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Abstract: This report describes shortcomings in current experimental exposure systems to study climate change impacts, and limitations of designs used in ecosystem functioning and biodiversity research.

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1 Executive summary

Work package 8 focuses on the advancement of techniques for creating future environmental conditions and on designing new approaches for experimental ecosystems, including new biodiversity experiments. The quantification of weaknesses and shortcomings in currently used experimental approaches to study climate change impacts on ecosystems (e.g. greenhouses, infrared heaters and monolith translocation) is tackled in the first deliverable presented here. The report also analyses important limitations of designs used in biodiversity-ecosystem functioning research. Ultimately, solutions will be proposed and tested in the next deliverables. The following issues are specifically addressed in Deliverable 8.1:

- Shortcomings of experiments simulating future elevated temperatures
- The use of Computational Fluid Dynamics (CFD) to design CO₂ enrichment technologies
- Designing new approaches for experimental ecosystems
- New generation of biodiversity/climate change experiments

2 Designing realistic warming experiments (Task 8.1)

2.1 Unrealistic air temperatures in warming experiments

2.1.1 Warming experiments in the field with infrared irradiation (UA)

Effects of high leaf-to-air VPD

Infrared heating as a method to simulate climate warming has been applied since the middle of the nineties of the last century (Harte et al. 1995; Nijs et al. 1996). Its main advantages are that it (i) is a method that can be actively controlled, (ii) can be applied in the free air and therefore avoids most artefacts associated with enclosures, (iii) warms both vegetation and soil, and (iv) warms the surface directly, which improves both responsiveness and energy efficiency. While this technique has attracted some criticism, this has until now mainly been restricted to oral objections, with little formal critiques in scientific journals. An exception has been a recent comment of Amthor et al. (2010) to a study by Aronson & McNulty (2009) that compared warming methods. This comment was partly a rightful criticism of the way in which infrared heating was proposed, namely as a method that creates warming similar to that expected under global warming. Since then, the original authors have published an erratum (Aronson & McNulty 2010) in which they support the consensus view that global warming will for the largest part encompass rising air temperatures rather than a drastic increase in infrared irradiation. Another, more relevant part of the criticism of Amthor et al. (2010) was directed towards the **changing vapour pressure differences associated with infrared heating** (caused by higher temperature differences between leaf and air), which tend to increase water loss from

plants and the soil surface (Nijs et al. 1997). A flux is determined by a gradient multiplied by a conductance. For water losses from the leaf, this gradient is the difference in vapour pressure between the leaf's stomatal cavities and the ambient air. If leaves are irradiated by infrared heaters, they will become warmer with little change in air temperature (which is only warmed indirectly). If the air is warmed (naturally or experimentally), then the leaf temperature will also warm, but the temperature difference between leaf and air will change little, although deviations can occur depending on wind, radiation, leaf morphology (size, hairs, etc.) and stomatal conductance (Körner 2003, De Boeck et al. 2011). The problem of altered water loss underneath infrared heater systems was already partly addressed by Kimball in his 2005 study and then again in 2011, in which a first order correction mechanism was proposed, namely adding supplemental irrigation water in amounts calculated to make infrared warming equivalent to air warming at constant relative humidity.

	calculation 1		calculation 2 (heat wave)				calculation 3 (heat wave, drought)			
	IR heaters	warm air	normal	heat wave	IR heaters	warm air	normal	heat wave	IR heaters	warm air
$T_{\text{air}} (^{\circ}\text{C})$	25	29	19.5	27.5	19.5	27.5	19.5	27.5	19.5	27.5
$T_{\text{leaf}} (^{\circ}\text{C})$	30	30	20.5	28.5	28.5	28.5	20.5	33.5	33.5	33.5
RH (%)	70	70	75	62	75	75	75	62	75	75
wind speed (m s^{-1})	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
leaf dimension (m)	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
air pressure (kPa)	101.3	101.3	101.3	101.3	101.3	101.3	101.3	101.3	101.3	101.3
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	0.183	0.258	0.410	0.232	0.165	0.309	0.410	0.015	0.015	0.015
vapour gradient (kPa)	2.00	1.42	0.70	1.60	2.17	1.12	0.70	2.87	3.45	2.40
$g_{b,\text{free}}$ ($\text{mol m}^{-2} \text{s}^{-1}$)	0.172	0.115	0.115	0.115	0.200	0.115	0.115	0.180	0.223	0.180
$g_{b,\text{forced}}$ ($\text{mol m}^{-2} \text{s}^{-1}$)	0.805	0.805	0.805	0.805	0.805	0.805	0.805	0.805	0.805	0.805
g_{free} ($\text{mol m}^{-2} \text{s}^{-1}$)	0.089	0.080	0.090	0.077	0.090	0.084	0.090	0.014	0.014	0.014
g_{forced} ($\text{mol m}^{-2} \text{s}^{-1}$)	0.149	0.195	0.272	0.180	0.137	0.223	0.272	0.015	0.015	0.015
E_{free} ($\text{mmol m}^{-2} \text{s}^{-1}$)	1.755	1.114	0.621	1.213	1.940	0.927	0.621	0.393	0.478	0.327
E_{forced} ($\text{mmol m}^{-2} \text{s}^{-1}$)	2.948	2.731	1.875	2.837	2.943	2.464	1.875	0.418	0.501	0.348

Table 1: *Transpiration rate (E) determined from environmental and plant data (italics) through calculation of total conductance (g) from boundary layer (g_b , calculated) and stomatal (g_s , calculated) conductance (for both free and forced convection) and the gradient for water vapour. Comparison between conditions found underneath infrared heaters (warming leaves but not the air) and air warming while keeping relative humidity (RH) constant.*

A full quantification of how transpiration rates may be affected by infrared heating has yet to made, however. We believe that this is a necessary step to propel the discussion on artefacts potentially associated with infrared heaters forward. We use established physical relationships to quantify these artefacts. Results on the leaf level suggest that the transpiration rate under infrared heaters is indeed increased, but that ‘drying’ artefact in infrared heaters is less of a concern when simulating heat waves and taking into account the prevalent natural conditions (Table 1).

2.1.2 Warming experiments in enclosures (e.g. ecotrons)

Use of weather station data to emulate changing field conditions (IMPERIAL)

Mesocosm and microcosm experiments have a good track record of providing an indication of processes and mechanisms directing ecosystem functioning at much larger scales by eliminating confounding variables and increased statistical power (Benton *et al.* 2007). At present, there are two approaches to setup mesocosm experiments. One is to keep the mesocosms outside and exposed to the natural weather variation while the treatment of interest is applied. The other is to transfer the mesocosms to a controlled environment (greenhouse, growth chamber) and then keep these systems in stable conditions. Both of these approaches have important drawbacks which limit the conclusions that can be drawn, such as, unrealistic climatic conditions in controlled environments and *in situ* differences in environmental conditions. We proposed a novel technical approach that could significantly improve the predictive value of measurements obtained in controlled conditions. The biological processes that drive these systems are greatly affected by the natural variation of climatic conditions. If we are to model these processes, we need to demonstrate that we have a good handle on the relationship between climate and functioning of these systems. In addition, any climate change treatments we impose on such systems need to be realistic and resemble, as close as possible, the situation which we will encounter in the real world in the future.

However, environmental variables in controlled environments such as temperature, day length and precipitation do differ substantially from those in the field, limiting the scope for comparisons between the mesocosms and the field. Now we have the technological capacity to link the climatic and soil conditions observed in the field to those in controlled environment. This would allow us to emulate the field conditions while fully utilizing the experimental and observational advantages of a controlled environment. One of the most important advantages is the possibility of running replicate mesocosms in identical conditions which are directly relevant to field conditions. Further, we could superimpose a climate change (or any other treatment) onto natural weather variation. This approach should yield substantial benefits especially in the case of treatments such as increased temperature or decreased precipitation. Both of these factors are predicted to alter significantly due to climate change (IPCC, 2007), but their application to mesocosm field studies is notoriously difficult to test because of the presence of important artefacts.

For the controlled environment facility at Imperial College (The Ecotron; Lawton 1996) we would need to successfully modify the Trend (Trend Control Systems Ltd., Horsham, UK) control system from the 'pre-programmed' mode which only allows static environmental conditions to the 'responsive' mode. The latter mode allows for a pre-arranged array of data to be automatically uploaded to the Trend outstations and run dynamic and realistic weather patterns. The variables that we aim to realistically simulate are temperature, humidity, light intensity and mesocosms water table. The

Imperial College Ecotron in its present configuration is not equipped to emulate outdoors peak light intensity; however it is able to control and to vary the amount of photosynthetic active radiation (PAR) reaching the mesocosms according to setpoints. To address the light intensity issue and to bring the spectral properties of the light conditions inside the Ecotron closer to natural conditions, we aim to test the latest generation of plasma lighting (Hogewoning *et al.* 2010) in one of the chambers used for the proof-of-concept study.

