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Opposite trends in life stages of annual plants caused by daily rainfall variability

Interaction with climate change

OPPOSITE TRENDS IN LIFE STAGES OF ANNUAL PLANTS CAUSED BY DAILY RAINFALL VARIABILITY — INTERACTION WITH CLIMATE CHANGE

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ABSTRACT

Global Circulation Models of climate predict not only a change of annual precipitation amounts but also a shift in the daily distribution. To improve the understanding of the importance of daily rain pattern for annual plant communities, which represent a large portion of semi-natural vegetation in the Middle East, I used a detailed, spatially explicit model. The model explicitly considers water storage in the soil and has been parameterized and validated with data collected in field experiments in Israel and data from the literature. I manipulated daily rainfall variability by increasing the mean daily rain intensity on rainy days (MDI, rain volume/day) and decreasing intervals between rainy days while keeping the mean annual amount constant. In factorial combination, I also increased mean annual precipitation (MAP). I considered five climatic regions characterized by 100, 300, 450, 600, and 800 mm MAP. Increasing MDI decreased establishment when MAP was >250 mm but increased establishment at more arid sites. The negative effect of increasing MDI was compensated by increasing mortality with increasing MDI in dry and typical Mediterranean regions (c. 360–720 mm MAP). These effects were strongly tied to water availability in upper and lower soil layers and modified by competition among seedlings and adults. Increasing MAP generally increased water availability, establishment, and density. The order of magnitudes of MDI and MAP effects overlapped partially so that their combined effect is important for projections of climate change effects on annual vegetation. The effect size of MAP and MDI followed a sigmoid curve along the MAP gradient indicating that the semi-arid region (≈300 mm MAP) is the most sensitive to precipitation change with regard to annual communitie

INTRODUCTION

Drylands are characterized in the first place by the limitation of plant growth by low quantity of water. Another important characteristic is the spatial and temporal distribution and great variability of water, which play important roles in structuring ecosystems and maintaining biodiversity [17,35,44]. Comparisons of historic climate trends in the Mediterranean basin showed a more or less clear shift in the distribution of rainfall intensities from light to heavy or torrential rains [1]. Present global climate models suggest that these trends will continue [9]. Many vegetation processes are affected by daily rain variability: germination [11,23], plant growth [19], litter decomposition [37,39], and litter mineralization [4]. Despite the well-documented importance of water in drylands and their wide global distribution [32], just a quarter of the studies reviewed by DiTommaso and Aarssen [6] included a water treatment and only a single study assessed the variability of water. Only a handful studies have been added since this review. Thus, our knowledge about the effects of climate change with regard to changes in daily precipitation patterns remains limited [42]. Experiments to study the effect of daily water availability on plant growth and survival have concentrated on crop species or used unnaturally long intervals or only parts of the plants' life cycle. The majority of results from these studies suggest that greater rain intensities and longer intervals between rains, *i.e.*,
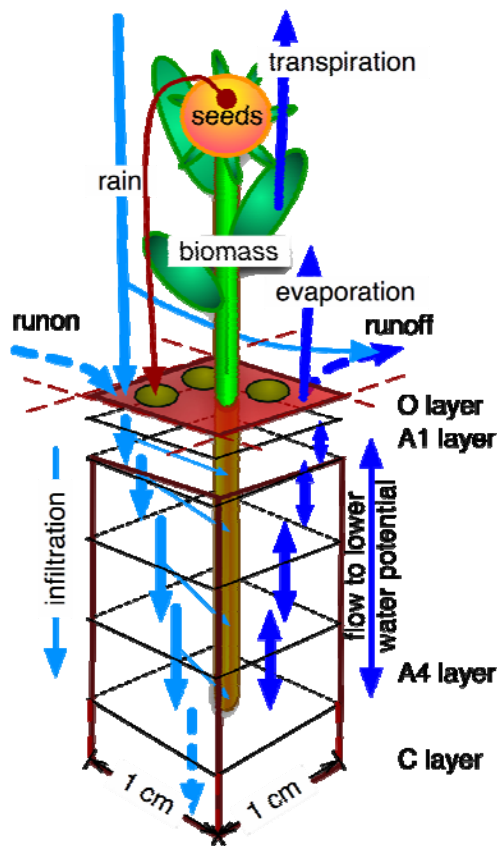
Figure 1. **Schematic overview of processes simulated in one cell of the model.**

