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The Use and Misuse of Climatic Gradients for Evaluating Climate Impact on Dryland Ecosystems - an Example for the Solution of Conceptual Problems

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1. Introduction

Current trends of emissions of greenhouse gases are expected to cause the global temperature to rise faster over the present and next century than during any previous period (Houghton et al., 1996, 2001; Zweirs, 2002). Climate models for the Middle East predict an increase in winter temperatures combined with changes in rainfall amounts and distribution (Ben-Gai et al., 1998; Black, 2009, Klafe and Bruins, 2009). These changes may alter ecosystem functioning, with direct effects on ecosystem, community and population processes such as plant litter decomposition, nutrient cycling, primary productivity, biodiversity, plant recruitment and survival (e.g., Aronson et al., 1993; Hobbie, 1996; Robinson et al., 1998; Sternberg et al., 1999; Chapin et al., 2000; Hughes, 2000; Sarah, 2004).

Considerable research has been directed at understanding the responses of terrestrial ecosystems to global environmental change. This topic is of great societal concern in the light of the potential impacts on the natural resources on which the human population depends on (Vitousek, 1994). Nevertheless, the challenge to predict ecosystem response to climate change is based on the multi-dimensional and multi-scale nature of the problem (Osmond et al., 2004). Complex ecological interactions make it difficult to extrapolate from individuals to communities and to predict the ecosystem response when only few levels of ecosystem organization are targeted. In addition, the lack of realistic climatic scenarios at relevant scales adds further complexity to the up-scaling process (Harvey, 2000).

Vast experimental research efforts have been invested in understanding the effects of global warming and CO_2 atmospheric enrichment on ecosystem functioning. These processes are considered key drivers of environmental change, particularly in northern latitudes.

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However, relatively little attention has been focused on assessing the responses of terrestrial ecosystems to potential changes in precipitation (Lavee et al., 1998; Svejar et al., 1999; Weltzin et al., 2003). This is probably because projected trends in precipitation changes differ widely between different regions of the world (Intergovernmental Panel on Climate Change, IPCC) therefore, downscaled climate scenarios are required. Precipitation changes are particularly important at mid-latitudes (e.g., around the Mediterranean Basin), where water availability is a key driver in ecosystem functioning, and where global circulation models agree that future precipitation will be lower than today (IPCC). In arid and semi-arid regions, anticipated changes in precipitation regimes may have an even greater impact on ecosystem dynamics than the separate or combined effects of rising temperatures and CO_2 levels. Therefore, studies focusing on the effects of changing patterns of rainfall on ecosystem functioning in these regions are much needed to improve our understanding of the impact of possible future climatic scenarios.

Current predictions of the effects of climate change on water-limited ecosystems are commonly based on empirical investigations of existing climatic gradients (Diaz and Cabido, 1997). However, such purely descriptive approaches alone do not provide sufficient information to enable accurate modelling of the effects of altered water availability caused by climate change. The greatest uncertainty stems from the assumption that climatic differences are the main single determinant of variation among communities along a gradient. There is little experimentally derived information that would allow mechanistic predictions of the impacts of these changes on natural plant and animal communities and ecosystem functioning (Walther et al., 2002; Dunne et al., 2004; Osmond et al., 2004).

Here we present an approach that was designed to overcome several of the major drawbacks of previous studies on the effects of climate change on natural ecosystems. The multidisciplinary project described here employs, in addition to observations along a natural aridity gradient, climate manipulations that are intended to close the gap between descriptive and experimental research approaches, and theoretical modelling. Our unique contribution is to base our study on integrative and complementary investigations of soil, overland flow, and vegetation and landscape processes, combined with consideration of the socio-economic impacts. We thus aim at a holistic approach to the assessment of the impact of climate changes on plant and human communities.

In the following we develop the rationale for combining different, complementary approaches in current climate change research. First, we review the advantages and drawbacks of commonly employed methodology. Based on this outline, we present an approach that takes these concerns into account. Finally, we present an ongoing research programme that is based on this rationale.

2. Methodology

2.1 Gradient approaches as space-for-time approaches

Natural climatic gradients, which include environmental factors such as altitude, topography, temperature and precipitation, provide a useful framework for studying the effects of climate change (Diaz and Cabido, 1997; Imeson and Lavee, 1998; Dunne et al., 2003). Comparisons of ecosystems and biotic communities along gradients provide powerful approaches to the investigation and understanding of the effects of climate variation on ecosystems (Le Houerou, 1990; Koch et al., 1995; Austin, 2002; Cocke et al., 2005). Approaches based on aridity gradients have been frequently used to study Mediterranean ecosystems (e.g., Boyko, 1947; Holzapfel et al., 1992; Holzapfel et al., 2006; Imeson et al., 1998; Kutiel et al., 2000; de Bello et al., 2005).

