

Impact of rainfall manipulations and biotic controls on soil respiration in Mediterranean and desert ecosystems along an aridity gradient

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Abstract

Spatially heterogeneous ecosystems form a majority of land types in the vast drylands of the globe. To evaluate climate-change effects on CO₂ fluxes in such ecosystems, it is critical to understand the relative responses of each ecosystem component (microsite). We investigated soil respiration (R_s) at four sites along an aridity gradient (90–780 mm mean annual precipitation, MAP) during almost 2 years. In addition, R_s was measured in rainfall manipulations plots at the two central sites where ~30% droughting and ~30% water supplementation treatments were used over 5 years. Annual R_s was higher by 23% under shrub canopies compared with herbaceous gaps between shrubs, but R_s at both microsites responded similarly to rainfall reduction. Decreasing precipitation and soil water content along the aridity gradient and across rainfall manipulations resulted in a progressive decline in R_s at both microsites, i.e. the drier the conditions, the larger was the effect of reduction in water availability on R_s . Annual R_s on the ecosystem scale decreased at a slope of 256/MAP g C m⁻² yr⁻¹ mm⁻¹ ($r^2 = 0.97$). The reduction in R_s amounted to 77% along the aridity gradient and to 16% across rainfall manipulations. Soil organic carbon (SOC) decreased with declining precipitation, and variation in SOC stocks explained 77% of the variation in annual R_s across sites, rainfall manipulations and microsites. This study shows that rainfall manipulations over several years are a useful tool for experimentally predicting climate-change effects on CO₂ fluxes for time scales (such as approximated by aridity gradients) that are beyond common research periods. Rainfall reduction decreases rates of R_s not only by lowering biological activity, but also by drastically reducing shrub cover. We postulate that future climate change in heterogeneous ecosystems, such as Mediterranean and deserts shrublands will have a major impact on R_s by feedbacks through changes in vegetation structure.

Keywords: climate change, CO₂ fluxes, CO₂ pulses, droughting, Mediterranean shrubland, shrub microsite, soil CO₂ efflux, soil organic carbon stock, supplemented rainfall

Received 10 February 2010; revised version received 17 May 2010 and accepted 13 June 2010

Introduction

Drylands cover 41–47% of the terrestrial surface (Le Houérou, 1996; Millennium Ecosystem Assessment, 2005) and contain 15.5% of the global soil organic carbon (SOC) stock (Lal, 2004). Climate-change scenarios predict changes (increase or decrease) in precipitation and increase in temperature in many dry regions of the globe (Christensen *et al.*, 2007). Changes in precipitation alter dynamics of soil water content, with significant consequences for ecosystem processes. In addition, higher temperatures increase the evaporative demand and subsequently decrease water availability, which can have extended effects on CO₂ and water fluxes (Arnone *et al.*, 2008).

Carbon sequestration and storage in terrestrial ecosystems are determined to a great extent by ecosystem respiration (Valentini *et al.*, 2000). Soil respiration (total soil surface CO₂ efflux, R_s) is the main component of ecosystem respiration in most ecosystems, and thus changes in R_s ultimately affect C storage. This is of interest for drought-affected regions, as drylands have a large potential for C sequestration (Grünzweig *et al.*, 2003, 2007). Soil respiration is driven in part by climatic factors, mainly temperature and soil moisture (Rustad *et al.*, 2000). Notably, in a recent global analysis across forests from various biomes, mean annual precipitation (MAP) explained over 50% of variation in R_s , while R_s did not significantly correlate with temperature (Grünzweig *et al.*, 2009). Therefore, potential climate-change induced alterations in rainfall are expected to have a major impact on R_s , particularly in dry regions.

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Rainfall-manipulation experiments in different biomes showed increased R_s following experimental water additions and decreased R_s following rain exclusion (Emmett *et al.*, 2004; Harper *et al.*, 2005; Borken *et al.*, 2006; Zhou *et al.*, 2006; McCulley *et al.*, 2007; Wan *et al.*, 2007; Fay *et al.*, 2008; Liu *et al.*, 2009). However, the R_s response to precipitation change differed according to moisture conditions. In temperate grasslands, R_s responded to water addition at drier sites only (Risch & Frank, 2007). In Mediterranean-type ecosystems, responses of R_s to rainfall manipulations varied with seasons and years, depending on respective rainfall amounts (Asencio *et al.*, 2007; Chou *et al.*, 2008).

Besides being controlled by climatic variables, R_s is regulated by biotic factors, such as vegetation (Ryan & Law, 2005; Wan *et al.*, 2007). Heterogeneous ecosystems, e.g. Mediterranean and desert shrublands, are comprised of relatively distinct microsites or patches, such as locations dominated by shrubs and open intershrub gaps dominated by herbaceous vegetation. Shrub microsites are often enriched in resources, such as water and nutrients, and are, thus, called 'islands of fertility' (Schlesinger *et al.*, 1996; Schade & Hobbie, 2005). Differences among microsites affect root and microbial activities, the main sources of respiratory CO_2 in the soil. Shrublands offer the opportunity to investigate vegetation effects on R_s by comparing microsite responses to changes in rainfall. Studies so far showed that rain pulses, such as monsoonal summer rainfall or one-time experimental water addition during summer increased R_s at shrub microsites to a larger extent than at open intershrub gaps (McCulley *et al.*, 2007; Sponseller, 2007; Potts *et al.*, 2008). To predict responses of the C cycle to climate change in dry, heterogeneous ecosystems, effects of rainfall changes on CO_2 fluxes need to be understood at the microsite level on an annual scale.