while keeping the total amount of rain constant, reduce plant performance [5,12,27,34,38]. The exceptions, however, suggest that the negative effect of daily rain variability may be caused by a low water holding capacity of the soil, confined rooting space or a shallow rooting habit [21,31,38,43]. Since the systematic variation of rain fall in field experiments while maintaining realistic rain intervals and intensities is a logistic challenge, I used a spatially explicit model to investigate the effect of daily rainfall variability on plant performance. The importance of rainfall variability is likely to decline from arid to mesic ecosystems. Therefore, I assessed its importance for a gradient of aridity. Furthermore, I compared the effect of changing daily variability to that of changing the annual rain volume.

Methods

I used a spatially explicit model to simulate the influence of daily rainfall variability on plant growth of individual annual plants on a 25 cm × 25 cm area subdivided in 1 cm² cells (Fig. 1).

Annual plants are the dominant herbaceous life form along a gradient from 100 to 800 mm mean annual precipitation in Israel. Furthermore, annual plants generally do not store water in their tissue and can therefore be expected to be especially responsive to daily rainfall variation. The model comprises four modules using equations or rules describing physical processes for time steps of one day. Seed bank processes, in contrast, use annual time steps. The climate module generates deterministically the daily temperature and stochastically the daily rainfall amount. The soil module simulates in each cell for five soil layers the infiltration, vertical movement, drainage, and evaporation of water. Excess water runs off the cell. The seed bank module tracks the density of seeds, their moisture and temperature-dependent germination, seed mortality, and density-dependent granivory. The plant growth module simulates the increase of individual biomass based on available moisture, competition for water, and temperature. Biomass is allocated to vegetative and reproductive tissue. The seeds produced by the plant are dispersed according to a negative exponential distribution. Details of the modules are described in [25]. The model has been validated with data from four field sites in Israel (Sede Boqer, 90 mm mean annual precipitation [MAP], Lahav, 300 mm, Matta, 537 mm, 'En Ya'qov, 780 mm [18]).

I used the stochastic time series generator ReGen [26] to vary the mean daily rain intensity on rainy days (MDI, rain volume/day) from –20 to +20% in 10% steps. For comparison, current regional climate change models project a change ranging from –3 to + 29% of the current

intensity in the Middle East [2]. Further, I varied MAP from –20 to +20% in 10% steps in a factorial way with MDI to provide a comparison for the magnitude of the effect of changing daily rainfall intensity. The simulations were performed for 5 sites on an aridity gradient: 100 (arid), 300 (semi-arid), 450 (dry Mediterranean), 600 (typical Mediterranean), and 800 mm MAP (mesic Mediterranean) to examine how the effect of daily rainfall intensity changes with climatic region.

I conducted the simulations for 30 years with five replications for each combination of change of intensity and annual precipitation for each point on the aridity gradient. To exclude inter-annual autocorrelation I reset the seed bank density each year to the same value (arid: 2000, semi-arid: 16'000, dry Med.: 17'000, typical Med.: 18'000, mesic Med.: 20'000 seeds/m^2 corresponding to typical values observed in the field). Runon (but not runoff) between cells in the model was excluded so that the direct effect of rainfall could be examined.

I report results for three variables: longest wet period (*LWD*, maximum number of consecutive days where soil water potential >–1.5 MPa [nominal permanent wilting point]), establishment (the ratio of seedlings to the number of seeds), and density of mature individuals. I examined the means of each variable for each 30-year series with analyses of covariance (ANCOVA). The full-factorial ANCOVA, using change of mean daily rain intensity and change of MAP as covariates and site as a nominal factor, had 605 degrees of freedom for the error term. Post-hoc comparisons of slopes and means were done using 95% confidence intervals. In addition, I calculated the change of each variable per 10% change of MDI and per 10% change of MAP.

