasing negative change in ANPP (%)						NO change	Recovery -increasing positive change in ANPP (%)						Current year rainfall	Average ΔANPP	S.D. ΔANPP	*p*-value
		−7 S.D.	−6 S.D.	−5 S.D.	−4 S.D.	−3 S.D.	−2 S.D.		2 S.D.	3 S.D.	4 S.D.	5 S.D.	6 S.D.	7 S.D.				
A																		
1980	1979							28.71	39.4	13.8	17.4	0.6	0.04		540.1	72.71	44.08	***
1981	1980		0.28	0.79	28.3	9.4	53.46	7.9							282.1	−112.5	53.16	***
1982	1981						0.18	18.04	14.43	67.4					215.1	29.86	12.32	***
1983	1982							26.41	41.13	13.0	18.7	0.68			394.9	119.4	69.65	***
1984	1983		0.76	0.3	28.3	9.75	52.38	8.5							156.3	−164.9	78.6	***
1985	1984							49.66	19.02	27.7	3.08	0.48			303.7	93.96	65.08	***
1986	1985			0.43	1	29.4	14.51	54.63							243.4	−45.64	34.78	***
1987	1986						17.96	54.79	26.26	0.74	0.28				356.7	−1.17	24.94	NS
1988	1987							0.58	1.32	2.99	5.36	54.4	18.9	15.95	369.6	112.6	23.05	***
1989	1988			1.6	29.2	14.4	50.66	4.07							275.1	−98.1	42.1	***
1990	1989							63.8	8.04	27.1	0.78	0.24			299.1	32.4	32.4	***
1991	1990							68.87	25.2	5.31	0.6	0.03			398.8	2.49	5.44	NS
1992	1991					0.2	17.8	45.12	36.88						527.5	2.5	6.74	NS
1993	1992							0.36	0.4	0.89	27.7	38.8	13.6	17.66	310.8	66.1	14.6	***
1994	1993		0.19	0.57	25.0	7.65	44.95	21.55							261.3	−73.3	39.5	***
1995	1994							6.81	51.05	11.6	29.3	0.8	0.4		422.7	45	20.35	***
1996	1995		0.19	0.76	26.3	8.67	50.49	13.55							248.9	−106.32	54.41	***
1997	1996							64.35	9.63	25.2	0.65	0.13			266	20.32	18.93	***
1998	1997							58.61	11.38	28.4	0.9	0.19			280.7	64.88	55.41	***

Table 1 (continued)

Current year	Previous year	Degradatio - increasing negative change in ANPP (%)						NO change	Recovery -increasing positive change in ANPP (%)						Current year rainfall	Average ΔANPP	S.D. ΔANPP	*p*-value
		−7 S.D.	−6 S.D.	−5 S.D.	−4 S.D.	−3 S.D.	−2 S.D.		2 S.D.	3 S.D.	4 S.D.	5 S.D.	6 S.D.	7 S.D.				
1999	1998			0.45	2.85	27.7	16.55	52.35							140.2	−136.09	98.33	***
2000	1999							31.47	36.69	13.3	17.8	0.63			198.3	57.27	35.31	***
2001	2000							3.03	47.12	18.5	29.6	1.16	0.43		358.7	166.49	69.23	***
2002	2001	4.21	49.8	15.6	29	0.64	0.52	0.07							324.7	−45.49	8.3	***
2003	2002		0.13	0.59	24.2	9.93	37.46	27.68							298.57	−33.38	18	***
2004	2003		0.19	0.68	25.3	8.83	47.1	17.87							268.65	61.27	32.85	***
2005	2004							0.22	0.33	0.93	17.3	45.6	11.3	23.96	261.32	64.56	14.81	***
2006	2005			0.48	1.6	31.9	22.49	43.5							204.9	−81.29	33.24	***
2007	2006								Positive change larger than 7 S.D.						238	49.73	6.07	***
2008	2007	0.18	0.7	26.8	10.0	51.3	10.89								202.9	−91.22	29.45	***
B																		
1987	1986							4.17	24.43	46.5	22.4	1.72	1.21		702.3	14.56	5.75	NS
1988	1987		20.77	20.77	41.45	19.39	3.92	0.57							532.5	−178.49	45.27	***
1989	1988							0.01	0.65	2.15	1.07	12.9	30.7	34.6	356.4	36.09	6.25	*
1990	1989			9.83	17.64	27.1	38.58	6.83							404	−96.53	40.46	***
1994	1993							0.02	0.09	0.2	2.08	13.7	22.76	40.54	355.6	430.78	71	***
1995	1994	Negative change higher than -7 S.D.													577.6	−284.77	22.44	***
1996	1995	0.63	3.59	14.8	28.07	43.91	7.39	1.59							565.9	−50.08	16.33	**
1997	1996			1.31	0.27	12.02	20.9	61.04	1.87	2.39					470.3	13.85	7.26	NS
1998	1997		3.02	13.42	18.92	37.77	26.4	0.11							554.4	47.41	17.99	**
1999	1998						13.8	67.86	13.32	3.53	0.26				283.2	−1.56	29.97	NS
2000	1999					0.93	4.17	42.99	38.46	11.7					495.4	46.29	58.69	NS

Table 1 (continued)