The varying effects of climate change on vegetation along gradients can be investigated directly and indirectly. The direct approach involves monitoring of dynamic, long-term vegetation changes in permanent plots (Schmidt, 1988), which necessarily involves long study periods. However, in many cases it is necessary to derive conclusions about successional trajectories from short-term observations. This indirect approach typically involves extrapolation from spatially distinct sites that are expected to represent certain stages in a temporal succession, to temporal patterns; i.e., space-for-time substitution or 'chronsequences' (Pickett, 1989). For example, this approach has been used to investigate the effect of chronic additions from the atmosphere to natural ecosystems. By assuming that all forests were principally N limited before industrialization, current differences in forest health along gradients of N deposition have been attributed to eutrophication (e.g., Lovett and Rueth, 1999), while other causes often have been neglected (Binkley and Högberg, 1997). This indirect and static approach is necessary in several fields of scientific inquiry where direct observation of chronsequences are feasible (e.g., palaeobotany, archaeology and geology, among others).

One has to keep in mind that indirect approaches are based on deductions and not on evidence obtained by direct observations. These deductions are clearly dependent on the subjective selection of sites used as reference for changes in time. Likewise, extrapolations from patterns formed by climatic and ecological gradients to temporal changes – especially in the context of climate change – have often proved to be problematic, as one cannot establish causal relationships on the basis of correlative studies alone (Rastetter, 1996; Dunne et al., 2004).

"Space-for-Time" approaches that use existing environments as proxies for environments under future changed climate are not, in themselves, sufficient to predict changes in species interactions within communities. Such substitutions involve comparisons with communities that have come into balance with local climates over long periods, and the development of such balances is not to be expected in the context of the current rapid pace of climate change (Rastetter, 1996). Moreover, the Space-for-Time approach works under the assumption that except for the climate, all ecosystem components and environmental factors are equally important. Clearly, this is not the case, and the detection of a causal relationship between changes in climate and in ecosystems necessitates more complex approaches. The Space-for-Time approach also neglects the effects of the current fast rate of climate change on ecosystem and community functions that have evolved over long periods. Populations are not likely to vary and move in unison, in response to climate change, and important changes in community composition are to be anticipated (Parmesan, 1996; Walther et al., 2002).

An additional problem is that short-term studies cannot mimic long-term environmental changes. Even if conducted over periods of several years, such studies necessarily present only snap-shots of slowly developing actual changes in climate regimes. In order to overcome the above-mentioned shortcomings of a space-for time approach, such descriptive studies need to be complemented by experiments that enable causal inference, and by theoretical methods that enable the development of scenarios over longer time periods (Sutherland, 2006).

2.2 Experiment vs. gradient approaches: combining efforts

One logical solution for the above problems with simple Space-for-Time approaches is to use climate change experiments *in situ*. The **Experiment-for-Time** approach provides a realistic solution, as climate change will happen in a given place and will be imposed on the biotic communities and ecosystem functions present in that place. This approach mimics the short-term responses of biotic communities and environments and, thereby, directly provides the needed causal relationships between the changes in climate change and in the ecosystem.

Combinations of descriptive gradient studies and experimental approaches have been extremely rare to date (Dunne et al., 2004) and, to the best of our knowledge, have not yet been applied to arid and eastern Mediterranean ecosystems.

The central idea and conceptual scheme behind a combined space-for time and experimental design is illustrated in Fig. 1. Comparisons of given ecosystem and community parameters (e.g., soil properties, biomass production, flora and fauna composition, sediment transport, etc.) along the climatic gradient (e.g., the north-south vertical comparison in Fig. 1) reflect combined changes in the community and climatic conditions. Comparison of the same parameters between climate manipulations within the same site (horizontal comparison in Fig. 1) reflects the effects of changes in climate only. Furthermore, comparisons of control