RESULTS

The longest wet period (*LWP*) varied significantly among sites, with MAP, MDI, all two-way interactions except MDI × MAP, and the three-way interaction between sites, MAP, and MDI (all $P < 0.0001$, Fig. 2a, b).

LWP (averaged across rain treatments) differed most strongly among sites ($F = 17802$) and increased along the humidity gradient (Fig. 2b). Within sites, *LWP* (averaged across all other factors) increased linearly with MAP ($F = 3886$) and with MDI ($F = 245$). The rates of increase differed among sites. The increase with MAP was steepest at the dry Mediterranean site and became flatter towards the arid and mesic ends of the climate gradient ($F = 35$, Fig. 2b). The increase with MDI was largest around 200 mm MAP and became smaller towards the ends of the climatic gradient ($F = 29$). Although the interaction between MAP and MDI was not significant across all sites, this interaction varied significantly among sites ($F = 5.9$), because the rate of increase of *LWP* with MDI rose with MAP at the arid site but sank with MAP at all other sites (Fig. 2b). At the moistest site, *LWP* did not change significantly with MDI. The relative increase of *LWP* with change of MAP and change of MDI was strongest at the arid site and decreased to the mesic Mediterranean site.

Establishment fractions varied significantly among sites, with MDI, with MAP, with the interaction of sites with MDI, with the interaction of sites and MAP, and with the three-way-interaction of all factors (all $P < 0.0001$, Fig. 2c, d). Establishment (averaged across MDI and MAP levels) varied around 18% depending on site ($F = 330$, Fig. 2c). Averaged across sites,

establishment increased with MAP ($F = 292$). An interaction of MAP with site ($F = 410$), however, arose because establishment decreased with increasing MAP at the Mediterranean sites (Fig. 2d). Increasing MDI at constant nominal MAP generally decreased establishment ($F = 6.8$), but this effect differed among sites ($F = 49$). At the arid site, a higher MDI increased establishment, whereas MDI generally caused establishment to decrease at the other sites (Fig. 2d). Since the density of seeds increased along the humidity gradient, the declining establishment suggests that density-dependent germination became more important as water supply increased. The three-way interaction ($F = 3.5$) indicated a maximum effect of MDI on establishment around 100 mm MAP and a minimum of MDI around 350 mm MAP.