The objective of the current study was to quantify the impact of rainfall changes on R_s at the microsite and ecosystem level. Furthermore, responses of R_s to climatic and biotic drivers were assessed. Soil respiration was investigated over almost two full annual cycles at the end of 5 years of rainfall manipulations (around +30% and -30%) and along an aridity gradient (90–780 mm MAP). We hypothesized that rainfall reduction decreases R_s directly by reducing water availability and indirectly by diminishing shrub cover, with supplemented rainfall acting in the opposite way. We further assumed that R_s under shrub canopies is more strongly affected by changes in rainfall than R_s between shrubs. It is assumed that biological activity under shrubs is higher and proceeds over the whole year as opposed to lower activity under ephemeral vegetation which is limited to the wet season.

Methods

Study sites and experimental setup

This study was conducted at four sites along a north–south aridity gradient (245 km long) in Israel (Table 1; Fleischer & Sternberg, 2006) as part of the GLOWA Jordan River (JR) project (<http://www.glowa-jordan-river.de>). All sites shared a Mediterranean-type climate characterized by a short, cool, wet winter and a long, hot, dry summer, with a dry-out transition season between spring and summer. Mean annual precipitation ranged widely among sites from 90 to 780 mm, while mean annual temperature range was narrow (17.7–19.1 °C, Table 1). Vegetation was dominated by the semideciduous, dimorphic shrub *Sarcopoterium spinosum* at the three northern sites and by the semideciduous shrub *Zygophyllum dumosum* at the southernmost site, with interspersed ephemeral herbaceous patches at all sites (for details, see Holzapfel *et al.*, 2006; Petru *et al.*, 2006). All sites were located on a southern aspect at similar elevation, and were on hard limestone bedrock overlaid with calcareous soil. Calcium carbonate content in the top soil (0–10 cm) increased from 0.15% at the Mesic Mediterranean site to 58.4% at the arid site (Oren & Steinberger, 2008).

Two climate-change scenarios were tested using rainfall manipulations: drought and increased rainfall. These contrasting scenarios were originally based on spatially variable changes in observed rainfall patterns in the region (Ben-Gai *et al.*, 1994; Alpert *et al.*, 2002), and were confirmed by recent observations and climate-change models (Christensen *et al.*, 2007; Black, 2009; Kafle & Bruins, 2009). Starting in winter 2002–2003, rainfall manipulations were applied at the two central sites, the Mediterranean and the semiarid site. Rainfall treatments mimic the natural timing, frequency and intervals of precipitation events at the sites (Sternberg *et al.*, in press). Rainout shelters (Dry treatment) similar to the ones described by Yahdjian & Sala (2002) were constructed to reduce precipitation by ~30% at each rainfall event. The fixed shelters utilized V-shaped bands of transparent plastic that were supported by a frame of galvanized aluminum (mean height = 2.5 m) and covered an area of 10 × 25 m. Intercepted rain was collected by gutters and drained outside the study site. Sides of the shelters were open to allow for air movement and minimizing temperature and humidity differences between sheltered and unsheltered areas. No significant shading effects due to shelters were noted. Irrigation systems (Wet treatment) were established to increase long-term MAP by ~30%. Irrigation was applied at the end of each rainfall event higher than 5 mm by means of drizzle sprinklers using tap water. Each treatment was applied to five plots (10 × 25 m), while five additional plots were left untreated (Control treatment). At the mesic Mediterranean and arid sites, five Control plots were maintained and no rainfall manipulations were conducted.

Soil respiration and auxiliary measurements

Soil respiration was measured on permanent collars (PVC, 90 cm² area, 5 cm high, installed to a depth of 4 cm) with a

Table 1 Site characteristics

Ecosystem type (site)	Latitude (N)	Longitude (E)	Elevation (m asl)	MAP (mm)	MAT (°C)	Vegetation formation	Soil type	Soil texture	Shrub cover (%)	Rock cover (%)
Mesic Mediterranean	33°00'	35°14'	500	780	18.1	Woodland, shrubland	Terra rossa	Clay	75.1	13.6
Mediterranean	31°42'	35°03'	620	540	17.7	Shrubland	Terra rossa	Clay	55.0	11.7
Semiarid	31°23'	34°54'	590	300	18.4	Dwarf shrubland	Brown Rendzina	Loam	35.4	15.3
Arid	30°52'	34°46'	470	90	19.1	Desert shrubland	Desert lithosol	Sandy clay loam	12.7	15.0

MAP, long-term mean annual precipitation; MAT, long-term mean annual temperature.

non-steady-state flow-through chamber (LI-6400-09 soil chamber, volume 1000 cm³) connected to the portable LI-6400 (LI-COR, Lincoln, NE, USA). The LI-6400-09 uses a fan to circulate the air between the chamber and the infra-red gas analyzer, and uses a pressure equilibration tube to eliminate pressure differentials between the chamber and the environment. Chamber and ambient temperature were similar, measurement time was 2–3 min, and R_s was calculated for ambient CO₂ on a regression line of fluxes vs. CO₂ concentrations (Instruction Manual, 6400-09 Soil CO₂ Flux Chamber, LI-COR, 2003). This system showed a very good agreement between known and measured R_s across the entire range of fluxes observed in the field (see NSF-1a in Table 1 of Pumpanen *et al.*, 2004).

Two microsites were selected for measurements: (a) below shrub canopy (shrub microsite) and (b) open gaps between shrubs (intershrub microsite). Two collars were randomly selected for each microsite in each plot, i.e. 60 collars at each of the two central sites (10 collars per each of three treatments and two microsites) and 20 collars at each of the two extreme sites (10 collars per each of two microsites). The two collars within each of the five plots were combined to 10 true replications because statistical analyses did not show any significant plot effect (data not shown). Regular measurements [10:00–15:00 Israel Standard Time (GMT + 2 h)] were carried out at high frequency (25–26 field campaigns; every 2–3 weeks between October and April) at the Mediterranean and semiarid sites, and at low frequency (8–9 campaigns) at the mesic Mediterranean and arid sites between January 2006 and September 2007. Three diel cycles (7–9 measurement cycles during 24 h) were performed at both the Mediterranean and the semiarid site (one cycle per site and season).