Simulating other than local climates (potential for decoupling of temperatures from outside conditions) (INRA)

INRA has started an experiment in the CNRS Ecotron of Montpellier in which monoliths of a grassland ecosystem are subjected to a future climate scenario, i.e. warmer, drier and with elevated atmospheric CO₂. The monoliths originate from a grassland of the French Massif Central (site of St Genès Champanelle: SGC, 03°02'44"E, 45°42'51"N, 800m a.s.l) located 360 km north of the Ecotron. Actual climate of SGC is different from that of Montpellier (mean annual temperature MAT = 8.4°C and 15.3°C, respectively). The aim of this experiment is to simulate at Montpellier a future climate of the SGC site for the 2040-2060 period, i.e. warmer (+2°C of annual T), drier (-20% summer rainfall) and +140 µmol mol⁻¹ of CO₂. However, solar radiation is not controlled in the Ecotron facility and is an important driver of air temperature. Thus the difficulty for this experiment is to cool the air temperature to match to values of future climate of SGC, especially in case target air temperature is low and solar radiation is high. The aim is to first analyze air temperature deviation between inside of macrocosm and target value of future climatic scenario, in relation with outside solar radiation, and second to propose improvement of air temperature simulation by taking into account global radiation. This progress report concerns the first aim: analysis of air temperature deviation between inside of macrocosm and target value of future climatic scenario.

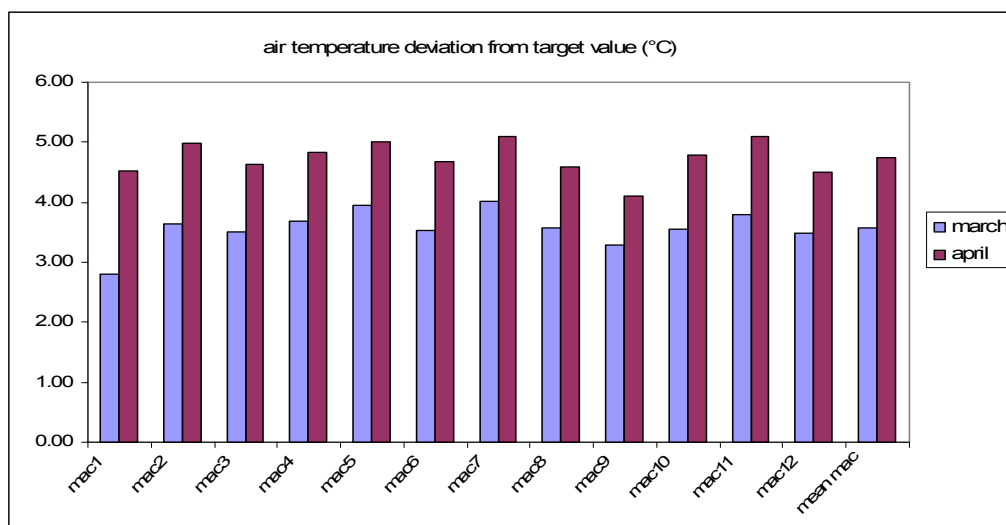


Figure 1: Air temperature deviation from target value (°C, monthly average) for each and for the average of the 12 macrocosms (mac1,..., mac12, mean mac, respectively).

In March and April 2011, air temperature was on average warmer (mean values +3.6 and +4.7°C) than the target value (Fig. 1). This deviation showed a high variability especially during sunny conditions (standard deviation = 3.7 and 3.1°C), as confirmed by the variation coefficient calculated within (0.062) and between (0.653) macrocosms in April.

These first data showed that the cooling system is not able to match the target values of the scenario. One possible way to reduce this artefact is to compensate high temperatures with lower ones for cloudy days, thus both global radiation and temperature should be taken into consideration. A first analysis of climatic data of both sites showed that the slopes of the relationship between air temperature (T) and global radiation (Rg) for the climate of SGC and that of Montpellier are similar:

$$\text{SGC: } T = 0.0054 \times R_g + 1.2926$$

$$\text{Montpellier: } T = 0.0054 \times R_g + 6.8989.$$

We propose the following equation to compensate for temperature deviation (Fig. 2):

$$T_{\text{Montpellier}} = T_{\text{SGC}} + 0.0054 \times (R_{g\text{Montpellier}} - R_{g\text{SGC}}) \quad (1).$$

The next step is to apply such an equation in the software of the Ecotron facility.

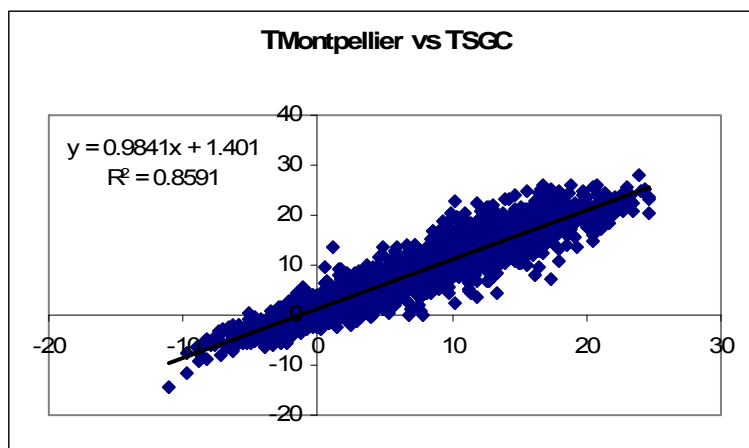


Figure 2: Relationship between Montpellier air temperature calculated from equation 1 and air temperature for SGC site.

2.2 Unrealistic canopy temperatures in warming experiments

2.2.1 Field warming experiments with infrared irradiation (UA)

Control methods for applying infrared irradiation

Despite the apparent growing popularity of infrared heating in ecological research, an issue which is still unresolved, is whether to control for air or for canopy temperature. In most studies, temperature control is based on canopy (surface) temperatures (e.g. Braun *et al.* 2002; Marchand *et al.* 2004; Morin *et al.* 2010). This seems a logical choice, as this is the variable that is directly affected by the applied heating. Moreover, the temperature that ultimately determines metabolic plant processes, is that of the plant itself, not of the air. Indeed, it is well documented that species from both cold and hot ecosystems are morphologically adapted to force the plant

temperatures to be closer to the metabolic optimum, in spite of adverse air temperatures (Larcher 2003). For example, alpine plants often form cushions which increase the effective characteristic dimension (acting as a big leaf) and decreases the wind speed, leading to leaf temperatures substantially above those of the surrounding air. In other studies, however, temperature control is based on air rather than canopy temperatures (e.g. Wan *et al.* 2002; Sherry *et al.* 2008; Mohammed & Tarpley 2009). Dissipation of sensible heat of the canopy under infrared heaters indeed increases air temperatures as well. As both historical records and climate change projections contain only information on air temperatures, and as these sources are commonly the basis for deciding which temperature regime to impose, using this same variable in the experiment seems rational. So, which temperature to control for? The problem is that increases in canopy temperatures are not necessarily equivalent to (natural) rises in air temperatures. A regression between canopy temperatures measured at experimental plots and air temperatures recorded at a nearby meteorological station in the study of Marchand *et al.* (2006), proved significant but showed marked variation (R^2 of 0.21). This is unsurprising as canopy temperatures depend not only on air temperatures, but also on wind speed, canopy conductance, air humidity and the general radiative environment. These variables exert an influence on air temperature as well, but less directly.

Kimball (2005) stressed the sensitivity of canopy temperatures under infrared heaters to the canopy conductance, noting that the power needed to warm the canopy by 1 °C is drastically reduced at night and in water-stressed canopies (i.e. when stomatal conductance is low). Marchand *et al.* (2006) also stated that the reduced soil water contents observed in their heat wave experiment likely reinforced the temperature increment, and that a heating treatment with the same soil moisture as in the ambient plots would therefore experience a less intense heat wave. A schematic based on standard energy balance equations (see equation 1 below), illustrates this (Fig. 3). At the same air temperature, the leaf temperature can differ substantially depending on stomatal behaviour. The fact that the plant water status affects the canopy temperature is problematic, as most infrared heating experiments do not allow for the canopy temperatures to vary freely and therefore the natural plant response is restricted. The problem is not resolved by using air temperatures as the control variable, because the warmer air results from the surface (canopy) warming generated by the infrared heaters. Indeed, the fact that the plant response and the level of warming influence each other under infrared heaters, is an unavoidable consequence of controlling the rate of warming based on a variable that is directly or indirectly a measure of the plants response.