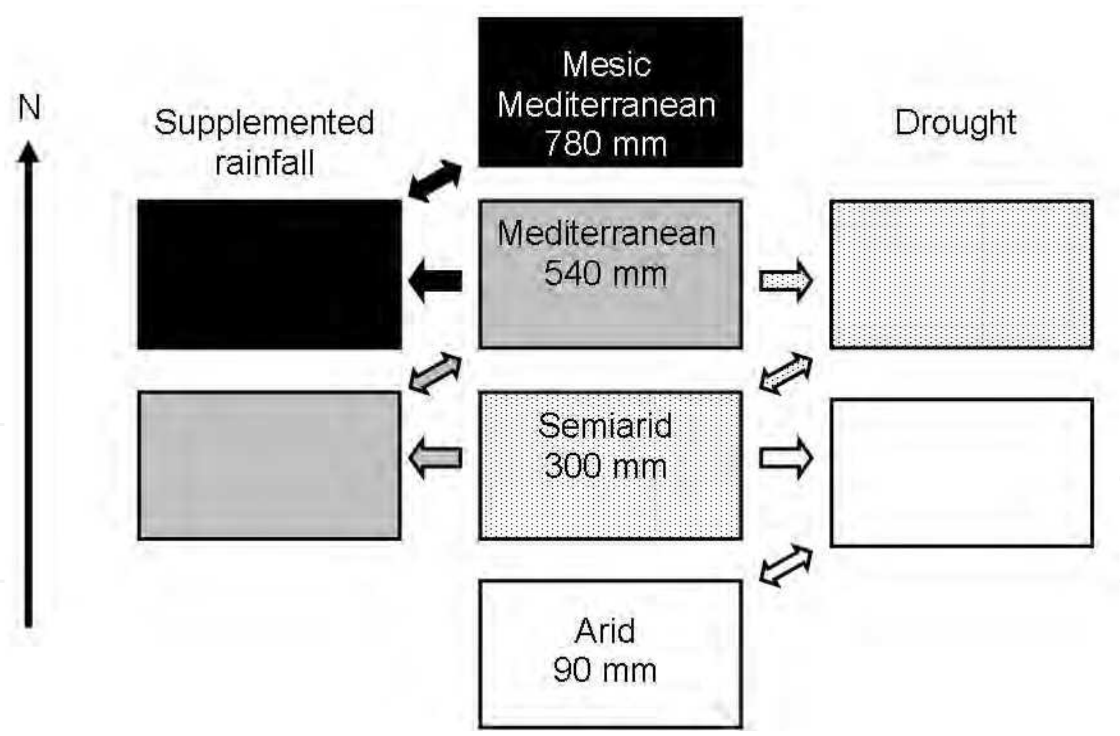

Fig. 1. Schematic illustration of comparisons of study sites along the gradient, with rainfall manipulations, representing the rationale of the experiment set up. Connecting arrows between squares illustrate meaningful comparisons (see text).

sites (i.e., natural precipitation) with manipulated climate treatments in adjacent sites along the gradient (diagonal comparison in Fig. 1) reflect mainly the effects of site differences, since their rainfall amounts tend to be similar. Thus, these three comparisons facilitate the separation of the effects of climate alone from the effects of site-specific community conditions. Furthermore, these comparisons highlight the interactions between climatic and other environmental effects. One prediction is that simple comparisons along an existing gradient will not necessarily enable direct forecasting of shifts in ecosystem conditions caused by climate change, since climatic and other environmental effects are likely to be confounded (Fukami and Wardle, 2005). Our research tests this prediction and evaluates the usefulness of this approach as compared with those used in previous studies of the effects of climate change.

The above outlined approach tests whether purely descriptive gradient approaches are sufficient to enable prediction of the effects of climate change. The present project is carried out within the framework of the research initiative, GLOWA–Jordan River (for details see: http://www.glowa-jordan-river.de). Besides contrasting direct and indirect approaches, as stated above, the project has two specific applied goals: (1) to understand the effects of global climate change on soil, run-off, populations, biotic communities and ecosystem properties and dynamics in ecosystems in Israel that range from Mediterranean to arid; and (2) to provide empirical data for modelling, economic analysis and prediction of ecosystem responses to climate change in an environmentally sensitive area.

2.3 Integration by modelling: extending the time-scale

The addition of experimental studies to the space-for-time approach should improve our understanding of relevant processes linked to short-term changes in precipitation patterns. However, this experimental approach is limited in space and time, and the limited number of years available for observation and experimental manipulation may not be sufficient for complete exploration of the long-term dynamics. This is because rainfall in more arid regions is highly variable and annual precipitation may be autocorrelated between consecutive years, which may lead to long-term fluctuations. In addition, technical and logistic constraints restrict the size of the area that can be manipulated in experiments to a scale that is necessarily smaller than scales relevant for land users and nature conservation. Furthermore, the type of climate-change scenario that can be mimicked by experiments is constrained by the practicability of active manipulation of the climate. Therefore, complex scenarios such as increased frequency of extreme events, as predicted for our study region (Kunstmann et al., unpubl.), cannot be directly addressed in the empirical study.