At the end of the R_s measurement period in 2007, a soil sample of 10 cm depth and 5 cm diameter was collected from the center of each R_s collar. Air-dry samples were sieved with a 2 mm screen, oven-dried (105 °C) and analyzed for SOC concentration by the Walkley–Black method (Nelson & Sommers, 1996). SOC stock was calculated for the top 10 cm of the soil profile as the product of SOC concentration and bulk density (determined as mass of sieved soil per total soil volume). Total soil depth was determined by hammering a 1 cm diameter iron rod into the ground at four points around each R_s collar.

Climatic variables

At each study site, data were continuously collected at an interval of 1 h for precipitation (automatic rain gauge; Campbell Scientific, Logan, UT, USA), solar radiation (LI200X Pyranometer, LI-COR), volumetric soil water content (θ) at 5 cm depth (time domain reflectometry, TDR, calibrated following differences in soil water capacity at each study site; Theta-Probe, Delta-T, Burwell, Cambridge, UK) and soil temperature (T_s) at 5 cm depth (thermocouples; Meteo-Tech, Bnei Brak, Israel). Rainfall was also measured in rainfall-manipulation plots using wedge rain gauges. Soil moisture and T_s were measured at three locations per site and microsite for the Control and at two locations per site and microsite for Wet and Dry treatments. To determine potential contribution to R_s by moisture in deeper soil layers, soil water content was also determined gravimetrically from 5 cm diameter cores drilled to depths of 0–10 and 10–20 cm in areas adjacent to the study plots (thus representing only the Control treatment). Long-term rainfall data (55–58 years) was obtained from the Israel Meteorological Service for stations in the vicinity of the study sites. Precipitation over all treatment years (2002–2007) were used when plotting dependent variables against precipitation because of the legacy of rainfall treatments for biological activity.

Relative extractable water (REW) was calculated from the θ dataset for each of the four study sites, as follows: $REW = (\theta - \theta_{\min}) / (\theta_{fc} - \theta_{\min})$, where θ_{\min} was minimum θ and θ_{fc} was θ at field capacity (determined as θ in the field 1 day after maximum θ to allow for drainage of potentially excessive water) (Granier, 1987). Daily REW values (ranging 0–1) were used to define wet and dry seasons for the hydrological year between October 2006 and September 2007, as follows: At each site, the wet season was defined as a period starting with at least 1 week of $REW > 0.15$, the dry season as a period starting with at least 1 week of $REW < 0.15$.

Soil-respiration algorithms

Annual R_s for the hydrological year 2006–2007 was calculated by a combination of a parabolic equation for θ and a second-order exponential equation for T_s . Because of severe moisture limitation to R_s at high T_s we used a temperature algorithm

that enabled R_s to decrease with increasing T_s after reaching a maximum (Tuomi *et al.*, 2007). Moreover, θ and T_s have an integrated effect on R_s rather than an additive one (Rustad *et al.*, 2000; Ryan & Law, 2005). Therefore, a multiplication of the parabolic equation and the second-order exponential equation was used, as follows:

$$R_s = e^{aT_s + bT_s^2}(c\theta + d\theta^2), \quad (1)$$

where a , b , c and d were fitted parameters. For each combination of site, treatment and microsite along the gradient (total of 16 combinations, means across 10 replications), a different set of parameters (a – d) was fitted. All measured data were used for equation fitting, except of measurements taken during R_s pulses. Disproportionally high pulses of R_s are induced by the first small rain events following the extended dry season.

Annual R_s was calculated by summing up hourly R_s fluxes obtained by applying Eqn (1) to the continuous θ and T_s data. Pulses were added to model results by interpolating between field data. For calculation of annual R_s at the ecosystem level, R_s of each of the two microsites was weighted by its spatial cover (CO₂ emission from large rocks was assumed to be zero; Table 1).

Hysteresis of the R_s response to diel changes in T_s can cause an overestimation of almost 20% in seasonal R_s calculated from T_s (Riveros-Iregui *et al.*, 2007). In order to test the reliability of the model results for annual R_s , we calculated an additional estimate of R_s by bypassing the hysteresis of diel cycles, as follows: Regular field measurements (close to the diel peak of R_s) were corrected to mean diel R_s by a factor obtained from the 24 h R_s cycles (data not shown). The resultant diel fluxes throughout the years 2006–2007 were linearly interpolated and summed up to an annual R_s estimate that was compared with the model results. This estimate was reasonably close to R_s fluxes calculated by Eqn (1) and corrected for pulses (Table 2), namely 4% and 12% lower on average across treatments and microsites for the Mediterranean and the semiarid sites, respectively.

Statistical analyses

Soil moisture at 5 cm depth, REW and T_s were analyzed along the gradient by two-way ANOVA (site, microsite), and across treatments by three-way ANOVA (site, treatment, microsite). Instantaneous R_s and θ from soil cores were tested by repeated-measures analysis using multivariate ANOVA (MANOVA). Multiple comparisons of means were performed with the Tukey–Kramer HSD test. The shrub–intershrub ratio for R_s ($R_{s\text{-shrub}}/R_{s\text{-intershrub}}$) was log-transformed for linear averaging and analysis by the nonparametric Wilcoxon's/Kruskal–Wallis test, and was subsequently back-transformed to present values as regular ratios. Slopes of linear regression lines were compared by analysis of covariance (ANCOVA).

Results

Climatic variables

Mean annual precipitation over the years 2002–2007 was representative of long-term MAP at all sites (maximum variation of 12%; Tables 1 and 2). In accordance

with the steep aridity gradient, θ decreased on average by 66% (Fig. 1) and REW by 32% ($P < 0.001$; data not shown) from the mesic Mediterranean to the arid site in the wet season. In the dry season, θ was significantly higher only at the mesic Mediterranean site, while REW did not differ across sites ($P = 0.420$). Regarding rainfall treatments, θ across the two central sites decreased from the Wet to the Control and Dry treatments, both during the wet season (–26%) and the dry season (–33%). Because of large variability among samples differences were statistically significant only for the dry season (Fig. 1).