A method where the warming is independent of plant responses is the application of a constant energy flux (e.g. Saleska *et al.* 2002). However, the resulting warming (i) increases temperature variability due to the dependence on fluctuating environmental conditions (mainly air temperature, wind and radiation) (ii) is uncontrolled – no target temperatures can be set. Also, the amount of energy that needs to be applied is unclear, as for example merely adding the extra radiative forcing from climate

projections to simulate a future climate will hardly affect temperatures (Kimball 2005). The use of a constant energy flux therefore seems an inadequate solution for many experiments, especially those testing specific scenarios of average temperature increases or extreme deviations from normal (heat waves). What is needed is an adjustable amount of warming that avoids the artefacts associated with the plant response and does not rely on the uncontrolled constant flux approach. To achieve this, the amount of heat that is added should be independent of plant responses. UA has started to develop such a regulation concept and associated infrared heating prototype (theoretical results see Fig. 3). The concept allows for drought – which is often associated with heat waves – to increase canopy temperature in a realistic way, contrary to approaches that maintain a fixed temperature difference between warmed and reference plots. The system will be described in detail and performance test results will be presented in Deliverable 8.2.

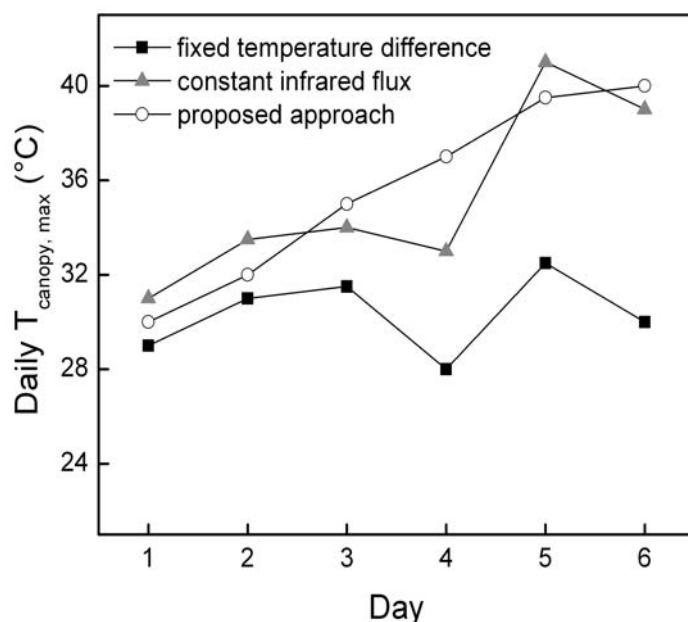


Figure 3: Conceptual comparison of how a heat wave with developing drought imposed by infrared (IR) heating affects canopy temperatures using: (1) a typical control that maintains a fixed difference of canopy or air temperatures between the treatment and the reference plots (black squares); (2) a predefined constant radiative flux emitted by IR heaters (grey triangles); (3) a new theoretical alternative approach that maintains radiative output of infrared heaters independent of plant responses (white circles).

2.2.2 Warming experiments in enclosures (e.g. ecotrons)

Effects of wall temperature and cover material (UA)

In the context of a warming world (IPCC, 2007), the research field studying effects of higher temperatures on plant and ecosystem responses has been steadily gaining ground. Methods of experimental warming are varied, ranging from the exclusive heating of the soil (Bergh & Linder, 1999), growth chambers with an artificial light environment (Swindell *et al.*, 2007), infrared heating of canopy and soil (Marchand *et al.*, 2004), climate-controlled greenhouses (Gielen *et al.*, 2005), to passive warming in open top chambers (Henry & Molau, 1997).

In greenhouses, the radiative environment is different from outside. The temperature of clear skies is often well below 0°C (Nobel, 2005), while the 'sky' inside the greenhouse consists of the cover materials which in most circumstances will be warmer than the outside sky. Sky temperatures determine the downward longwave radiation and therefore directly affect the energy balance and thus canopy temperatures. Other properties of the greenhouse such as the total light transmission and the reflectance of long-wave radiation could also affect the leaf temperatures. In open top chambers, a substantial proportion of the sky is not artificial, while the absence of a roof precludes an isolation of convective heat exchange with the outside (this is the most important warming mechanism in closed chambers). We hypothesize that a (canopy) warming effect would be mainly caused by the important reductions in wind speed inside such open top chambers (OTCs).

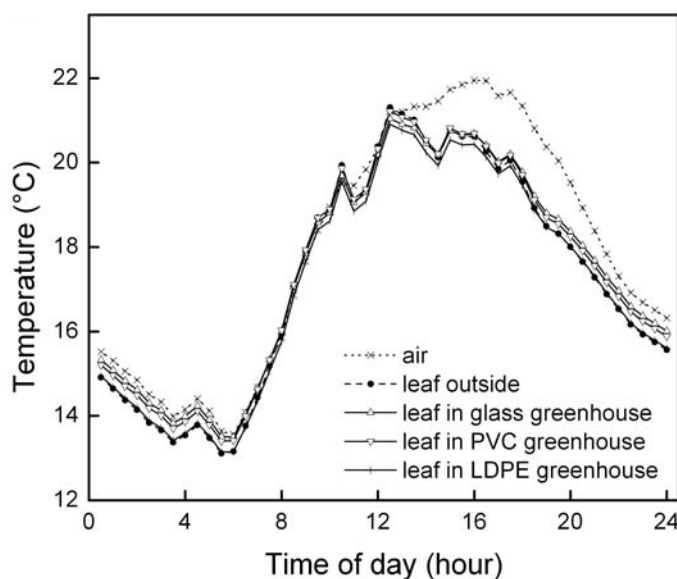


Figure 4: Air and leaf temperatures during an entire summer day, on a bright day. Leaf temperatures outside and inside climate-controlled greenhouses (at outside temperature) were modeled using half-hourly data on shortwave radiation, air temperature, and relative humidity from the Fluxnet site in Brasschaat, Belgium, with wind speed set at 2.9 m s^{-1} , the long term average during summer in Belgium.

No peer-reviewed study has formerly quantified wind speeds inside and outside of passive OTCs such as the standard hexagonal chambers used in the International Tundra Experiment (ITEX), although this subject has been reported upon in a PhD thesis (Dalen, 2004). These measurements show that the wind speeds inside these OTCs were reduced more than 3-fold in a forest and over 8-fold on a mountaintop. Such important reductions in wind speed inevitably have an effect on energy exchange, as the calmer conditions reduce the heat exchange through convection. If greenhouses and passive OTCs do indeed distort leaf temperatures significantly, it would imply that the amount and possibly the variability of true (canopy) heating achieved differs from prior estimates of attained warming. This in turn suggests that extrapolations from greenhouse and OTC studies may have to be reconsidered. In the case of the actively regulated greenhouses, any discrepancies between leaf temperatures inside the greenhouses and outside could be buffered or mitigated by an altered heating control.

Using an energy balance model, we investigate possible effects of two widely used warming methods (greenhouses and passive OTCs) on leaf temperatures. The

model applies standard energy balance formulae, supplemented with data on optical properties of greenhouse materials and wind conditions inside OTCs. Results show that the different radiation environment inside temperature-controlled greenhouses did not produce large leaf temperature deviations compared to outside (Fig. 4). Poor greenhouse design with significant radiation blockage by the structure or with insufficient ventilation did affect tissue temperatures more significantly. The drastic wind speed reduction inside passive OTCs generally doubled the actual (canopy) warming compared to earlier reported increases in air temperature provided by this technique – an effect that was inflated if the plants' stomates closed (Table 2).

Table 2: Comparison of leaf temperatures (T_{leaf}) inside and outside passive Open Top Chambers (OTCs) under varying conditions of air temperature (T_{air}) radiation (R_s), relative humidity (RH), leaf dimension (d), adaxial and abaxial stomatal conductance (g_{vs}), and cloud cover. First and second row for each set of conditions refer to outside and inside OTCs, respectively. Reduction of wind speed inside OTCs is based on data from Dalen (2004).

T_{air} (°C)	R_s (W m ⁻²)	RH	u (m s ⁻¹)	d (m)	$g_{vs,ad}$ (mol m ⁻² s ⁻¹)	$g_{vs,ab}$ (mol m ⁻² s ⁻¹)	cloud cover	T_{leaf} (°C)	ΔT (OTC - out) (°C)
10	750	0.6	1.22	0.02	0.3	0.3	0	12.43	
10	750	0.6	0.19	0.02	0.3	0.3	0	14.92	2.49
5	0	0.6	1.22	0.02	0.05	0.05	0	4.44	
5	0	0.6	0.19	0.02	0.05	0.05	0	3.84	-0.60
10	200	0.6	1.22	0.02	0.3	0.3	1	10.19	
10	200	0.6	0.19	0.02	0.3	0.3	1	10.80	0.61
5	0	0.6	1.22	0.02	0.05	0.05	1	5.30	
5	0	0.6	0.19	0.02	0.05	0.05	1	5.65	0.35
10	750	0.6	1.22	0.02	0.05	0.05	0	13.85	
10	750	0.6	0.19	0.02	0.05	0.05	0	17.75	3.90
10	750	0.6	1.22	0.02	0.3	0.3	0	12.43	
11.5	750	0.6	0.19	0.02	0.3	0.3	0	16.03	3.59
10	750	0.6	1.22	0.02	0.05	0.05	0	13.85	
11.5	750	0.6	0.19	0.02	0.05	0.05	0	18.96	5.11
10	750	0.9	1.22	0.02	0.3	0.3	0	13.31	
10	750	0.9	0.19	0.02	0.3	0.3	0	16.19	2.87
5	0	0.9	1.22	0.02	0.05	0.05	0	4.67	
5	0	0.9	0.19	0.02	0.05	0.05	0	4.31	-0.36
10	750	0.6	1.22	0.005	0.3	0.3	0	11.35	
10	750	0.6	0.19	0.005	0.3	0.3	0	12.94	1.59
5	0	0.6	1.22	0.005	0.05	0.05	0	4.69	
5	0	0.6	0.19	0.005	0.05	0.05	0	4.31	-0.38