The effects of rain manipulations on density of mature plants were similar to that on *LWP*. Density varied significantly with site, MDI, and MAP and their interactions (all $P < 0.0001$, Fig. 2e, f). The greatest absolute differences among levels were among sites ($F = 13381$). Density (averaged across sites and MDI) increased with MAP ($F = 936$, Fig. 2e). This slope of increase (averaged across daily patterns) differed among sites ($F = 275$). It was maximal at the semi-arid site (Fig. 2f). Further, density (averaged across sites) increased with increasing MDI ($F = 45$), but the rate was generally smaller than that caused by a similar change in MAP. The rate of increase with MDI (averaged across levels of MAP) varied among sites ($F = 20$). The greatest average slope occurred in the semi-arid site (Fig. 2f). The confidence interval of the average slope at the typical Mediterranean site included zero. The effects of MDI and MAP on density interacted ($F = 16$). Inspection of means indicated that the effect of MDI was the stronger the more MAP was reduced. This interaction further varied among sites ($F = 8$). At the arid site, the effect of increasing MDI was positive and increased with MAP (Fig. 2f). At the three intermediate sites the effect of MDI decreased with increasing MAP so that it became insignificant. At the mesic Mediterranean site, the effect of increasing MDI was negative, but the size of this effect also decreased with MAP. Generally, the effect of MDI was smaller than that of MAP at each site. In summary, increasing mean daily rain intensity and, more strongly, mean annual precipitation both increased density, but their relative effects generally decreased from the semi-arid to the mesic Mediterranean site.
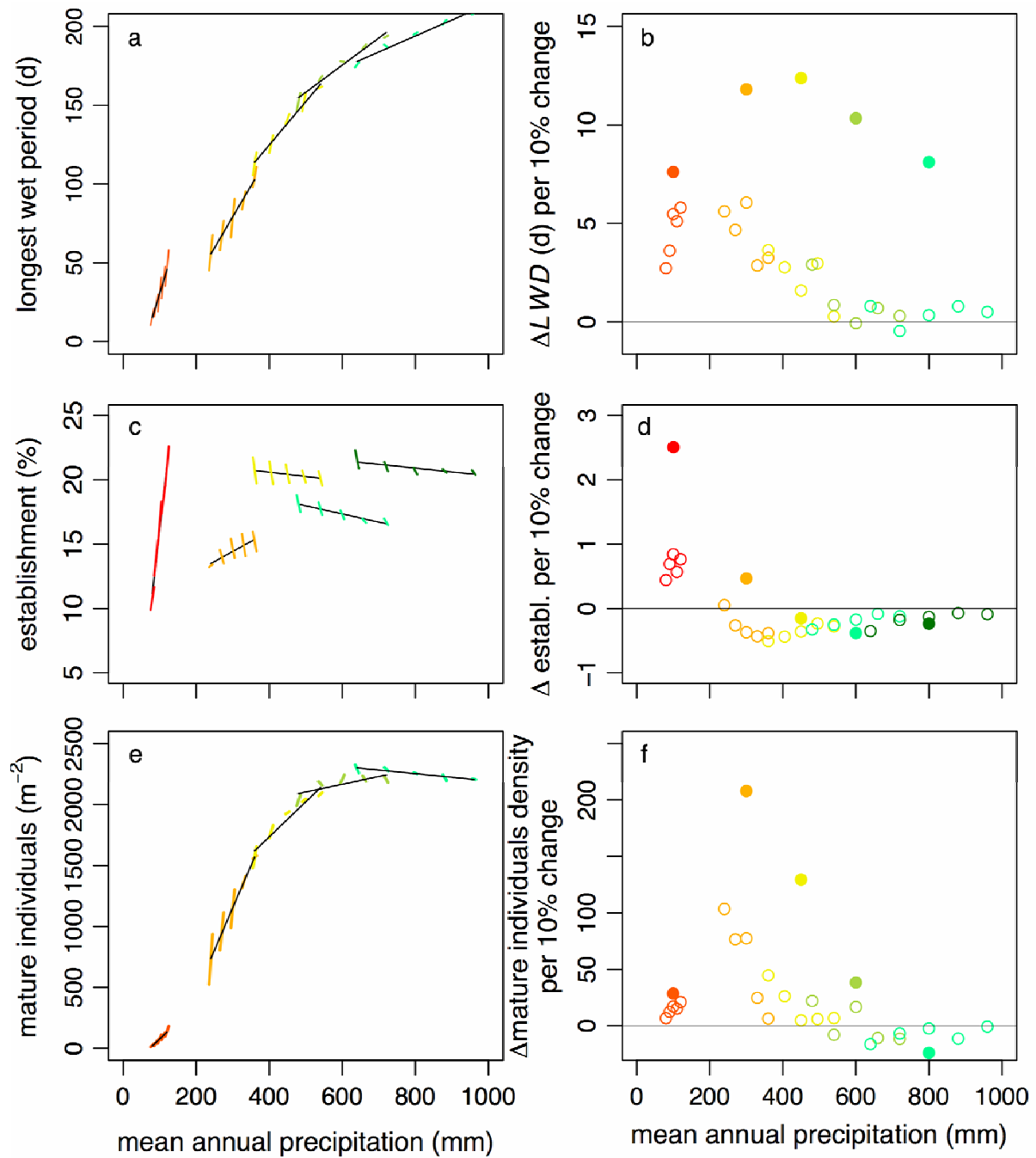
Figure 2. Change of (a) longest wet period (*LWP*, maximum number of consecutive days with soil water potential > -1.5 MPa), (c) establishment fraction, and (e) density of mature individuals with mean annual precipitation (MAP, thin, black lines) and with daily mean rain (MDI, thick, grey lines, 20% change of MDI scaled to 10 mm MAP). The slope of the thin lines corresponds to the effect of absolute change of MAP. b), d), f) Slopes of panels in the left column expressed per 10% change of MAP (filled circles) or 10% change of MDI (outline circles). This corresponds to the effect of the relative change of MDI and MAP.