Soil moisture at 5 cm depth measured by TDR did not differ between shrub and intershrub microsites along the gradient (Fig. 1). However, θ as determined by coring was higher under shrub canopies than in intershrub patches by 23% at 0–10 cm and by 9% at 10–20 cm depth during the dry season ($P = 0.010$ – 0.001 at the three northern sites). At the arid site, θ was higher under shrubs during the wet season by 22% at 0–10 cm and by 16% at 10–20 cm depth ($P = 0.014$).

Changes in T_s along the aridity gradient were small, with mean annual T_s differing by a maximum of 3 °C for shrub and 2 °C for intershrub microsites (Table 2). Mean T_s during the dry season was lower by 2.3 °C under shrub canopies than in open intershrub patches ($P = 0.007$), which mainly resulted from up to 20 °C lower maximum daily T_s under shrubs (data not shown). Rainfall manipulation treatments did not show any effect on T_s ($P = 0.181$).

Seasonal fluxes of soil respiration

The seasonal cycle of R_s was characterized by low R_s during the dry season when plant activity and θ were minimal and T_s was high, and by high R_s fluxes through the wet season which is the main growing season in these shrublands (Fig. 2). Rates of R_s were highest in spring when T_s increased after winter, soils were not yet desiccated and biological activity (substrate supply) was at its maximum. In addition, a notable pulse of R_s immediately following the first rain events (October 2006) was a major characteristic of the R_s annual cycle. At the Mediterranean site, the maximum R_s flux during this pulse was more than twice the R_s fluxes at any other time throughout the research period (Fig. 2), but those high fluxes did not differ significantly among microsites ($P = 0.169$) and rainfall treatments ($P = 0.171$). At the semiarid site, pulses of R_s were similar to maximal fluxes measured at other periods throughout the study. Low measuring frequency did not allow for observation of significant pulses at the mesic Mediterranean and arid sites. Analyses of observed R_s across all measuring dates showed statistically significant interactions

Table 2 Annual rate of soil respiration (R_s) on the microsite and ecosystem scale, and microclimatic and soil variables along aridity gradient (ecosystem types) and rainfall manipulations (treatments)

Ecosystem type (site)	Treatment	Annual R_s ($g C m^{-2} yr^{-1}$)*			Precipitation		Mean annual T_s ($^{\circ}C$)		SOC stock ($kg m^{-2}$)†		Soil depth (cm)‡		
		Shrub	Intershrub	Eco-system	$R_{s-shrub} / R_{s-ecos}$		MAP (mm)	CV	Shrub	Intershrub	Shrub	Intershrub	
		906	689	758	0.90	0.65	820	0.18	19.2 (0.7)	21.4 (1.1)	2.72 (0.25)	2.49 (0.24)	36.5 (4.2)
Mesic Medit. Mediterranean	Control	754	660	634	0.65	602	0.21	19.1 (0.4)	21.2 (0.7)	1.94 (0.13)	1.19 (0.13)	18.8 (4.0)	17.3 (4.5)
	Wet	860	725	715	0.66	751	0.22	20.6 (0.3)	21.6 (0.0)	1.90 (0.22)	1.40 (0.11)	15.4 (1.8)	11.1 (1.2)
Semiarid	Dry	748	567	600	0.69	440	0.27	21.0 (0.3)	22.2 (0.1)	1.92 (0.15)	1.51 (0.24)	17.8 (2.9)	10.8 (1.0)
	Control	731	345	429	0.60	301	0.29	21.7	22.9	1.35 (0.16)	0.90 (0.10)	25.2 (4.2)	14.6 (2.2)
	Wet	585	724	564	0.37	386	0.25	21.0	21.9	1.12 (0.19)	1.20 (0.12)	20.0 (3.9)	39.0 (9.8)
Arid	Dry	507	594	472	0.38	233	0.38	21.7	23.7	1.33 (0.12)	0.99 (0.10)	13.0 (1.5)	22.9 (3.6)
	Control	295	193	177	0.21	94	0.43	22.2 (1.0)	23.4 (0.3)	0.67 (0.07)	0.34 (0.04)	28.2 (5.1)	25.7 (5.0)

Annual R_s [according to Eqn (1)] and soil temperature (T_s) were calculated for the year 2006–2007; mean annual precipitation (MAP) and coefficient of variation in precipitation (standard deviation divided by the mean, CV) were calculated over all rainfall manipulation years (2002–2007). For T_s ($n = 1-3$ sensors), soil organic carbon (SOC) stock and soil depth ($n = 10$ locations), values represent means (± 1 SE).

*Ecosystem-scale R_s was weighted by surface rock cover (Table 1); $R_{s-shrub} / R_{s-ecos}$ is shrub R_s times relative shrub cover divided by ecosystem R_s , i.e. the contribution of R_s under shrub canopies to ecosystem R_s .

†Soil organic carbon stock (0–10 cm) differed significantly among sites ($P < 0.001$; mesic Mediterranean > semiarid > arid, Tukey–Kramer HSD test) and microsites ($P < 0.001$; shrub > intershrub), but not among treatments ($P = 0.675$). Soil depth differed among sites ($P < 0.001$); treatment interacted with microsite at the semi-arid ($P = 0.014$), but not at the Mediterranean site ($P = 0.640$).