2.3 Unrealistic biosphere-atmosphere exchange in monoliths

2.3.1 Artefacts from excavating, translocating and re-installing large soil cores on soil biosphere-atmosphere exchange (KIT)

Temperatures in soil cores vs. natural soils. In the framework of the German Helmholtz Association funded infrastructure project TERENO (*TER*restrial *E*nvironmental Observatories), KIT is running the (Pre-) Alpine Observatory covering several research sites in the Ammer catchment, South-Bavaria, Germany. TERENO was designed to study long term effects of climate change on terrestrial ecosystems. For this purpose KIT has installed 36 lysimeters with undisturbed intact grassland soil cores (diameter approx. 1 m, depth 1.4 m) and is operating them at three sites (Graswang, Rottenbuch, Fendt). Lysimeters were partly moved along an altitudinal gradient, with some soil cores remaining at the original sites as controls. In consequence, lysimeters with intact soil cores from higher elevation were translocated to sites at lower elevation with higher temperatures ($\delta 1.5^{\circ}\text{C}$ Graswang-Rottenbuch and $\delta 3.2^{\circ}\text{C}$ Graswang-Fendt) and slightly lower annual rainfall (Fig. 5).

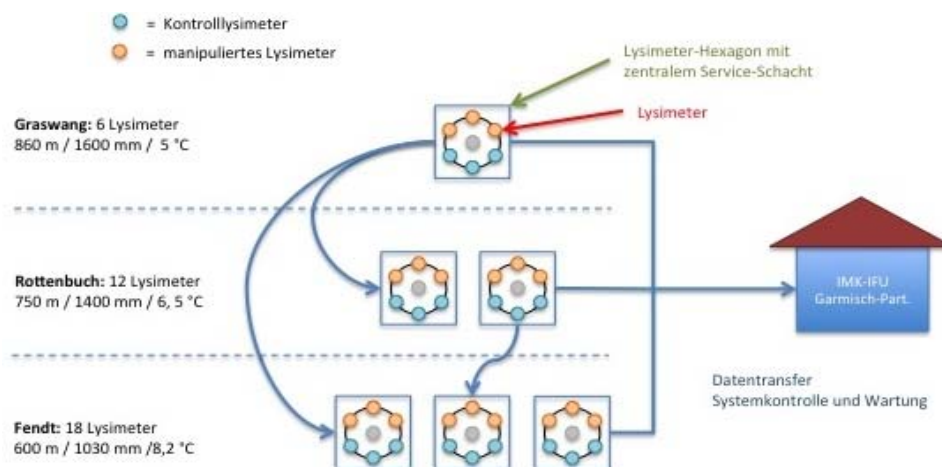


Figure 5: Climate change lysimeter setup of KIT in the frame of the TERENO (Pre-) Alpine Observatory

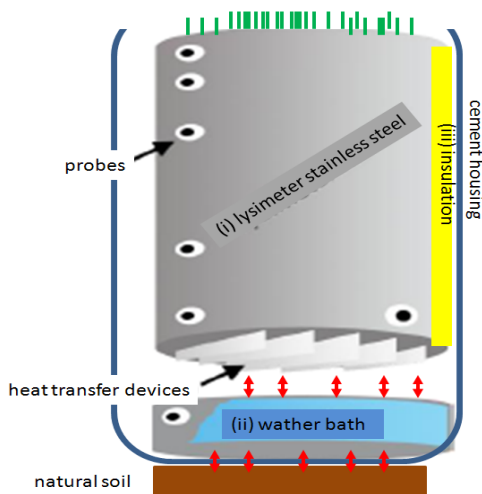


Figure 6: Lysimeter setup in 3 different designs: (i), (ii) and (iii)

Main research interest of this in-situ climate change experiment is to detect impacts of changes in climate on grassland soil hydrology, C and N turnover and associated losses in gaseous and liquid form as well as biodiversity. Since September 2011, KIT is operating 36 lysimeters arranged in hexagons with a central service unit storing data loggers and other

steering and sampling devices (6 in Graswang, 12 in Rottenbuch and 18 in Fendt, see Fig. 5) The lysimeters have an area of 1m² and a weight of about 3t, which varies due to changes of soil water content.

One of the main problems while using lysimeters for climate change studies is that the soil cores are taken out from the field, thereby cutting the soil at the base and at the sides. In consequence, boundary conditions, in particular with regard to soil water and temperature exchange, are disturbed, most severely with regard to the lower boundary condition. In recent years introducing of suction cups steered by the water tension delivered from reference tensiometers in undisturbed soil helped to significantly improve the lower boundary condition for soil water contents and percolation. However, this does not apply if soil cores are removed from their place of origin. If soil texture and soil hydraulic significantly differ from the original place a modeling approach is needed. In contrast to soil moisture, differences of the temperature profile within lysimeter soil and natural conditions have not been in the centre of discussion so far, though some studies have tackled the problem (e.g. Todd et al., 2000; Evett et al., 1995). I.e. potential effects of temperature changes due to the transfer of intact soil cores in lysimeters have largely been neglected and not sufficiently addressed in designing lysimeters. However, in the frame of a climate change study, this is of particular interest, since soil C and N turnover processes are largely governed by temperature. For that reason KIT installed a detailed field pre-experiment which aimed at the comparison of soil temperatures in lysimeters as compared to those in soils under natural conditions. The experiment was installed in April 2010, also as a contribution to EXPEER, and soil temperatures were monitored

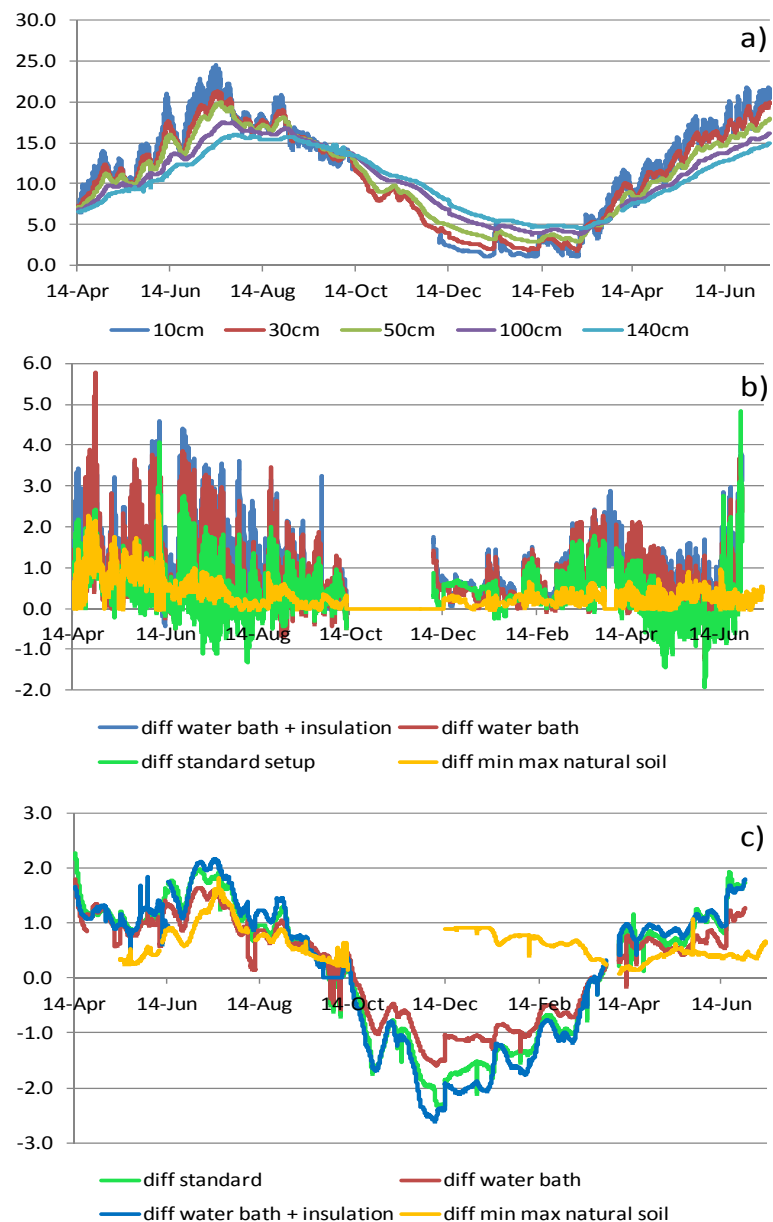


Figure 7: Temperature evolution in the natural soil profile (a) and temperature differences of lysimeters vs. natural soil (b 10cm; c 140cm)

over a 14-month period lasting until June 2011. Thereby three different types of lysimeter designs were tested: i) standard stainless steel lysimeter, (ii) stainless steel lysimeter with a new, innovative heat transfer device, consisting of metal plates dipping in a water bath which is in direct contact with the underlying soil, (iii) stainless steel lysimeter with heat transfer devices, water bath and insulation (Fig. 6). Each lysimeter design was set up in 3 replicates, i.e. we used 9 lysimeters in total for this experiment. All lysimeters and in addition three natural soil profiles were equipped with temperature sensors at 10, 30, 50, 100, and 140cm soil depth.