Modelling provides useful tools to close these gaps. Spatially explicit, stochastic simulation models have been found successful in using short-term and small-scale information to gain understanding of and to predict longer-term and larger-scale processes, as described by Jeltsch and Moloney (2003). Grid-based, modular simulation models of vegetation dynamics are especially able to link information on differing scales (Jeltsch et al., 1996, 1997; Jeltsch et al., 1999). However, in the type of climate change studies proposed in the present paper, phenomena on at least three different spatial scales have to be distinguished: (1) responses of individual plants, e.g., growth, seed production, mortality and, possibly, physiological adaptation mechanisms (e.g., Petru et al., 2006); (2) small-scale intra- and interspecific interactions between individuals of contrasting growth forms, among which interactions between herbaceous and woody vegetation, including competition and facilitation mechanisms, are of especial importance (Holzapfel et al., 2006); and (3) the effects of these interactions on vegetation pattern formation on the landscape level, with feedbacks to spatial processes such as runoff, soil moisture distribution and availability, fire, grazing, and other types of land use. At all these levels, the models need and use data obtained in the detailed field investigations and experiments, and thus also function as integrators of collected information.

It is, however, not feasible to collect all the necessary information on all scales in full detail. Therefore, we apply a cascade of models that differ in spatial and temporal resolution. With increasing scale, spatial resolution of data has to be aggregated to reduce the otherwise immense complexity of the model. Since, in contrast to previous studies, realistic climatic scenarios at biologically meaningful scales are produced within the larger framework of the GLOWA–Jordan River programme (see website), we will be able to utilize these scenarios for generating more realistic predictions. Field monitoring and experiments can be used for model testing and validation, and additional simulation experiments, such as increasing the frequency of extreme years, can be conducted that are not feasible in the experimental plots.

The combination of hierarchical modelling and experiments with the space for time approach provides a powerful strategy for gaining understanding of the impact of climatic changes by examining processes that link individuals, patches, and the landscape (up-scaling procedure). Only such a multi-scale approach is capable of predicting consequences of changed climatic conditions on a level that is relevant to land use and management.

2.4 Socio-economic evaluations: a need for a stronger link with nature

Linking the ecological and socio-economic approaches at the landscape level provides improved tools to analyze the impacts of global change on society and nature. Scientists are responding to the demands to estimate potential local impacts of climate change and to produce relevant information that can be used at regional and local scales, and can be related to public and natural needs (Cash and Moser, 2000). However, most of the papers that analyze this issue place little emphasis on the link between ecosystem processes and socio-economic impacts. This topic deserves to be investigated in more detail, in light of the multi-scale nature of the global climate change problem

The impact of climate change on agricultural activities and their economic consequences has received much attention from economists (Mendelsohn et al., 1994; Nordaus, 1994). The general approach is to assume changes in temperature and precipitation and to determine their effects on the income generated from agriculture. Fewer scientists have dealt with evaluation of the loss of welfare caused by changes in ecosystems (Layton and Brown, 2000). In both types of analysis changes in vegetation, soil and water processes are regarded as external agents; Layton and Brown (2000), for example, used arbitrary values of forest loss depicted in computer-enhanced photographs.

In the present study, we link the climate to changes in biomass and ecosystem processes via changes in the landscape, and hence to societal welfare. In order to link the changes in biomass to the welfare level of society a stated preference approach was used. In this approach a survey of the urban population was conducted, in which the biomass level was expressed in the form of landscape photos of the experimental stations (see Fleischer and Sternberg, 2006). Previous studies have shown that the recreational value of agricultural landscape can be much higher than the returns obtained from farming (Fleischer and Tsur, 2000). In our experimental stations, in which the land is mainly and extensively used for grazing, this difference is even greater, because emphasis was put mainly on the changes in utility that accrue to the individuals exposed to the landscape. Since these changes will occur only in the future we were able to use only a stated preference approach, within which we used a choice modelling approach. Data were collected by means of a face-to-face survey of a representative sample of the urban population in Israel, where more than 91% of the population are city dwellers. The landscape in the photos varied along the north-south environmental gradient, from a typical mesic Mediterranean, through Mediterranean, semiarid to arid. By using the Random Parameters Logit (RPL) model it was possible to determine the population's Willingness To Pay (WTP) in order to prevent changes to the landscape. The WTP was, in fact, the monetary value of the welfare loss to the population caused by the changing landscape. The novel feature of this research was in the use of photographs of the experimental stations along the north-south gradient; photographs that provided a simulation of the expected impact of the climate change on the landscape (for full details see Fleischer and Sternberg, 2006).