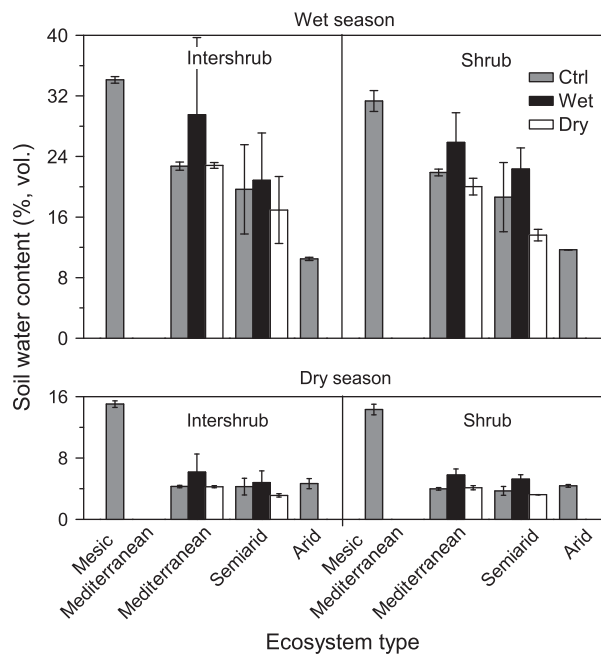


Fig. 1 Mean seasonal volumetric soil water content at 5 cm depth across ecosystem types, treatments and microsites during the hydrological year 2006–2007 (October 2006–September 2007). Mean \pm 1 SE, $n = 2$ –3. Two-way ANOVA across Control plots: sites, $P < 0.001$ for both seasons; microsites, $P = 0.596$ and 0.277 for wet and dry seasons. Three-way ANOVA across the two central sites: rainfall treatments, $P = 0.157$ and 0.043 for wet and dry seasons. Interactions were not statistically significant.

among date and treatment (central sites), date and microsite (all except of Mediterranean site), and treatment and microsite (semiarid site; data not shown).

Responses of instantaneous and annual soil respiration to climate change

Parabolic equations could explain the R_s – θ relationship for all site–treatment–microsite combinations ($r^2 = 0.74$ – 0.94). Soil respiration increased with θ in the dry and transition seasons up to a maximal value in spring, and decreased with θ beyond this value during wet and cool winter periods.

Fluxes of R_s predicted by the statistical model (Eqn (1)) correlated well with observed R_s along a nearly 1:1 relationship for all site–treatment–microsite combinations ($r^2 = 0.75$ – 0.92 , $P < 0.001$). Annual R_s calculated by the model for the year 2006–2007 on the ecosystem scale declined by 77% from the mesic Mediterranean to the arid site and by 16% from Wet to Dry treatments (Table 2). Early-season R_s pulses caused by the first rain events contributed 20% to the annual R_s flux at the Mediterranean site, but only 9% at the semiarid site.

Across all sites and treatments, R_s on the ecosystem scale decreased logarithmically with precipitation, with 97% of the variation in R_s being explained by MAP (Fig. 3a). The slope of this curve was $256/\text{MAP g C m}^{-2} \text{ yr}^{-1} \text{ mm}^{-1}$, indicating that annual R_s declined at a rate of only $0.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ with every mm at 900 mm rainfall, but at a rate of $2.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ with every mm at 100 mm rainfall. Notably, annual R_s decreased linearly with an increase in CV in precipitation along the gradient and across rainfall treatments (Fig. 3b). Annual R_s declined with decreasing mean annual θ and with increasing mean annual T_s (the latter over a narrow range of about 20–23 °C; Fig. 3c and d). In addition, annual R_s declined with wet-season θ ($r^2 = 0.97$, $P < 0.001$).

Biotic effects on soil respiration

Soil respiration was compared with SOC stocks at each combination of sites, treatments and microsites. Variation in SOC stocks explained 77% of the variation in annual R_s (Fig. 4). SOC stock was higher under shrubs than in intershrub gaps (Table 2), and decreased linearly along the aridity gradient (shrubs: $\text{SOC} = 0.3825 + 0.00295 \text{ MAP}$, $r^2 = 0.998$, $P = 0.001$; intershrub: $\text{SOC} = 0.0519 + 0.00293 \text{ MAP}$, $r^2 = 0.96$, $P = 0.022$). Annual R_s was only weakly related to above-ground shrub and herbaceous biomass (M. Sternberg, J. Kigel, D. Kanas and I. Konsens, unpublished results), a logarithmic relationship with $r^2 = 0.34$ (data not shown). Annual R_s at the microsite level correlated to a lower degree with precipitation than R_s at the ecosystem level mainly because of within-site variability in SOC stocks and soil depths, particularly at the semiarid site (Table 2). Upscaling to the ecosystem level compensated for part of this variation.

Observed fluxes of R_s tended to be higher under shrub canopies than in open gaps, particularly under drier conditions. The shrub–intershrub ratio ($R_{s\text{-shrub}}/R_{s\text{-intershrub}}$) was higher for the two drier compared with the two wetter sites along the gradient ($P < 0.001$) and for the Dry compared with the Control and Wet treatments at the Mediterranean site ($P = 0.004$). Annual R_s at the shrub microsite was 23% higher than R_s at the intershrub microsite on average across sites and rainfall treatments (Table 2). This difference was statistically significant when comparing linear regression lines of annual R_s vs. $\log_e \text{MAP}$ (Fig. 3a, legend). On the other hand, the decline in R_s with decreasing MAP was similar at the two microsites (similar slopes of the regression lines; legend Fig. 3a). As a result, the shrub–intershrub ratio of R_s increased with decreasing MAP, from 1.31 at the mesic Mediterranean to 1.53 at the arid site. Yet, the contribution of R_s under shrubs to