Current year	Previous year	Degradatio - increasing negative change in ANPP (%)						NO change	Recovery -increasing positive change in ANPP (%)						Current year rainfall	Average ΔANPP	S.D. ΔANPP	*p*-value
		−7 S.D.	−6 S.D.	−5 S.D.	−4 S.D.	−3 S.D.	−2 S.D.		2 S.D.	3 S.D.	4 S.D.	5 S.D.	6 S.D.	7 S.D.				
2001	2000								Positive change larger than 8 S.D.						320.1	180.95	8.56	***
2002	2001	Negative change larger than -7 S.D.													562.2	−215.54	24.92	***
2003	2002						0.2	69.06	19.62	9.17	1.84	0.1			721.7	18.96	29.13	***
2004	2003					0.35	4.66	39.42	46.13	9.23					581.3	52.49	59.06	NS
2005	2004	10.2	14.88	26.7	39.7	4.32	1.14	0.12							370.7	−22.95	5.95	NS
2006	2005	0.1	3.84	18.03	36.73	28.02	12.6	0.59							508.4	−67.95	21.98	*
2007	2006							0.13	0.25	40.5	49.1	9.77			502.7	145.67	25.02	***
2008	2007			33	32.82	20.02	11.3	1.74							327	−296.45	88.65	***

during the growing season. Soil moisture accumulation in the DME depends on a thick, clayey soil profile (>50 % clay) that can accumulate and store water during the wet season. Such accumulation is probably the reason that scenarios **end_season** and **season-begin** showed a reduction in ANPP values compared with observed long-term data. It also may explain the change in spatial coverage of the low- to medium-productivity groups (up to 600 gm^{-2}). In the **end_season** and **season-begin** scenarios, the season became shorter than in the other scenarios, and even inclusion of both effective and ineffective rainfall events did not compensate for the season shortening; additional rainfall at the end of the growing season was not utilized by annual vegetation, either to extend the production period or to increase peak production. Moreover, although the growing season usually starts during autumn, the air temperature is still warm and helps to create adequate conditions for germination and ANPP processes. However, when the growing season starts late, i.e., during the coldest period of December to mid-February, the low air temperature inhibits these processes (Noy-Meir 1973). Consequently, although ANPP values under the **end_season** and **season-begin** scenarios were within the actual long-term ANPP range, there were consistent reductions in the simulated ANPP, which indicated changes in the vegetation-covered area.

A decrease in the area of the high-productivity groups is expressed in negative feedback between vegetation growth and soil-water availability. Such a decrease generates more bare soil, and the vegetation faces difficulties in recolonization (Rietkerk et al. 2004). In contrast, recovery of plant cover enhances the positive feedback between soil moisture and plant cover (Rietkerk and van de Koppel 2008). As more-productive groups develop, the vegetation becomes denser and each group accumulates more water, nutrients and sediments than less productive one (Ludwig et al. 2005; Arnau-Rosalén et al. 2008). The resulting improvement in local conditions may stimulate further productivity increase in the course of the season (Ludwig et al. 1999).

In the SAE the **season-begin** scenario led to the lowest ANPP values: a decrease by 27–31.9 gm^{-2} under a rainfall reduction of 30–35 %. This may imply that if future seasons start later than they do now, and if annual rainfall amounts decrease by more than 35 %, the ecosystem could lose its resilience and become desertified (Scheffer et al. 2001). Unlike the DME, the SAE showed a decline in ANPP after rainfall reductions of 30–35 % in all scenarios: for example, under the **rainfall** and **season-begin** scenarios rainfall reduction of 30 % led to ANPP reductions of 77.28 and 27.05 gm^{-2}, respectively. Under all scenarios, the combination of rainfall reduction by 30–35 % with increases in numbers of rainfall spells (in scenarios **tmp_evop**, **frequency-magnitude** and **begining/end_season**) caused reductions in ANPP to lower values than recorded actual ANPP data. When annual rainfall is reduced to less than 250 mm in the SAE, changes in ANPP values and the size of the high-productivity group are likely to occur. In this case, it is the shallow soil profile and the silty-sandy soil texture (< 23 % clay) that make this ecosystem more sensitive to rainfall reduction. Water storage depends more on the rainfall “interpulsing” since long dry periods are accompanied by high evaporation. The differences in hydraulic conductivity and soil depth between the sites indicate that there is a permanent potential for water stress in the SAE, once dry conditions occur. Moreover, none of the examined scenarios led to high long-term average ANPP values in this ecosystem, which indicates the high importance of both annual rainfall amounts and numbers of effective rainfall events, for supporting production processes.

Under the predicted climate-change scenarios the frequency of dry seasons, especially in dry environments, is expected to increase. A comparison between the worst outcomes under each scenario in the two respective environments shows that the reduction of ANPP can lead to the largest changes in subsequent ANPP amounts and the cover of more-productive groups. Thus, in dry environments, less-productive growing seasons are not necessarily caused by seasonal rainfall reduction but could be an outcome of changes in rainfall distribution, especially at the beginning and end of the growing season.

Even though there is no carry-over effect of soil moisture from previous seasons, and the stored water dries out during the summer, there still remains a contribution of seeds from previous seasons (Petru et al. 2006). Therefore, reductions in ANPP to values lower than expected, because of more extreme rainfall patterns, are considered to be manifested mostly in changed spatial patterns of productivity during the following season, but they could lead to new patterns of seed dispersal, survival and establishment (Lundholm and Larson 2004). Therefore, it can only be assumed that climate changes that involve changes in the distribution of rainfall events, even if they are associated with rainfall reductions by less than 35 % of the annual average, will cause ANPP decreases. The ability of grasslands to persist during drought years may be indicative of the resistance of those grasslands to climate changes (Robertson et al. 2009). Future studies, that examine effects of climate change on natural vegetation, should examine the responses of dry-ecosystem resilience to extreme weather events during the course of growing seasons; and specifically to more extreme events than have been predicted in the scientific literature.

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