Evolution of the temperature (hourly time step) at different soil depths of the natural soil profile is shown in Fig 7a. Temperature variation as well as the temperature amplitude is highest in the upper soil layers, with maximum soil temperature of up to 25°C. From October to March the soil temperature profile is inverted, i.e. deeper soil temperature sensors showed higher temperatures compared to those installed in the upper soil layers. In winter minimum temperature at 10cm is close to 0°C and temperature at 140cm soil depth never dropped below 5°C. Figure 7 also shows differences in temperature of the 3 lysimeter designs (standard, water bath and water bath + insulation, n=3 each) compared to the mean soil temperature of the natural soil for 10 and 140cm soil depth. Values are compared to the maximum difference in temperature across the 3 natural soil profile measurements which were mostly <1°C (yellow line). For 10cm soil depths temperature amplitude observed in soil cores of all 3 lysimeter designs were higher as compared to those of the natural soil. Differences were highest in summer, when soil temperatures at 10 cm soil depth of the lysimeters were up to 4°C warmer as compared to the directly adjacent soil. Soil temperature differences between natural and lysimeter soil were lowest in winter (0.5-1°C). Independent from the lysimeter design temperatures were always higher than in the natural soil with differences increasing from standard < water bath < water bath + insulation. The higher temperatures in the top soil of the lysimeters are a result of heating up the stainless steel frame (about 5cm higher than the vegetation surface) by solar radiation. However, heat flow might not be the only reason since reflection of radiation could also play an important role for warming. This hypothesis is supported by the fact that there was only little difference between the summer months in 2010 and 2011, though lysimeter frames were covered by white tape in spring 2011. With increasing distance from the lysimeter frame the warming effect decreases and in the centre of the lysimeter (56cm from the lysimeter frame) temperature did not differ significantly from the natural soil (data not shown). Temperature differences at 140cm (lower boundary condition) were with max. +/- 2°C much smaller compared to 10cm soil depth and did differ less from the maximum difference of the 3 measurements in the natural soil profile at the same depth. In contrast to the upper condition the lysimeter design had a significant influence on the temperature evolution. Best results, i.e. smallest temperature deviations of soil lysimeters temperatures at 140 cm depth from those of adjacent undisturbed soils, were obtained with the design of a water bath only. Water bath + insulation and standard lysimeters showed nearly the same high temperature differences from the natural soil. Taking into account the

higher heat input of the insulated lysimeter (most likely due to reduced cooling at night time) also here the water bath revealed to have a positive impact.

In conclusion, the introduction of water baths significantly improved the heat flow at the lower boundary condition of the lysimeters; insulation of lysimeter side walls did not prove to be successful to reduce temperature differences compared to adjacent natural soils. However, observed temperature increases of up to 3-5°C in the upper 10 cm due to introducing soil cores in lysimeters still reveal a major problem of energy fluxes in lysimeters at the upper boundary condition. KIT continues the temperature experiment with any of the 36 grassland lysimeters all of them equipped with water baths and heat transfer devices. We will test further insulation and cover options for reducing heating of the top soil and enhanced heat flow in the lysimeters compared to natural soil conditions.

3 Using Computational Fluid Dynamics (CFD) to design CO₂ enrichment technologies (Task T8.2)

Spatial scale of FACE systems: problem analysis (CNR)

Climate change is driven mainly by the recent increase in the atmospheric concentrations of anthropogenic greenhouse gases, but CO₂ also causes direct responses of plants. Most of our food comes from managed ecosystems and there is an urgent need to assess if food production will be sustained under future climate change scenarios and if the increasing demand will be finally met to nourish the nine billions of people that are expected to live on this planet by 40-50 years from now. This is the main reason why the response of agricultural land systems and terrestrial ecosystems to future atmospheric CO₂ concentrations requires careful and reliable predictions based on the best technology available to reproduce today the environmental conditions that the plants will experience tomorrow. Free Air Carbon dioxide Enrichment (FACE) facilities offer indeed such an opportunity. FACE are large open-air experiments, in which the atmospheric CO₂ concentration is locally elevated to the levels expected in the future. Fig. 8 gives a practical example of the limitation of a conventional FACE design for testing combinations with other factors. Plot size is often critical, reducing the number of species that can be studied. The relative position of each sub-plot within the study



Figure 8: An aerial view of the BIOCON FACE experiment in Minnesota. Several plant species and micro-cosms were arranged within the CO₂ fumigation area in sub-plots.

area is also problematic especially when replicates are considered. More details on the BIOCON experiment displayed in Fig. 8 can be found at <http://www.biocon.umn.edu/>

To identify possible improvement in FACE technology, we must at first identify what the requirements of a new generation of research infrastructures must provide, with specific reference to elevated CO₂ science:

- FACE systems must be accessible to interdisciplinary teams of scientists, including plant physiology, crop science, ecology, soil chemistry, hydrology, plant-microbe interactions and soil microbiology, microclimatology, and plant and ecosystem modeling. The design must ensure that they can address the most pressing scientific goals;
- The opportunity to test interactions of elevated CO₂ with nutrient supply, climatic variables such as temperature and water or gaseous pollutants must be ensured.

A recent workshop, “FACEing the future: planning the next generation of elevated CO₂ experiments on crops and ecosystems” financed by the European Science Foundation (ESF) promoted a dialogue between engineers and scientists who have been involved in research on how plants respond to elevated CO₂, and a wider circle of plant scientists, ecosystem researchers and modelers. The main questions to be tackled in the future were discussed, also to assess weaknesses and limitations of the current FACE designs.

It can be emphasized that current FACE facilities are not entirely adequate to meet the challenge posed by the need of predicting and understanding the response of crop plants and natural ecosystems to elevated CO₂. In particular, the type of technology adopted so far has not been used to explore whether genetic diversity affects the response of plants to elevated CO₂ which is known to have the potential to lead to increased crop productivity. This type of studies will require testing and examining the responses of a high number of cultivars (>100 sometimes) and each sub-plot will require some minimum space for sampling and growth analysis. This poses another challenge to the current FACE designs: sub-plots (and thus genotypes) located next to the releasing pipes may occasionally experience higher concentrations than those located in the centre of the FACE area where the concentrations are generally more uniform.

The existing FACE designs are also problematic when interactions between elevated CO₂ and other environmental drivers have to be studied. This type of interactive response is required by the models to finally predict the responses of managed and natural ecosystems, including short-rotation forestry systems. The availability of space is again a limitation, and the unavoidable contiguity that exists within a CO₂ fumigated space in conventional designs, is also problematic in interaction studies. For instance, if warming is to be applied concurrently with FACE, this can hardly be made in sub-areas within the same FACE ring without interfering with non-treated sub-areas.

Nowadays, the majority of FACE systems release CO₂ from a series of pipes or tubes located in rings or octagones around the experimental area. Control algorithms (mostly PID, Proportional-Integral-Differential) are used to adjust the flow of CO₂ on the basis of the wind direction/speed and CO₂ concentration measurements that are made inside the ring, above and around the vegetation. The current designs are typically 8-25 m in diameter but there is no inherent advantage to building much larger rings. The efficiency of gas use would in fact unavoidably decrease, and the control of temporal and spatial target concentrations could be lost, beyond a certain ring/octagone diameter.

New studies and new solutions are therefore urgently needed to tackle the changes in the scientific questions that will be examined in the future (applied genomic studies) and to provide alternative solutions for interactive studies. This is indeed one of the major challenges for a scientific infrastructure that has the ambition to provide unique and state-of-the-art services to the scientific community. The EXPEER work plan explicitly considers this issue and intends to overcome the current weaknesses and limitations of FACE systems by exploring new technological solutions.

4 Designing new approaches for experimental ecosystems (Task T8.3)

4.1 Lack of reproducible model systems in ecosystem science

The lack of reproducible model systems in ecosystem science is obvious in the sense that it limits intercomparison of studies with different associations of species, and is consequently not addressed in this report on weaknesses and limitations of current techniques. It will be addressed, however, in deliverable D8.2 (month 24) on solutions for these weaknesses. In D8.2, possible features of new types of model ecosystems in ecology will be proposed.