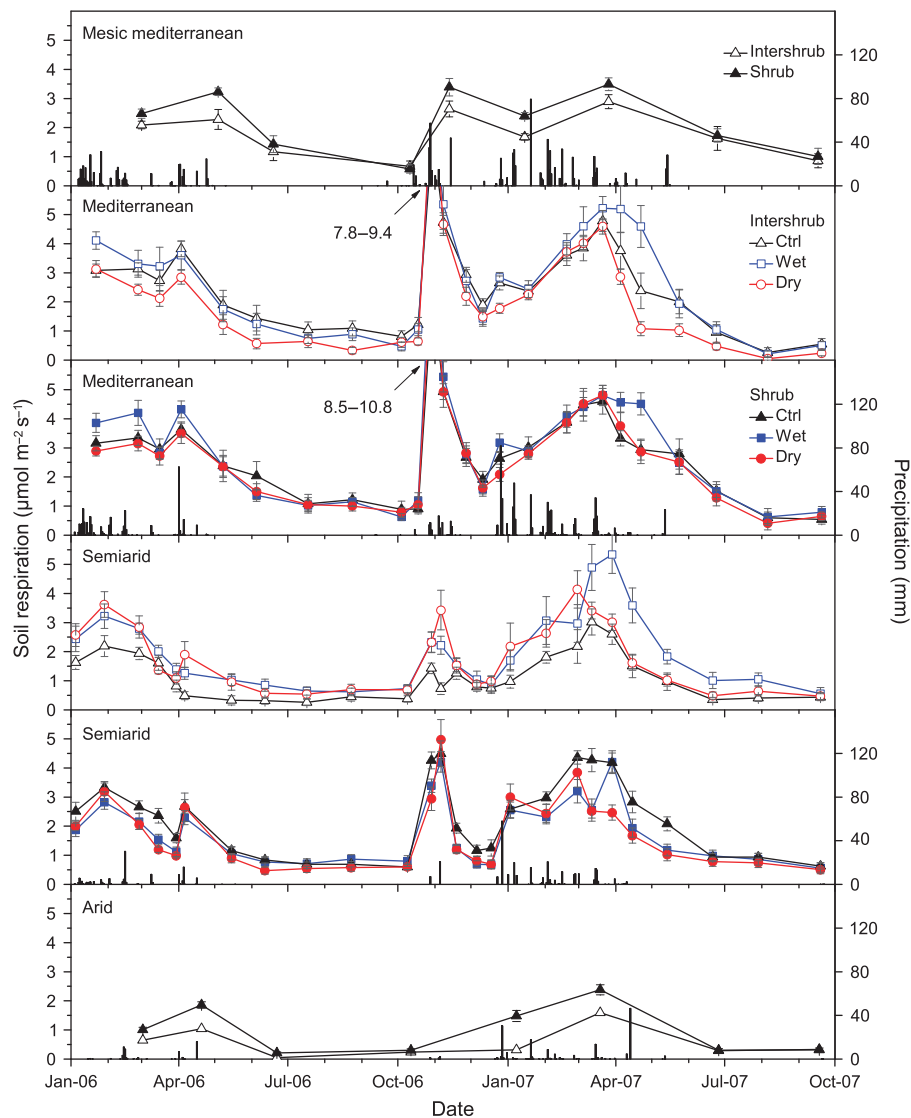


Fig. 2 Seasonal cycle of regular R_s measurements per site, treatment and microsite. Daily precipitation amounts were presented in bars for each site. Mean \pm 1 SE.

ecosystem-scale R_s ($R'_{s-\text{shrub}}/R_{s-\text{ecos}}$) decreased markedly with decreasing MAP on the ecosystem scale (Table 2) as a result of the drastic reduction in shrub cover from north to south (Table 1).

Discussion

Soil respiration under precipitation change

Soil respiration decreased considerably with decreasing water availability along the aridity gradient, as hypothesized. A reduction of 89% in MAP from north to south resulted in 77% decrease in R_s . In semiarid Arizona, a reduction of 40% in R_s was found in response to a 40% decline in MAP along an aridity gradient

(Conant *et al.*, 1998). Such gradients are a proxy for climate change on very large time scales which enable adaptive responses of the vegetation and soil components of the ecosystem (Sternberg *et al.*, in press). Ecosystem-scale R_s was only slightly altered by experimental drought, but increased by 22% following rainfall addition on average across the two central sites (see discussion below concerning variability at the semiarid site). Manipulation experiments revealed 3–30% decrease in seasonal or annual R_s following various drought treatments (Emmett *et al.*, 2004; Harper *et al.*, 2005; Borke *et al.*, 2006) and 9–103% increase in R_s following rainfall additions of two to four times MAP (Zhou *et al.*, 2006; McCulley *et al.*, 2007; Fay *et al.*, 2008; Liu *et al.*, 2009). Notably, R_s along the gradient and R_s