3. A case study along an aridity gradient

During 2001 four experimental sites were established in Israel, along a 245-km-long climatic gradient running from Galilee in the north to the Negev Desert in the south (Fig. 2). These sites represent respectively, Mesic Mediterranean (MM), Mediterranean (M), semiarid (S), and arid (A) climatic conditions (see Table 1). All the sites rest on the same calcareous (hard limestone) bedrock and are positioned on south-facing slopes, i.e., the drier aspect. The study sites were fenced to exclude the main domestic grazers, i.e., cattle, sheep and goats. The basic climate is Mediterranean, with mild and rainy winters (October-April) and prolonged rainless, hot summers. The plant-growing season is closely associated with the temporal distribution of rainfall. Germination of annuals, and growth of most perennials starts soon after the first rains, between October and December each year (Table 1).

3.1 Climatic manipulations: rationale and application

Experimental approaches to climate-change studies, particularly those that address the impacts of precipitation on ecosystems, typically involve the use of rainout shelters to exclude natural precipitation, and artificial irrigation to increase rainfall (Fay et al., 2000; Sarah and Rodeh, 2004). Rainout shelters provide control over the daily or seasonal timing and extent of dry and wet periods. Global climate change is predicted to alter rainfall patterns during the growing season, and this may lead to either reductions or increases in the total amount of precipitation in different cases, in addition to causing shifts in the temporal distribuion of the rainfall during the growing season. Such changes may affect numerous ecosystem processes, through the temporal and spatial redistribution of water, and ultimately may have impacts on rates of primary productivity and decomposition, as well as on biological diversity (Hulme, 2005).

Rainfall manipulations are applied in only two of the four sites. These sites are located in the two intermediate locations along the climatic gradient and they represent the transition from mesic to arid conditions: the Mediterranean (M) and the semi-desert (S) regions. The rationale of climatic manipulations at these sites is based on predicted potential climate-change scenarios in which the strongest changes occur in the transition zone between mesic Mediterranean and arid desert areas (Fig. 2). The mesic Mediterranean and the desert stations (MM and A) at the ends of the gradient, are kept under natural climatic conditions and serve as controls for the climate-manipulated areas.

Ecosystem type	Rainfall & CV (mm - %)	Temperature (°C) Min. Mean Max.	Elevation (a.s.l)	Soil type	Vegetation formation
Arid (N 30°52' E 34°46')	90 - 51	13.6 - 19.1 - 26.1	470 m	Desert Lithosol	Open vegetation dominated by small shrubs and semi-shrubs such as *Zygophyllum dumosum*, *Artemisia sieberi* and *Hammada scoparia* and sparsely growing desert annuals, geophytes and hemicryptophytes.
Semiarid (N 31°23' E 34°54')	300 - 37	13.2 – 18.4 – 24.8	590 m	Light Brown Rendzina	Dwarf-shrubs of *Sarcopoterium spinosum* and *Coridothymus capitatus* associated with herbaceous (chiefly annual) plant species
Mediterranean (N 31°42' E 35°3')	530 - 30	12.8 – 17.7 - 23.6	620 m	Terra Rossa	Dwarf-shrubland dominated by *Sarcopoterium spinosum* and a high diversity of herbaceous (mostly annual) plant species.
Mesic Mediterranean (N 33°0' E 35°14')	780 - 22	13.5 - 18.1 - 23.4	500 m	Montmorillonitic Terra Rossa	Closed oak maquis (*Quercus calliprinos*) and open garrigue formations dominated by shrubs (*e.g. Calicotome villosa, Sarcopoterium spinosum, Cistus* spp.) and associated herbaceous plants.

Table 1. Physical and biotic characteristics of the study sites along the aridity gradient. Temperature refers to annual means (mean minimum, mean and mean maximum) Rainfall coefficient of variance (CV) is presented as percent (Modified from Fleischer and Sternberg, 2006).

Two climate-change scenarios are currently being tested in the sites with winter, i.e., growing season, rainfall manipulations: increased rainfall and drought. These scenarios arebased on existing climate-change models for the region (Ben-Gai et al., 1998; Zangvil et al., 2003) and on scenarios generated within our own project (Kunstmann et al., unpubl.) and represent two extreme boundary conditions. In each site, plots of 10 × 25 m are subjected to simulations of either wetter or drier winters. There are three treatments per site: 1) control (natural conditions); 2) artificially augmented winter rainfall (30% more than average annual precipitation); and 3) winter drought (30% less than average annual precipitation), simulated by means of rainout shelters. The climatic manipulations are each applied to five plots.