DISCUSSION

Global climate change models predict a change in the daily rain pattern characterized by a shift to more high-volume rain events [22]. I simulated this shift by increasing the seasonal variation of mean daily rain volume (MDI) matched by a decrease in the seasonal variation of likelihood of rainy days so that the mean annual volume remained unchanged.

Changing annual rain volume and daily rain pattern clearly affected the average longest wet period (*LWP*, number of consecutive days where moisture in at least one soil layer >-1.5 MPa) (Fig. 2a, b). A change of mean annual precipitation (MAP) had a stronger effect than a change of MDI and keeping MAP constant. As expected, average *LWP* increased among sites along the humidity gradient. The slope of increase of *LWP* with *relative* change of MAP was greatest at the dry Mediterranean site (Fig. 2b). Thus, this region is the most sensitive with regard to water availability. Based on the *absolute* change of MAP, however, the slope of increase of *LWP* became flatter with the humidity of the climate (Fig. 2a). This pattern is due to the roughly reciprocal relationship between soil water potential and soil water content. At the arid site, soil moisture is on average low and almost each additional rainfall raises the soil water potential considerably and prolongs the wet period. With increasing climatic humidity, the soil is moister on average. The moister the soil, the more water is needed to raise the water potential by the same magnitude. In addition, the soil becomes saturated and additional water drains to lower soil layers or runs off at the surface. Changing MDI produced a complex response of *LWP*. In almost all instances, a greater amplitude of MDI, *i.e.*, more days with rainstorms, extended the wet period because a rainstorm fills up the soil immediately and to a greater depth than light rains. This is confirmed by measurements at the field sites. Water stored at greater depths evaporates more slowly than it does near the surface because soil dries out from the surface downwards and soil permeability decreases as the soil dries out [30]. Thus, both the responses of *LWP* to a change in MDI and to a change in MAP are strongly tied to the non-linear relation between soil water potential and soil water content.

The average percentage of established seeds was 18% across sites (Fig. 2c, d). The increase of establishment with MAP within sites was positive at the arid and semi-arid sites but negative at the three Mediterranean sites (Fig. 2d). This is the outcome of combining the concept of hydrothermal time for germination [26] with density-dependent germination fractions [16] in the model. Evidently, additional rain enhanced the number of days when conditions for germination were met and increased establishment at the two arid sites. In contrast, more frequent rainfalls at the Mediterranean sites did not greatly improve the conditions for germination. On the other hand, more rain raised the potential germination fraction, intensifying the competition among germinating seeds. As a consequence establishment along the Mediterranean part of the humidity gradient decreased. Independent of changes to MAP, increasing MDI increased seedling density till about 200 mm MAP and decreased establishment beyond that point on the humidity gradient. This indicates that under arid conditions establishment is improved by heavy rainfalls that penetrate the soil more deeply and provide the opportunity to grow deep roots. Under moister conditions, this effect becomes less important so that germination and establishment are enhanced by more regular rainfalls. Without density regulation, heavy rainfalls would cause mass germination and strong competition among adult plants. Therefore, density-dependent germination is an evolutionary stable strategy [40]. Evidence for density-dependence in natural communities is accumulating

[3,8,16,20,33,40]. In summary, seedling establishment is determined mostly by seed availability, number of rainstorms under arid conditions, and regularity of rain under more mesic conditions.