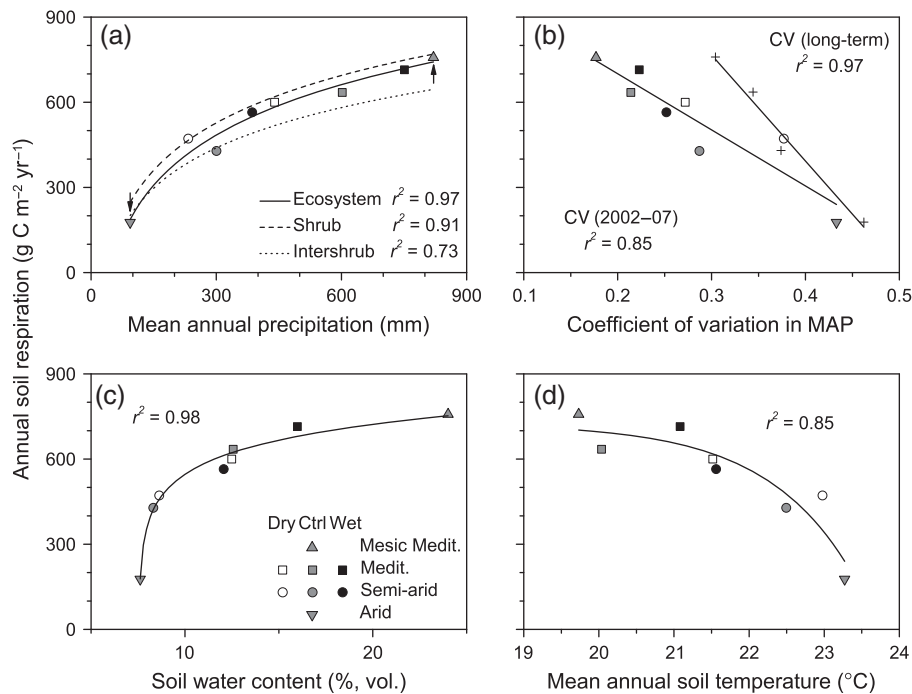


Fig. 3 Change of annual soil respiration rate (R_s) at the ecosystem scale with (a) mean annual precipitation (MAP) 2002–2007, (b) coefficient of variation (CV) in short-term (2002–2007) and long-term MAP, (c) mean annual soil water content (θ) 2006–2007, (d) soil temperature (T_s) 2006–2007. (a) Dashed and dotted lines are regression lines fitted to R_s vs. MAP for shrub and intershrub microsites, respectively (annual R_s rates weighted for rock cover); probabilities from ANCOVA with microsite as main effect and \log_e MAP as covariate: microsite, $P = 0.036$; \log_e MAP, $P < 0.001$; interaction, $P = 0.583$ (lack of interaction means that slopes are similar); arrows indicate the trend of ecosystem R_s moving from values close to shrub R_s at the mesic end of the gradient to values close to intershrub R_s at the arid end; equation for R_s vs. MAP (ecosystem scale): $R_s = -975 + 256 \log_e(\text{MAP})$, $P < 0.001$. (b) Crosses (+) represent the relationship between annual R_s and long-term CV in precipitation (55–58 years); equation for R_s vs. CV (2002–2007): $R_s = 1096 - 1976 \text{ CV}$, $P = 0.001$; equation for R_s vs. CV (long-term): $R_s = 1514 - 2981 \text{ CV}$, $P = 0.014$. (c) $R_s = 449 + 108 \log_e(\theta - 7.54)$, $P < 0.001$. (d) $R_s = 725 - 8.90 \cdot 10^{-7} e^{0.864 T_s}$, $P < 0.001$.

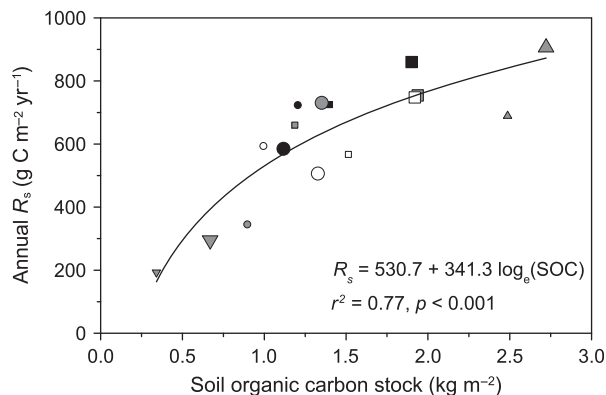


Fig. 4 Change in annual soil respiration (R_s) with soil organic carbon (SOC) stock. Upward triangles, squares, circles and downward triangles represent mesic Mediterranean, Mediterranean, semiarid and arid sites; grey, closed and open symbols represent Control, Wet and Dry treatments; large and small symbols represent shrub and intershrub microsites. Separate curves for microsites were not significantly different ($P = 0.184$).

across rain manipulations covaried along a common curve with climatic and edaphic variables (Fig. 3). This indicates that R_s in settings that simulate climate change on different time scales (gradient vs. manipulations) responded to the same extent to change in water availability. It appears, therefore, that multiyear rainfall manipulation is a useful tool for experimentally predicting climate-change effects on C fluxes for times scales that are beyond common research periods.

Soil respiration declined at an increasing rate with reductions in MAP and θ , i.e. the drier the conditions, the larger was the effect of reduction in water availability on R_s . This trend was especially pronounced below 10% mean annual θ . Progressive reduction in R_s with falling MAP was also obtained in a recent global analysis of forests where R_s was measured with modern technology (Grünzweig *et al.*, 2009), but not in a classical analysis across various vegetation types (Raich & Schlesinger, 1992). Lack of moisture increasingly reduces plant and microbial activity (Rey *et al.*, 2005),

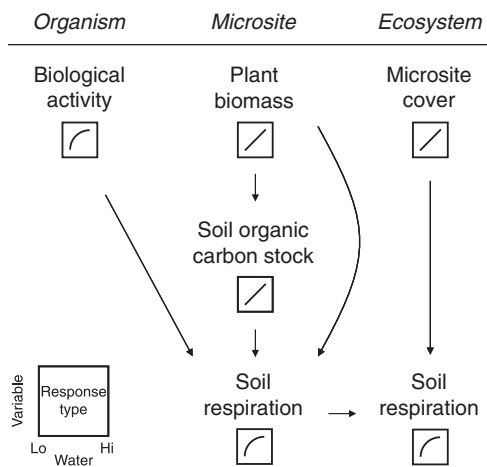


Fig. 5 Conceptual model on response of soil respiration and its main biotic controls to change in water availability across different scales. The small schematic figures depict the type of response of each variable to change in water availability. Scale within the model increases from left (plant, microorganism) to center (shrub, intershrub microsite) and right (ecosystem). The response of biological activity (CO_2 production per unit biomass or SOC stock) to water availability was obtained from laboratory incubations of Mediterranean shrubland soil under different moisture conditions (Rey *et al.*, 2005). Herbaceous biomass decreases linearly along the aridity gradient, the response of shrub biomass is not yet resolved (M. Sternberg, J. Kigel, D. Kanas and I. Konsens, unpublished results).

and poses limitations to diffusion of substrates to soil microorganisms. Decrease in R_s is being enhanced by linear reductions in SOC and cover of more active vegetation, such as shrubs. Those mechanisms appear to interact and result in progressively lower R_s on the microsite and ecosystem scale under reduced water availability (Fig. 5).