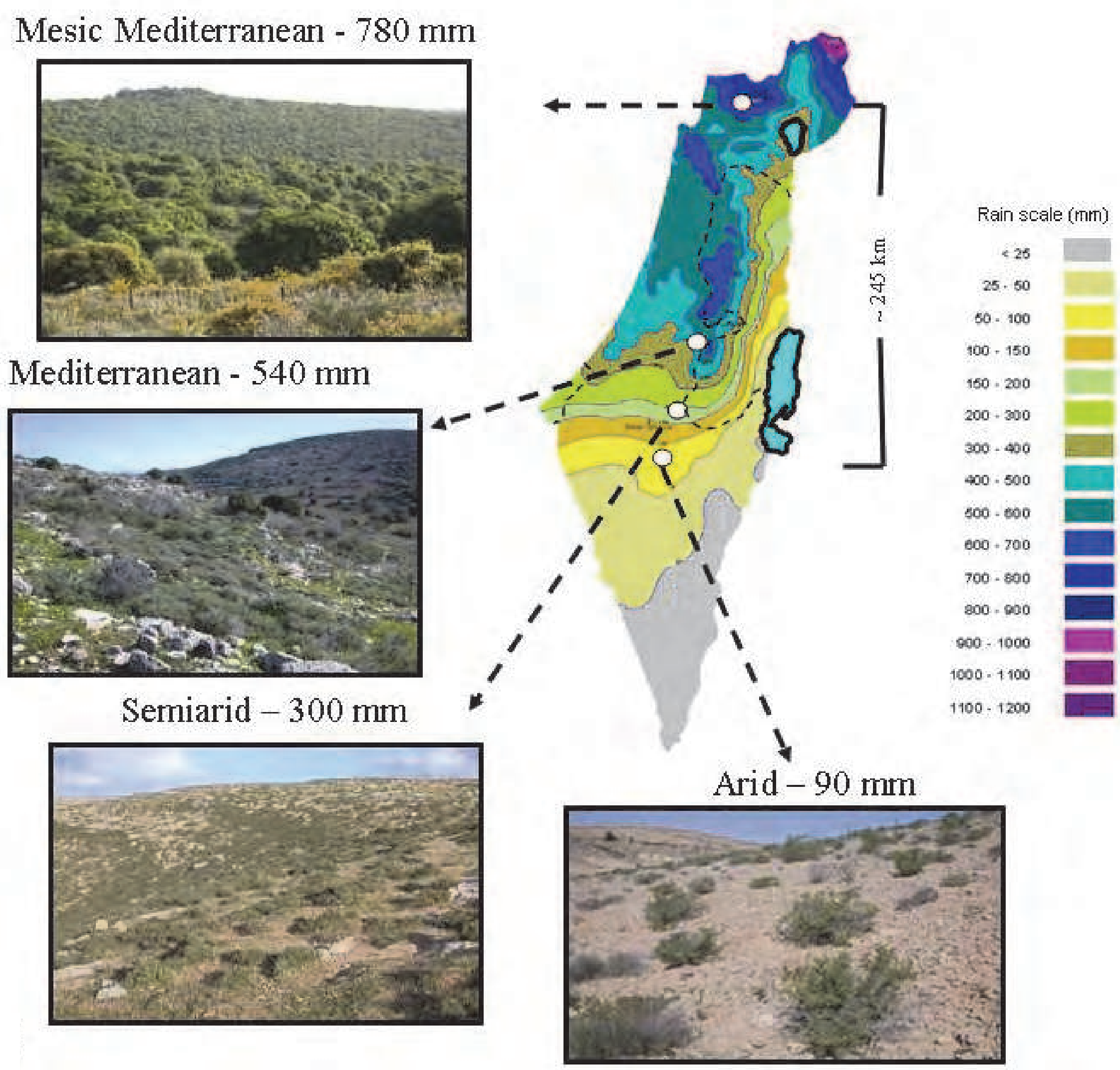

Fig. 2. Location of the experimental sites along the aridity gradient. Photographs: Claus Holzapfel

The rainfall treatments mimic the natural timing, frequency and intervals of rainfall events at the sites. Irrigation is applied at the end of each rainfall event by means of drizzle sprinklers. Drought treatment will be achieved by using plastic rainout shelters as described by Yahdjian and Sala (2002) to intercept 30% of the precipitation arriving at a site (Figure 3). These fixed rainout shelters utilize V-shaped bands of greenhouse plastic to intercept a given amount of rainfall. The bands are supported by a frame of galvanized aluminum (mean height = 2.5m) and cover a total surface of 25m x 10m. The roofs are angled and drain to gutters at the downslope edge of the roof. Gutters leading to collecting pipes that drain the water intercepted outsite the study plots. Sides of the rain shelters are open to allow for air movement and minimize temperature and humidity differences under and outside the shelter (Fay et al., 2000).