Generally, the effect of rain manipulations on the density of mature individuals followed a similar pattern as that on *LWP* (Fig. 2e, f). Thus, density increased in a sigmoid way with mean annual precipitation along the gradient (Fig. 2e), was more strongly affected by a change in MAP than by a change in MDI (Fig. 2f), and increasing either MAP or MDI had positive effects on density, except in the mesic Mediterranean region. The tight correlation between density and *LWP* indicates the strong control that water as a limiting resource exerts on plant growth. In the arid and semi-arid regions, individuals grew sparsely so that competition was weak. With increasing MAP the importance of rainstorms and *LWP* for growth decreased, while that of competition among the more densely growing individuals increased. This resulted in a negative effect of increasing MAP on density. At the dry and typical Mediterranean sites establishment fractions had decreased with MAP due to seedling competition. This was compensated later by higher mortality of established plants at lower MAP and thus *LWD*, resulting in an increase of density of mature individuals with MAP. At the mesic Mediterranean site, the small increase of *LWP* was less effective so that the density of mature individuals still decreased with increasing MAP. Similarly, the decrease of establishment with increasing MDI was not changed by the increase of *LWP* at the mesic Mediterranean site during growth so that the density of mature individuals also decreased with MDI. The decrease of density, however, was compensated by higher production per individual so that peak community shoot mass increased with MAP at this site as it did at the other sites [24]. To summarize, the sigmoid increase of plant density with mean annual precipitation MAP resulted from non-linear relations between soil water volume and soil water potential, a larger effect of rainstorms on establishment in arid than in mesic regions, and increasing importance of competition for water. The increase of density with daily mean rain MDI was the net effect of a positive effect on establishment at arid sites, a negative effect on germination at Mediterranean sites, and a positive effect on the longest wet period *LWP* resulting in more intense competition but also higher production with increasing MAP.

Experiments that manipulate rainfall frequency in natural vegetation [12] or use wild species are rare [27,34,38,43]. More effort has been invested in studies of irrigation frequency of crops [5]. Most of these studies agree that established plants perform better when the same amount of water is distributed in more frequent, smaller volumes than in fewer, larger volumes, especially when roots are close to the surface [5]. Exceptions [21,27,31,43] suggest that positive effects are observed predominantly in intact natural vegetation, whereas negative effects are found when root space is limited as in pot experiments or roots are concentrated near the soil surface as in crop species. This conclusion is corroborated by irrigation experiments [10] and the model's sensitivity analysis [24] that showed that soil depth is the fourth most important factor across all sites controlling the longest wet period *LWP*. Seeds and seedlings in my simulation were in a similar situation as plants in pot experiments. They had access only to water in the surface and A1 layer. Consequently, I found a negative effect of rainstorm frequency on seedling density (Fig. 2d) but positive effects on the density of mature individuals in all regions but the mesic Mediterranean (Fig. 2f).

My study showed that effects of precipitation pattern in more arid climates are primarily related to the time soil moisture is available to plants. The length of the moist period depends not only on soil characteristics that vary with soil texture, but also on the "context" of rain events [36], *i.e.*, on the soil moisture before rains and on the clustering of events. Therefore, my results support Reynolds et al. [36] that in terms of the pulse-reserve hypothesis [35] "pulse" must refer directly to the form of the resource as it is available to the plant and not to the resource as it is supplied. Thus, pulse here must refer to the available soil moisture and not to the rain event.

Using the simulation results one can estimate the effect of precipitation changes projected by global circulation models. The RegCM3 model generally predicts a 10 to 20% increase of MDI, but the change of MAP varies between –20 and +10% in simulated regions [2,14,15]. Although the community response to an increase of MDI has an opposite trend to the response to a decrease in MAP (Fig. 2), the latter is much stronger. Consequently, the net effect is negative. At sites with soils that might cause a negative response of community mass to the increase of MDI the effect of decreasing MAP would be amplified. In contrast, where the decrease in MAP is small and the increase in MDI is strong, the net effect might be even positive. Projected changes of mean temperatures, CO_2 concentrations or nitrogen deposition from the atmosphere may interact with effects of precipitation changes. A multi-factorial experiment in an annual grassland, however, showed that interactions among these factors become rare and nitrogen deposition produced the strongest effect [7]. Nonetheless, in the long-term, aboveground production of herbaceous arid communities is most strongly correlated with annual precipitation [28], which is also shown by the tight correlation of community biomass with annual precipitation along my gradient [24].