Changes in biotic effects on soil respiration

Various studies showed higher R_s under shrub canopies than in intershrub gaps, at least during part of the year (McLain & Martens, 2006; Sponseller, 2007; Potts *et al.*, 2008). The 23% higher R_s under shrubs in the current study were possibly caused by both direct and indirect biotic factors. Higher SOC stocks and possibly higher root biomass under shrub canopies likely supplied larger amounts of substrates (direct biotic effect). In addition, microclimatic conditions during the transition and dry seasons were more moderate under shrubs (indirect biotic effect), given that θ was higher and maximum T_s was less extreme compared with intershrub patches. Those conditions could have contributed to the higher shrub–intershrub ratio at more arid sites and in the Dry treatment.

Soil respiration at both microsites responded similarly to rainfall reduction, which contradicts our hypothesis and the evidence from other shrublands that showed stronger responses under shrub canopies than in intershrub patches (McCulley *et al.*, 2007; Sponseller, 2007; Potts *et al.*, 2008). Shrub roots are probably active throughout the year as opposed to roots of ephemerals which desiccate during the spring–summer transition season. Even though microbial activity continues into the dry season at both microsites (Dirks *et al.*, 2010), microorganisms are assumed to be more active under shrubs than between shrubs during the dry season because of the more moderate microclimatic conditions. Continuing biological activity should have rendered the shrub microsite more sensitive to drying than the intershrub microsite. The lack of such a difference indicates great robustness of shrub roots and soil microbes to climate change, possibly reflecting a high degree of adaptation of organisms to the large interannual variation in water availability in the Mediterranean region.

The ratio of shrub to intershrub R_s tended to increase under drier conditions which is in agreement with the islands-of-fertility theory, since differences between microsites in C and N pools and fluxes are higher at drier compared with more moist sites (Schade & Hobbie, 2005). However, the decrease in shrub cover with increasing aridity was more pronounced than the increase in the shrub–intershrub ratio. Therefore, R_s under shrubs contributed less to ecosystem-level R_s at drier sites than at more mesic ones (Table 2). Climate-induced variability in vegetation structure significantly influenced CO_2 fluxes also in desert ecosystems along an aridity gradient (Conant *et al.*, 1998). This has consequences for larger spatial scales where climate change is expected to affect vegetation dynamics, with major impacts on the regional and global C cycle (Cramer *et al.*, 2001). Rainfall treatments did not result in a significant short-term shift in composition of herbaceous species (M. Sternberg, unpublished results), therefore precipitation effects on R_s at intershrub microsites were not caused by vegetation change.

Spatial and temporal variation in soil respiration

Soil respiration did not correlate with climatic factors at the semiarid site, which was probably caused by heterogeneity in soil depth and SOC stocks. Shallow compared with deeper soil results in lower organic C stock in the total profile and less nutrients for root development, hence less substrate for respiratory activity. Moreover, shallow soils limit access of roots to soil water at deeper layers, a critical mechanism for activity and survival under conditions of drought stress. Potential carbonate dissolution and precipitation is considered

not sufficient to explain annual CO₂ fluxes (Serrano-Ortiz *et al.*, 2010).

Soil respiration pulses are commonly observed under Mediterranean-type climates (e.g. Tang *et al.*, 2005; Chou *et al.*, 2008; Grünzweig *et al.*, 2009). The first small rain events result in enhanced microbial decomposition of labile organic matter which is probably abundant following an extended dry period (Kieft *et al.*, 1987; Fierer & Schimel, 2003). Although theoretically postulated (Serrano-Ortiz *et al.*, 2010), carbonate-derived CO₂ did probably not contribute significantly to R_s pulses (Inglima *et al.*, 2009). Root respiration is an additional source of pulses at a later stage or after slightly larger rain events (Huxman *et al.*, 2004; Tang *et al.*, 2005). Pulses constituted a significant part of the annual R_s flux at the Mediterranean site (20%), but were less prominent at the semiarid site (9%). The contribution of R_s pulses to the annual R_s balance was relatively low in Mediterranean-type grassland (up to ~5%, Chou *et al.*, 2008) and pine forests (11%, Tang *et al.*, 2005; up to 9%, Grünzweig *et al.*, 2009), values that were similar to the ones at the semiarid site in the current study. The high R_s pulse at the Mediterranean site might be related to disruption of soil macroaggregates by wetting of dry soil, thus exposing free soil organic matter and microaggregates to microbial decay (Denef *et al.*, 2001). Such a mechanism was suggested for clayey soils (Borken & Matzner, 2009), which is applicable to the Mediterranean site.

Conclusions

Reduction in precipitation across Mediterranean and desert ecosystems resulted in a progressive decline in R_s at both shrub and intershrub microsites, i.e. the drier the conditions, the larger was the effect of reduction in water availability on R_s . The impact of low water availability on R_s is enhanced across scales: basic moisture constraints on biological activity at the organismic level (plants, microorganisms) is followed by reductions in the respiring mass and in substrates (biomass, SOC stock) at the microsite level (Fig. 5). Since R_s and SOC stocks were higher under shrubs than at the intershrub microsite, drastically lowered shrub cover further reduced R_s with increasing aridity. Therefore, changes in vegetation structure under climate change might have a large impact on ecosystem-scale R_s in these heterogeneous systems compared with changes in respiratory activity of each vegetation component.

Acknowledgements

We wish to thank Jaime Kigel, Irit Konsens and Dina Kanas for providing biomass data. We further acknowledge the technical

assistance of Rita Dumbur, Gil Yogev, Yaniv Kriger, Anatoly Shavlevitch, Johannes Metz, Ofer Kor, Yonatan Berkowitz, Ran Drailich, Ifat Granat, Ilan Noy-Meir, Yaniv Blatner and Eran Reznik. This study was supported by the International Arid Lands Consortium (IALC) and the FP6 Integrated Project Climate Change and Impact Research: the Mediterranean Environment (CIRCE). The study was carried out within the framework of the project GLOWA Jordan River supported by the German Federal Ministry of Education and Research (BMBF) in collaboration with the Israeli Ministry of Science and Technology (MOST).

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