Summaries of the soil properties, overland flow and vegetation studies, and the measured parameters are presented in Table 2. The selection of the type of data collected is based on the need to couple between climate and vegetation responses and to cover a whole range of spatial, temporal and organizational scales.

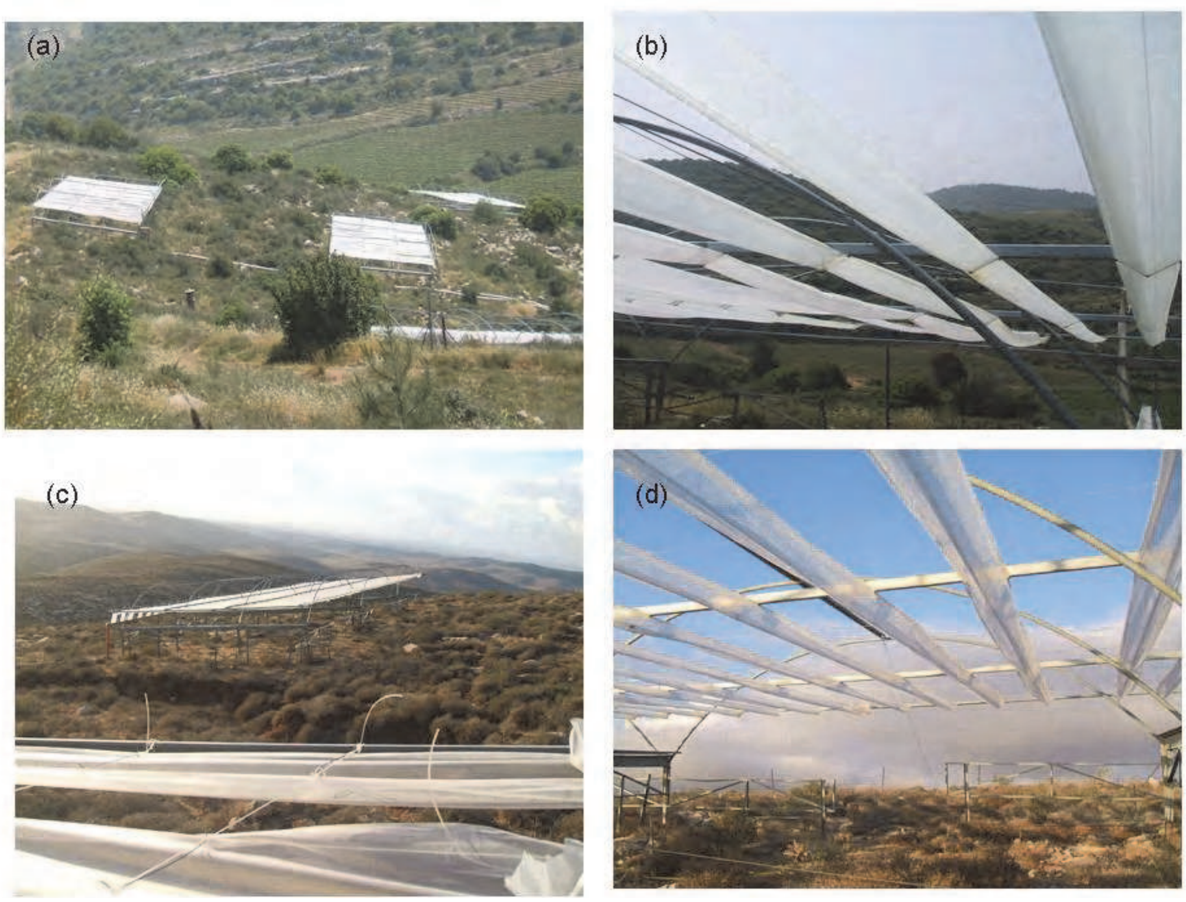

Fig. 3. View of the study sites with the rainout shelter structures at the Mediterranean (a and b) and at the semiarid site (c and d). Photographs: Claus Holzapfel and Marcelo Sternberg.