 Among the communities along the humidity gradient from arid to mesic Mediterranean, those in the semi-arid region are the most sensitive to changes in annual precipitation as shown by my simulations (Fig. 2) and field data [18]. Despite its low mass, annual vegetation is important in drylands. Annual plants represent the bulk food for livestock, reduce soil erosion, and increase rain infiltration. The attractiveness of their species diversity is an economical factor in the tourism industry [13,41]. Therefore, this "marginal" vegetation must be included in regional assessments of global change to provide a full picture of the effects on regional ecosystems and socio-economy[29].

In conclusion, my simulations demonstrate that changes to daily rain patterns have strong effects on annual plant communities in arid regions through the amount of water stored in the soil. These effects were smaller but of the same order of magnitude as changes to mean annual precipitation. Therefore, these effects should be included in assessments of global climate change.

REFERENCES

1. Alpert P, Ben-Gai T, Baharad A, *et al.* (2002) The paradoxical increase of Mediterranean extreme daily rainfall in spite of decrease in total values. Geophysical Research Letters 29: 31.1-31.4.
2. Alpert P, Krichak SO, Dayan M, *et al.* (2005) Regional climate modeling over the E. Mediterranean. Scientific Assembly of the International Association of Meterology and Atmospheric Science. Beijing, China.
3. Bergelson J, Perry R (1989) Interspecific competition between seeds: relative planting date and density affect seedling emergence. Ecology 70: 1639-1644.
4. Burke I, Lauenroth WK, Parton WJ (1997) Regional and temporal variation in net primary productivity and nitrogen mineralization in grasslands. Ecology 78: 1330-1340.
5. Clothier BE, Green SR (1994) Rootzone processes and the efficient use of irrigation water. Agricultural Water Management 25: 1-12.
6. DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: a review. Vegetatio 84: 9-29.
7. Dukes JS, Chiariello NR, Cleland EE, *et al.* (2005) Responses of grassland production to single and multiple global environmental changes. PLoS Biology 3: e319.
8. Dyer AR, Fenech A, Rice KJ (2000) Accelerated seedling emergence in inter-specific competitive neighborhoods. Ecology Letters 3: 523-529.
9. Easterling DR, Meehl GA, Parmesan C, *et al.* (2000) Climate extremes:observations, modelling, and impacts. Science 289: 2068-2074.
10. English NB, Weltzin JF, Fravolini A, *et al.* (2005) The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. Journal of Arid Environments 63: 324-343.
11. Facelli JM, Chesson P, Barnes N (2005) Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology 86: 2998-3006.
12. Fay PA, Carlisle JD, Knapp AK, *et al.* (2003) Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia 137: 245-251.
13. Fleischer A, Sternberg M (in press) The economic impact of global climate change on Mediterranean rangeland ecosystems: a space-for-time approach. Ecological Economics.
14. Giorgi F, Bi X, Pal J (2004) Mean, interannual variability and trends in a regional climate change experiment over Europe. II: climate change scenarios (2071-2100). Climate Dynamics 23: 839-858.
15. Giorgi F, Bi X, Pal JS (2004) Mean, interannual variability and trends in a regional climate change experiment over Europe. I. Present-day climate (1961-1990). Climate Dynamics 22: 733-756.
16. Goldberg DE, Turkington R, Olsvig-Whittaker L, *et al.* (2001) Density dependence in an annual plant community: variation among live history stages. Ecological Monographs 71: 423-446.
17. Hansson L (2003) Why ecology fails at application: should we consider variability more than regularity? Oikos 100: 624-627.
18. Holzapfel C, Tielbörger K, Parag HA, *et al.* (2006) Annual plant-shrub interactions along an aridity gradient. Basic and Applied Ecology 7: 268-279.
19. Huxman TE, Smith MD, Fay PA, *et al.* (2004) Convergence across biomes to a common rain-use efficiency. Nature 429: 651.