4.2 Miniaturised analogues/physical models of larger scale systems

Designing analogue/physical models of the carbon cycle and problems related to incorporating an artificial ocean (IMPERIAL)

Currently, computer-based simulations of the Earth system (Earth system models) are the only available tool to estimate the global impact of biotic feedbacks on future atmospheric CO₂ and temperatures. In most areas of science and technology, at some point, use has been made of analogue (physical) models to force progress (Frigg and Hartmann 2006). For example, the wind tunnel was and still is an essential tool in aeronautical and structural design despite extremely complex and well-tested computer simulations. When dealing with complex systems, an analogue is frequently constructed at an early stage. We believe that in the scientific dash to

provide climate change predictions this initial step of potential importance has been omitted. For example, an analogue model of the carbon cycle could provide an alternative and independent tool capable of assessing the impacts of future CO₂ concentrations and temperatures on biotic C feedback. Established in materially closed, energetically open systems (just as the Earth), we argue that such physical/analogue models of the C cycle are well suited to model biotic C feedbacks (Milcu et al. 2011). This is due to two essential features: i) ability to continuously and simultaneously allow the two-way feedbacks between the biotic and abiotic components to take place and ii) ability to perform detailed mass balance analyses.

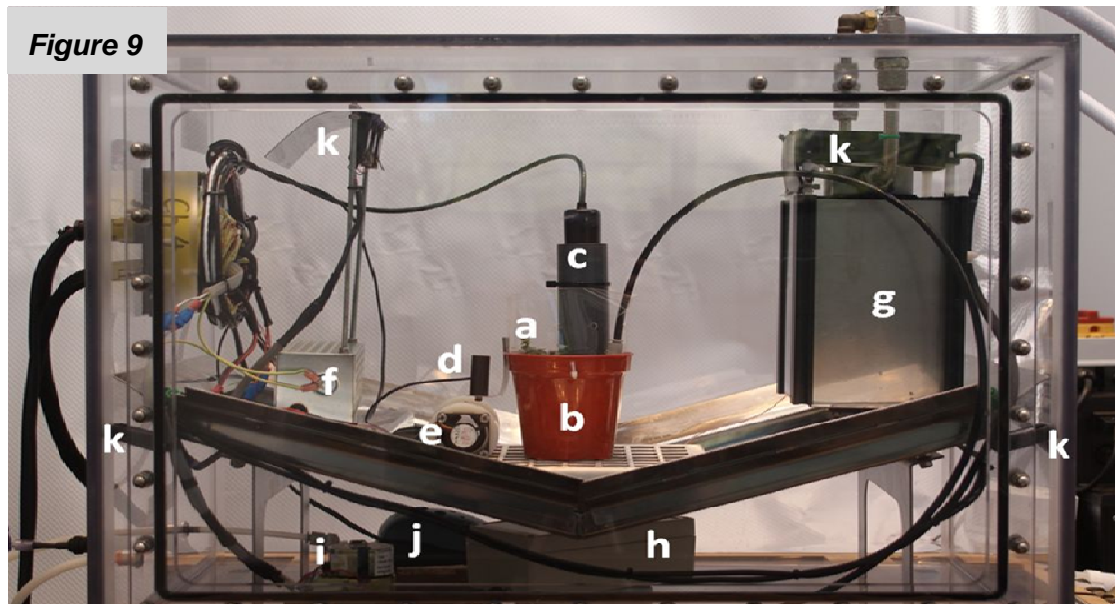


Figure 9
Side elevation of a materially closed chamber (MCC): (a) plant, (b) pot containing carbon free sand and soil, (c) soil moisture probe, (d) light (PAR) sensor, (e) pressure and temperature sensors, (f) heater, (g) cooler, (h) water reservoir, (i) peristaltic irrigation pump, (j) air pump, (k) air fans.

Using this alternative approach we recently showed that it is possible to setup analogue models of the terrestrial carbon cycle (Lukac et al. 2011 and Milcu et al. 2011). We represented a simple terrestrial only analogue model of the pre-industrial C cycle with total volume of ~120 L which could represent (pro rata) the 2011 GtC in soil, 900 GtC in vegetation and 560 GtC in the pre-industrial atmosphere by adding e.g. 2.85 g of dry arable soil (2.13% C), 0.53 g with 0.528 g FW (14% DW) plant biomass and adjusting the atmospheric CO₂ at 280 ppm (Fig. 9). We found that the atmospheric CO₂ concentration tends to stabilise (i.e. weekly slope of CO₂ concentration was not different from zero) near the preindustrial atmospheric CO₂ concentrations within a couple of weeks post-closure (Fig. 10). Using this approach we simulated different CO₂ emission scenarios and estimated the biotic C feedbacks (Milcu et al. 2011 – under review in Nature Climate Change).

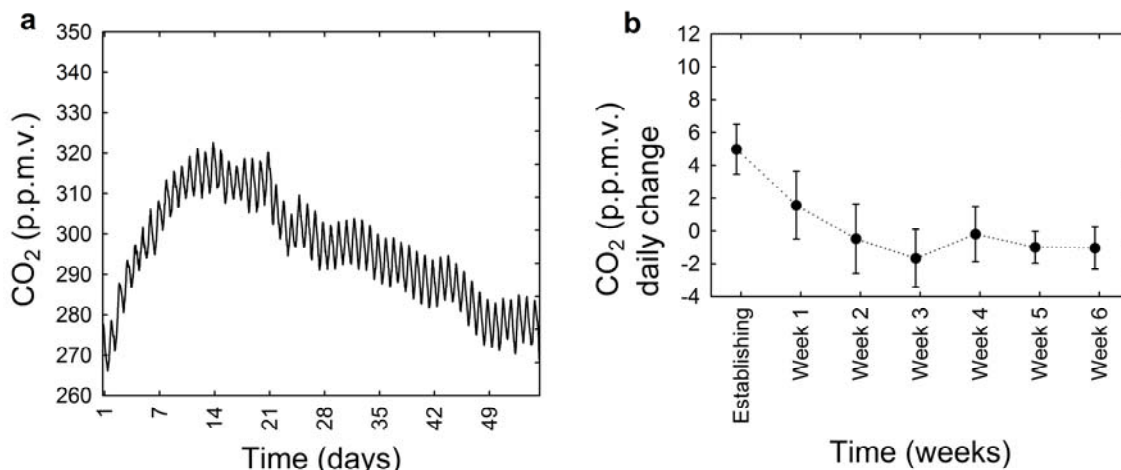


Figure 10: Average atmospheric CO₂ concentrations trends (a) and daily rate of CO₂ change (b) in analogue models of the terrestrial carbon cycle; $n=5$.

The next logical step is to link the terrestrial analogue to an artificial ocean which will capture the physico-chemical properties of the ocean (e.g. CO₂ uptake and release driven by the chemical equilibrium $\text{CO}_2 + \text{H}_2\text{O} \leftrightarrow \text{H}_2\text{CO}_3$). As this hasn't been done before, we think that is sensible to start with a sterile aquatic compartment and not introduce another level of biological complexity (i.e. without aquatic primary producers). Challenges of linking an artificial ocean to the terrestrial analogue of the C cycle are: (i) produce artificial sea water with the right alkalinity and chemical composition, (ii) achieving and maintaining a sterile aquatic compartment and (iii) ensuring that surplus CO₂ dissolved in the artificial seawater is degassed before linking the aquatic compartment to the terrestrial one

5 New generation biodiversity/climate change experiments (Task T8.4)

Limitations of existing methods in ecosystem functioning and biodiversity research (UP, IMPERIAL, UFZ, UA)

The relationship between biodiversity and ecosystem function (BD-EF) has been intensively studied over the past few decades. Despite the emerging consensus that more biodiversity is often found to enhance ecosystem functioning and services, the relationships revealed in many detailed studies are complicated, context-specific and hard to generalise. Below we discuss methodological limitations and artefacts associated with biodiversity-ecosystem functioning research.

Most biodiversity experiments to date have been relatively short-term and in fact much of the early criticism of biodiversity experiments suggested that their findings might be an artifact of studying transient dynamics. It is now becoming clear, from studies that have been run for longer periods, that diversity effects increase in

strength with time, in particular complementarity effects become more important over time (Cardinale et al. 2007), in addition a couple of recent analyses have shown that more species are required to maintain function across a larger number of years (Isbell et al. 2011; Allan et al. 2011). This shortcoming of studying short-term processes is therefore being addressed as experiments keep running for longer; however recent results underline the importance of continuing diversity experiments and running them for decades not years, as different patterns may emerge over the long-term. Such studies are particularly required for forests, as our knowledge on the BD-EF relationship is still dominated by studies on grasslands and aquatic systems (Cardinale et al. 2006). In addition to small temporal scale, biodiversity experiments are normally conducted at a small spatial scale. Although the justification for the importance of studying biodiversity effects on ecosystem functioning usually makes reference to global declines in biodiversity or species extinctions, almost all biodiversity-ecosystem functioning studies actually examine diversity losses at the local scale, and in systems that are fairly homogenous. However, biodiversity might be more important for the maintenance of function in more heterogeneous environments (Tylianakis et al. 2008) or across landscapes, if there is spatial turnover in the species driving function, meaning that the focus on studying biodiversity at small scales in homogenous conditions could also underestimate its importance for functioning. More scaling up of biodiversity studies from the local to the landscape scale is therefore necessary to address this shortcoming. Moreover, more biodiversity experiments should include explicit manipulations of spatial or temporal environmental heterogeneity.