4. Current directions

The results obtained from this innovative project provide useful tools for refining predictions of the responses of ecosystems ranging from Mediterranean to desert to global environmental change. The combination of methodologies that was achieved by up-scaling and down-scaling specifically targeted processes provides a more accurate means of coping with the great uncertainty inherent in studying global climate change. Moreover, the results of this project will lead to a better understanding of the mechanisms that determine changes in community structure, ecosystem functioning and soil erosion in these ecosystems. Another innovation is that the results we obtain will enable us to obtain realistic down-scaled climate scenarios for the region, to be integrated into our models (in collaboration with the climate modellers participating in the GLOWA – Jordan River Project – see web page). Finally, our results can be utilized directly for evaluating the socio-economic consequences of climate change for ecosystems. Although such an integrated approach has been advocated previously (Weltzin et al., 2003), to our knowledge, no similar study, which combines gradient and experimental approaches with modelling and socio-economic approaches, has addressed the effects of global climatic change in Mediterranean and desert ecosystems.

Parameter	Methology	Objective
Soil structure (aggregate stability and aggregate size distribution), organic matter content, soluble salts, electrical conductivity, pH, microbial enzymes (arylsulphatase activity) and nitrogen content in the soil (NO_2, NO_3 and NH_4).	Soil sampling three times a year – autumn, winter and spring – in different microhabitats: a) shrub understorey , b) open patches between shrubs , c) beneath rock fragments and d) tree understorey. Soil samples include two layers: 0-2 cm and 5-10 cm depth.	Understanding changes in soil properties linked to nutrient turnover and susceptibility to erosion.
Overland flow and sediment properties.	Small run-off plots set up in several microhabitats: a) shrub understorey; b) open patches between shrubs, and c) a combination of shrubs and open gaps. The area of each plot is about 0.15 m^2 and that of shrub-open gap matrix is about 0.3 m^2.	Redistribution of water-accepting patches (sink) and overland flow-contributing patches (source) as a strategy of water conservation.
Aboveground biomass, species richness, species diversity, species composition, plant density, phenology, soil seed banks, germination strategies, species interactions	Comparisons for all parameters are between microhabitats: a) shrub understorey; b) open patches between shrubs. Destructive and non-destructive biomass estimations using allometric estimations. Species richness, diversity and density per quadrat of seedlings is determined with repeated counts, taking into account separate germination events. Soil seed bank is collected from all stations every year, in autumn before the onset of rainfall and watering, for 3 consecutive years to deplete dormant seeds. Adaptation to the climate via germination strategies and adaptation to biotic conditions are studied for selected plant species and functional groups.	Understanding of mechanisms behind plant population and plant community dynamics. Baseline for theoretical predictions of species and community response to climate change.
Plant litter decomposition	Plant litter bag experiment including microhabitat comparisons (shrub understorey and open gaps between shrubs) along the climatic gradient. Reciprocal plant litter transplantation among study sites	Estimations of nutrient cycling and carbon turnover.

Table 2. Description of biotic and abiotic parameters measured in all study sites along the climatic gradient (includes the experimental climatic manipulations).

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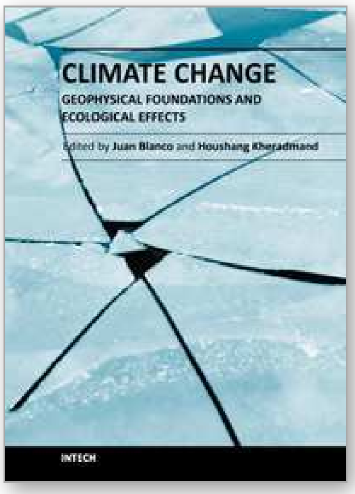

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This book offers an interdisciplinary view of the biophysical issues related to climate change. Climate change is a phenomenon by which the long-term averages of weather events (i.e. temperature, precipitation, wind speed, etc.) that define the climate of a region are not constant but change over time. There have been a series of past periods of climatic change, registered in historical or paleoecological records. In the first section of this book, a series of state-of-the-art research projects explore the biophysical causes for climate change and the techniques currently being used and developed for its detection in several regions of the world. The second section of the book explores the effects that have been reported already on the flora and fauna in different ecosystems around the globe. Among them, the ecosystems and landscapes in arctic and alpine regions are expected to be among the most affected by the change in climate, as they will suffer the more intense changes. The final section of this book explores in detail those issues.

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