20. Inouye RS (1980) Density-dependent germination response by seeds of desert annuals. Oecologia 46: 235-238.
21. Jankju-Borzelabad M (2005) Responses of arid land plants to simulated changes in rain frequency and intensity. Presentation at the 90th Annual Meeting of the Ecological Society of America held jointly with the IX International Congress of Ecology. Montréal, Canada.
22. Karl TR, Trenberth KE (2003) Modern global climate change. Science 302: 1719-1723.
23. Kigel J (1995) Seed germination in arid and semiarid regions. In: Kigel J, Galili G, eds. New York, New York, U.S.A.: Marcel Dekker. pp. 645-699.
24. Köchy M (manuscript) Change of productivity of annuals with daily rain distribution switches trend along a gradient of aridity.
25. Köchy M (manuscript) Stochastic time series of daily precipitation for interior Israel.
26. Köchy M, Tielbörger K (in press) Hydrothermal time model of germination: parameters for 36 Mediterranean annual species based on a simplified approach. Basic and Applied Ecology. (doi: 10.1016/j.baae.2006.04.002)
27. Laporte MF, Duchesne LC, Wetzel W (2002) Effect of rainfall patterns on soil surface CO_2 efflux, soil moisture, soil temperature and plant growth in a grassland ecosystem of northern Ontario, Canada: implications for climate change. BMC Ecology 2: 10.
28. Lauenroth WK, Sala OE (1992) Long-term forage production of North American shortgras steppe. Ecological Applications 2: 397-403.
29. Le Houérou HN (1982) The impact of climate on pastoralism. In: Kates RW, Ausubel RN, Berberian M, eds. 27. New York, New York, U.S.A.: J. Wiley. pp. 155-185.
30. Maidment DR, ed. (1993) Handbook of Hydrology. New York, U.S.A.: MacGraw Hill.
31. Mermoud A, Tamini TD, Yacouba H (2005) Impacts of different irrigation schedules on the water balance components of an onion crop in a semi-arid zone. Agricultural Water Management 77: 282-295.
32. Middleton N, Thomas D, eds. (1997) World Atlas of Desertification. London, U.K.: United Nations Environment Program (UNEP).
33. Murray BR (1998) Density dependent germination and the role of seed leachate. Australian Journal of Ecology 23: 411-418.
34. Novoplansky A, Goldberg DE (2001) Effects of water pulsing on individual performance and competitive hierarchies in plants. Journal of Vegetation Science 12: 199-208.
35. Noy-Meir I (1973) Desert Ecosystems: environment and producers. Annual Review of Ecology and Systematics 4: 25-51.
36. Reynolds JF, Kemp PR, Ogle K, *et al.* (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141: 194-210.
37. Salamanca EF, Kaneko N, Katagiri S (2003) Rainfall manipulation effects on litter decomposition and the microbial biomass of the forest floor. Applied Soil Ecology 22: 271-281.
38. Sher AA, Goldberg DE, Novoplansky A (2004) The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. Oecologia 141: 353-362.
39. Taylor AR, Schroter D, Pflug A, *et al.* (2004) Response of different decomposer communities to the manipulation of moisture availability: potential effects of changing precipitation patterns. Global Change Biology 10: 1313-1324.

40. Tielbörger K, Valleriani A (2005) Can seeds predict their future? Germination strategies of density-regulated desert annuals. Oikos 111: 235-244.
41. Vaughan D (2000) Tourism and biodiversity: a convergence of interests? International Affairs 76: 283-297.
42. Weltzin JF, Loik ME, Schwinning S, *et al.* (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53: 941-952.
43. Williams KJ, Wilsey BJ, McNaughton SJ, *et al.* (1998) Temporally variable rainfall does not limit yields of Serengeti grasses. Oikos 81: 463-470.
44. Wilson SD (2000) Heterogeneity, diversity and scale in plant communities. In: Hutchings M, John EA, Stewart AJ, eds. Oxford, U.K.: Blackwell Science. pp. 53-69.