Land use change is the major driver of biodiversity loss and also has direct effects on ecosystem functioning. Therefore in order to predict what negative effects loss of species will have on ecosystem functioning, it is important to understand the relative importance of these direct and indirect land use effects (Manning et al. 2006). Studies carried out in differently managed systems could aid substantially in disentangling these processes. More studies should manipulate diversity in natural or semi-natural systems to estimate the relative importance of biodiversity effects compared with other drivers (e.g. Stein et al. 2008).

The vast majority of biodiversity experiments manipulated plant diversity. However, diversity effects on ecosystem functioning may also be due to microorganismal or faunal diversity of different guilds, including pollinators, herbivores, carnivores, parasites, parasitoids, mycorrhizal or pathogenic fungi, soil pathogens such as nematodes and many more. Experiments addressing the diversity effects of non-plant groups and interactions between diversity effects of different groups are likely to be very important in nature, but, despite early attention (Naeem et al. 1994; van der Heijden et al. 1998) have hardly been addressed. Ecologists have traditionally portrayed soil biota as a black box of “decomposers”, essentially a highly functionally redundant trophic level through which all aboveground material is recycled. There is now mounting evidence that soil communities are every bit as complex and diverse as those aboveground. Furthermore, it is increasingly becoming apparent that biotic

drivers such as soil pathogens may be equally important (Maron *et al.* 2010; Schnitzer *et al.* 2011). Biodiversity research needs to focus more on understanding the relative importance of different mechanisms and more manipulative experiments, such as spraying pesticides or fungicides or adding limiting nutrients, carried out within biodiversity experiments, are necessary to achieve this.

Recent studies have also shown that alongside losing species, the loss of intraspecific genetic diversity (GD) within populations (Crutsinger *et al.* 2006; Bailey *et al.* 2009) has extended detrimental effects on ecosystem functioning and services. The few studies that investigated the impact of GD on ecosystems processes suggest that it plays a role analogous to species diversity (SD) and that it may play a larger role in community and ecosystem processes than previously realised (Reusch *et al.* 2005; Crutsinger *et al.* 2006).

There is also evidence that the loss of functional diversity (FD), the extent of morphological, anatomical, physiological, biochemical and phenological characteristics of plants species in a community, is an important determinant of ecosystem processes (Petchey & Gaston 2002; Cadotte *et al.* 2009). The rationale behind this is that communities consisting of species assemblages with more diverse functional traits are assumed to access more of the total resources and allow multiple competing species to coexist (Cadotte *et al.* 2009). However, whether to account for intraspecific trait variability when measuring FD remains one of the main current debates (Albert *et al.* 2011).

Understanding the relative contribution and potential interactions of SD, GD and FD to ecosystem performance, resilience and stability has been identified as a major knowledge gap (Hersch-Green *et al.* 2011) that we need to address if we are to devise effective conservation/restoration strategies aiming to simultaneously maximise biodiversity and ecosystem functioning (Hersch-Green *et al.* 2011). Experimental work which simultaneously manipulates SD, GD and FD in a factorial approach, and which could provide important information on their relative importance, is currently lacking. Another shortcoming of biodiversity–ecosystem functioning experiments with artificially assembled communities is the fact that they usually simulate random extinctions of taxa. However, in nature, extinctions are often aggregated within phylogenetically related taxa which share certain particular traits.

A major scientific challenge of the next years is to assess the impact of global environmental change on biodiversity and ecosystems and on the services they provide. The increasing atmospheric carbon dioxide concentration and the subsequent climatic change, as well as the accelerated land use change are main components of global change. Besides empirical studies and modelling approaches, manipulative field experiments are urgently needed to enlighten and quantify processes, deduce indicators and develop strategies for sustainable land use and the management of biodiversity. In this context, several field experiments have been conducted during previous years, but most of them have focused on single factors such as decline of biodiversity (Cedar Creek Experiment, USA; Jena Experiment,

Germany), increase of CO₂ (a total of 15 large FACE experiments worldwide), or change in temperature and precipitation (Jasper Ridge Experiment, and WARM Project, USA). A great scientific task that remains unexplored is to forecast the combined effects of these factors, which could be profoundly different from the sum of single effects.

Experimental approaches such as the one proposed by the Helmholtz Centre for Environmental Research – UFZ could address some of these challenges (Figs. 11, 12). The approach includes a large experimental facility that will enable scientists to assess the combined impact of climate change and land use change on biodiversity and on the functioning and services of ecosystems. This “Global Change Experimental Facility” (GCEF) is still in the establishment phase; it will constitute a big infrastructure facilitating integration of research among different research groups within Germany and Europe and will build capacity in the field of biodiversity and global change research. The GCEF will comprise the technical infrastructure for field experiments to simulate:

- (1) scenarios of climate change (including extreme events) versus ambient climate considering (i) precipitation regimes and (ii) temperature regimes;
- (2) scenarios of land use, ranging from agricultural crops for biomass production to (semi-)natural vegetation such as extensive grasslands or successional communities.

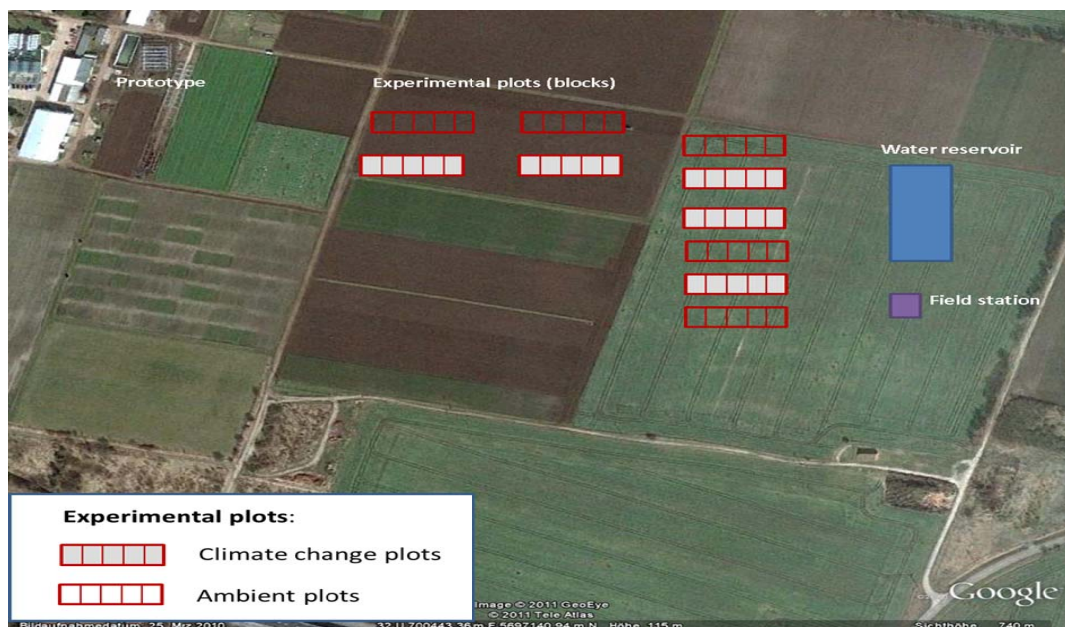


Figure 11: GCEF – Design and field site in Bad Lauchstädt. Principle design: Climate change plots (with roofs) and ambient climate plots (without roofs).



Figure 12: GCEF: prototype of a single roof.

6 References

- Albert, C. H., F. de Bello, I. Boulangeat, G. Pellet, S. Lavorel, and W. Thuiller. 2011. On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* doi: 10.1111/j.1600-0706.2011.19672.x.
- Allan E., Weisser W., Weigelt A., Roscher C., Fischer M. & Hillebrand H. (2011). More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences*, **108**, 17034-17039.
- Amthor J.S., Hanson P.J., Norby R.J. & Wullschleger S.D. (2010). A comment on “Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality” by Aronson and McNulty. *Agricultural and Forest Meteorology*, **150**, 497-498.
- Aronson E.L. & McNulty S.G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, **149**, 1791-1799.
- Aronson E.L. & McNulty S.G. (2010). Reply to comment on “Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality” by Aronson and McNulty. *Agricultural and Forest Meteorology*, **150**, 499-500.
- Bailey, J. K., J. A. Schweitzer, F. Úbeda, J. Koricheva, C. J. LeRoy, M. D. Madritch, B. J. Rehill, R. K. Bangert, D. G. Fischer, and G. J. Allan. 2009. From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1607.
- Balvanera P., Pfisterer A.B., Buchmann N., He J.S., Nakashizuka T., Raffaelli D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology letters*, **9**, 1146-1156.
- Bergh J. & Linder S. (1999). Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. *Global Change Biology*, **5**, 245-253.
- Braun, V., Buchner, O. & Neuner, G. (2002) Thermotolerance of photosystem 2 of three alpine plant species under field conditions. *Photosynthetica*, **40**, 587-595.
- Cadotte, M., J. Cavender-Bares, D. Tilman, and T. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PloS One* **4**, 843-845.
- Cardinale B.J., Srivastava D.S., Duffy J.E., Wright J.P., Downing A.L., Sankaran M. & Jouseau C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989-992.
- Cardinale B.J., Wright J.P., Cadotte M.W., Carroll I.T., Hector A., Srivastava D.S., Loreau M. & Weis J.J. (2007). Impacts of plant diversity on biomass production increase through time

because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123.

Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, **313**, 966.

Dalen L. (2004). Dynamics of mountain birch treelines in the Scandes mountain chain, and effects of climate warming. Unpublished Doctoral Thesis, NTU, Trondheim, Norway.

De Boeck H.J., Dreesen F.E., Janssens I.A. & Nijs, I. (2011). Whole-system responses of experimental plant communities to climate extremes imposed in different seasons, *New Phytologist*, **189**, 806-817.

Evetts S.R., Warrick A.W., Mathias A.D. (1995). Wall material and capping effects on microlysimeter temperatures and evaporation. *Soil Sci. Soc. Amer. J.*, **2**, 329-336.

Frigg R, Hartmann S (2006) Models in science. Stanford Encyclopedia of Philosophy.

Gielen B., De Boeck H.J., Lemmens C.M.H.M., Valcke R., Nijs I. & Ceulemans R. (2005). Grassland species will not necessarily benefit from future elevated air temperatures: a chlorophyll fluorescence approach to study autumn physiology. *Physiologia Plantarum*, **125**, 52-63.

Harte J., Torn M.S., Chang F.R., Feifarek B., Kinzig A.P., Shaw R. & Shen K. (1995) Global warming and soil microclimate – results from a meadow-warming experiment. *Ecological Applications*, **5**, 132-150.

Hersch-Green, E. I., N. E. Turley, and M. T. J. Johnson. 2011. Community genetics: what have we accomplished and where should we be going? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 1453.

Hogewoning, S. W., P. Douwstra, G. Trouwborst, W. Van Ieperen, and J. Harbinson. 2010. An artificial solar spectrum substantially alters plant development compared with usual climate room irradiance spectra. *Journal of Experimental Botany*, **61**, 1267.

IPCC. (2007). Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M. & Miller H.L., eds. Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge, UK & New York, NY, USA: Cambridge University Press.

Isbell F., Calcagno V., Hector A., Connolly J., Harpole W.S., Reich P.B., Scherer-Lorenzen M., Schmid B., Tilman D. & van Ruijven J. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199-202.

Kahmen, A., Perner, J. and Buchmann, N.: Diversity-dependent productivity in semi-natural grasslands following climate perturbations, *Funct. Ecol.*, **19**, 594-601, 2005.

Kimball B.A. (2005) Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, **11**, 2041-2056.

Kimball, B.A. (2005) Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, **11**, 2041-2056.

Kimball, B.A. (2011) Comment on the comment by Amthor et al. on "Appropriate experimental ecosystem warming methods" by Aronson and McNulty. *Agricultural and Forest Meteorology*, **151**, 420-424.

Körner, C. (2003) Alpine plant life, 2nd edn. Springer, Berlin.

Larcher, W. (2003) *Physiological plant ecology*, 4th edition. Springer-Verlag, Berlin, Germany.

Lawton, J. H. 1996. The Ecotron facility at Silwood Park: The value of "big bottle" experiments. *Ecology*, **77**, 665-669.

- Lukac, M., A. Milcu, D. Wildman, R. Anderson, T. Sloan, and P. Ineson. 2011. Non intrusive monitoring of atmospheric CO₂ in analogue models of terrestrial carbon cycle. *Methods in Ecology and Evolution*, **2**, 103-109.
- Manning P., Newington J.E., Robson H.R., Saunders M., Eggers T., Bradford M.A., Bardgett R.D., Bonkowski M., Ellis R.J. & Gange A.C. (2006). Decoupling the direct and indirect effects of nitrogen deposition on ecosystem function. *Ecology Letters*, **9**, 1015-1024.
- Marchand F.L., Nijs I., De Boeck H.J., Kockelbergh F., Mertens S. & Beyens L. (2004). Increased turnover but little change in the carbon balance of High-Arctic tundra exposed to whole growing season warming. *Arctic Antarctic and Alpine research*, **36**, 298-307.
- Marchand F.L., Nijs I., De Boeck H.J., Kockelbergh F., Mertens S. & Beyens L. (2004) Increased turnover but little change in the carbon balance of High-Arctic tundra exposed to whole growing season warming. *Arctic Antarctic and Alpine research*, **36**, 298-307.
- Maron J.L., Marler M., Klironomos J.N. & Cleveland C.C. (2011). Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecology Letters*., **14**, 36–41.
- Milcu, A., M. Lukac, and P. Ineson. 2011. The role of closed ecological systems in carbon cycle modelling. *Climatic Change*, doi: 10.1007/s10584-011-0234-2
- Mohammed A.R. & Tarpley L. (2009) Instrumentation enabling study of plant physiological response to elevated night temperature. *Plant Methods*, **5**, 7.
- Molau U. & Shaver G.R. (1997). Controls on seed production and seed germinability in *Eriophorum vaginatum*. *Global Change Biology*, **3**, 80-88.
- Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010) Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist*, **186**, 900-910.
- Marcel G.A., van der H., Klironomos J.N., Ursic M., Moutoglis P., Streitwolf-Engels R., Boller T., Wiemken A. & Sanders I.R. (1998). Mycorrhizal fungal diversity determinates plant biodiversity, ecosystem variability and productivity. *Nature*., **396**, 69-72.
- Naeem S., Thompson L.J., Lawler S.P., Lawton J.H. & Woodfin R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-737.
- Nijsl., Ferris R., Blum H., HendreyG. & Impensl. (1997) Climate-warming effects on transpiration: a field study using free air temperature increase (FATI) and free air CO₂ enrichment (FACE). *Plant, Cell and Environment*, **20**, 1041-1050.
- Nijs I., Kockelbergh F., Teughels H., Blum H., HendreyG. & Impensl. (1996) Free air temperature increase (FATI): A new tool to study global warming effects on plants in the field. *Plant, Cell and Environment*, **19**, 495-502.
- Nobel P.S. (2005). Physicochemical and environmental plant physiology, third edition. Burlington, USA, Elsevier Academic Press.
- Petchey, O. L. and K. J. Gaston. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402-411.
- Reusch, T. B. H., A. Ehlers, A. Hämmerli, and B. Worm. (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 2826.
- Saleska, S.R., Shaw, R.M., Fischer, M.L., Dunne, J.A., Still, C.J., Holman, M.L. & Harte, J. (2002) Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. *Global Biochemical Cycles*, **16**, 1055.
- Schnitzer S.A., Klironomos J.N., HilleRisLambers J., Kinkel L.L., Reich P.B., Xiao K., Rillig M.C., Sikes B.A., Callaway R.M. & Mangan S.A. (2011). Soil microbes drive the classic plant diversity-productivity pattern. *Ecology*, **92**, 296-303.

- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor, and H. Miller. 2007. IPCC, 2007: Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press.
- Stein C., Auge H., Fischer M., Weisser W.W. & Prati D. (2008). Dispersal and seed limitation affect diversity and productivity of montane grasslands. *Oikos*, **117**, 1469-1478.
- Tilman D., Lehman C.L. & Thomson K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, **94**, 1857.
- Todd R.W., Evett S.R., Howell T.A., Klocke N.L. (2000). Soil temperature and water evaporation of small steel and plastic lysimeters replaced daily. *Soil Science* **165**, 890-895.
- Tylianakis J.M., Rand T.A., Kahmen A., Klein A.M., Buchmann N., Perner J. & Tschardt T. (2008). Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biology*, **6**, e122.
- Van Peer L., Nijs I., Reheul D. & De Cauwer B. (2004). Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. *Functional Ecology*, **18**, 769-778.
- Van Ruijven J. & Berendse F (2010). Diversity enhances community recovery, but not resistance, after drought, *Journal of Ecology*, **98**, 81-86.
- Wan, S., Yuan, T., Bowdish, S., Wallace, L., Russell, S.D. & Luo, Y.Q. (2002) Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology*, **8**, 754-768.