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Spiders in mofette fields—Survival of the toughest in natural carbon dioxide springs?

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ABSTRACT

In mofette fields, natural carbon dioxide springs, organisms have to stand extreme CO_2 concentrations up to 100%. These hostile conditions are spatially small-scaled and further influenced by earth tides, wind and temperature. The present project investigated the influence of increased atmospheric CO_2 concentration on spiders as representatives of above-ground organisms by means of pitfall traps in three mofette fields, differing in habitat conditions in the Plesná valley, eastern Cheb Basin, Czech Republic.

Among the 71 recorded spider species four were rarely found in the Czech Republic. A canonical correspondence analysis revealed significant influences of environmental parameters on the spider assemblages. Two groups of spiders are clearly distinguishable, one being positively influenced by humidity and the second by temperature. A cluster analysis showed distinct and congruent results: spider assemblages of pitfall traps at spots with a mean CO_2 concentration above 7.6% grouped close together and this grouping was independent of site. At >7.6% CO_2 significantly fewer individuals and species were found in comparison to areas with lower CO_2 concentration. Between 2.5 and 10% CO_2, spiders indicated increased CO_2 concentrations much more sensitively than endogeic organisms (Nematoda, Collembola) in a nearby mofette field. Unlike in nematodes, collembolans and plants, no mofettovageous or mofettophilous spiders were detected. In contrast to humidity, CO_2 concentration and temperature, the vegetation cover was not among the factors, which significantly influenced spiders. This is explained by the fact that mofettophilous plants occurred at spots where almost no spiders could live. In a field experiment, most *Pardosa pullata* males tested passed a 30 cm long corridor with increased carbon dioxide concentration. These results and that of pitfall traps showed that relatively large and wandering specimens respectively were able to transit moderately hostile spots. Further experiments are necessary to find out if there is any active avoidance of high-CO_2 areas by spiders.

1. Introduction

Mofette fields are locally restricted areas with naturally increased carbon dioxide concentrations. They are located at recent or post-volcanic areas where carbon dioxide leaks from magma reservoirs of the earth crust or mesosphere (Pfanz, 2008; Weinlich et al., 2013; Pfanz et al., 2014). At mofette fields, CO_2 may reach concentrations up to 100% in soil pores as well as in the atmosphere close to the soil surface. Earlier investigations have shown large small-scale differences of carbon dioxide concentrations depending upon released CO_2 volume, horizontal and vertical transport processes, physical and chemical soil properties, as well as fine root and biomass concentration (Miglietta et al., 1993; Vodnik et al., 2006). Furthermore, diurnally and seasonally fluctuating carbon dioxide concentrations are influenced by earth tides, weather conditions and vegetation (Van Gardingen et al., 1995; Hamada and Tanaka, 2001; Faber et al., 2009; Kies et al., 2015). Nevertheless, Pfanz et al. (2004) and Faber et al. (2009) discovered that at plots with high CO_2 pressure the concentrations are generally higher than in plots with minor pressure.

In addition to direct toxic effects, rising carbon dioxide concentrations cause hostile conditions to organisms by decreasing oxygen concentrations and increasing soil acidity (Heinicke et al., 2009; Weinlich et al., 2013). Some studies investigated the response of life under such extreme conditions. For example Pfanz et al. (2004) and Saßmannshausen (2010) analyzed the vegetation in mofette fields and found that plant species responded differently to increased CO_2 concentrations. Species-specific differences were

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also reported by Russell et al. (2011) and Hohberg et al. (2015) for the endogeic soil fauna, both for inhabitants of the water-filled soil pores (Nematoda) and for air-breathers (Collembola). An outstanding result is the finding of a new collembolan species that is known from mofette fields exclusively (Schulz and Potapov, 2010). Besides, short-time influence of carbon dioxide on different species was investigated under specific conditions in laboratory experiments (Zinkler and Platthaus, 1996; Rasman et al., 2012; Pilz and Hohberg, 2015). In contrast to plants and endogeic animals there is next to nothing known about the impact of highly elevated atmospheric CO_2 on ground living arthropods like spiders.

Walking across a mofette field in the Cheb Basin at NW Bohemia (Czech Republic) spots of high carbon dioxide concentrations attract attention not only in having a different or missing vegetation compared to the surroundings but also by accumulations of dead animals: single vertebrates such as toads or birds and many invertebrates in particular Coleoptera and Diplopoda. At some of these places fox faeces are regularly found because this predator quickly learns to use this comfortable food source. This illustrates spectacularly the amount of consistently incurred dead specimens. In contrast to the taxa mentioned, Araneae are only rarely found dead. This is not because spiders are rare: In general, there are a number of spider species occurring in high densities at the mofette fields, reflected by the name of one area which is called "Spider-Mofette". The question arises why spiders are rarely found dead at these spots. Is it because of their minor sclerotisation and the consequently more rapid degradation of remains in comparison to beetles and diplopods or can spiders survive higher CO_2 concentrations via physiological adaptations? Alternative explanations for the lack of dead spiders may result from their high motility by quickly moving in and out of high CO_2 areas or from avoidance of hostile spots by spiders.

2. Materials and methods

2.1. Site descriptions

The investigations were carried out in the carbon dioxide degassing area of the flood plain of the Plesná River, which is part of the swarm-quake region in the eastern Cheb Basin at NW Bohemia, Czech Republic (Bankwitz et al., 2003). The mofette fields in this area are characterized by an almost pure CO_2 emission, without the usual reactive magma-derived components (H_2S and CO) and with only occasional traces of hydrogen (Kämpf et al., 2013). We examined three separate sites situated between the villages Vackovec and Milhostov with different soil water conditions. Height, coverage and species composition of vegetation differed within each site as a function of carbon dioxide concentration and other environmental factors. Soil surface in the area was usually fully covered by plants with the exception of spots of extreme CO_2 concentrations, which were completely bare.

2.1.1. Thistle-Mofette (pitfall traps T1–T7)

The Thistle-Mofette (50.1472°N, 12.4514°E) covers about 200 m^2. It is bordered by uncultivated wet meadows spotted with some willow bushes and in the west by a hay meadow. The soil is sandy and nutrient poor in comparison to the other mofette fields resulting in relatively scarce vegetation. According to Saßmannshausen (2010), it belongs to the *Calluna-Nardus* mofette type and is dominated by the positive CO_2 indicator plants *Nardus stricta* and *Festuca ovina* as well as the mofettovagous *Poa angustifolia*. Average carbon dioxide concentration at the soil surface (measured as described below) ranged from 0.8% to 10.3% at the seven pitfall traps. This mofette field is situated at higher altitude than the other mofette fields investigated (434 m a.s.l.).

2.1.2. Spider-Mofette (pitfall traps S1–S7)

The Spider-Mofette is situated within the flooding zone of the Plesna River (50.1420°N, 12.4502°E, 432 m a.s.l.) and is surrounded by a wet uncultivated meadow dominated by *Filipendula ulmaria* and *Deschampsia caespitosa*. In this ca. 1300 m^2 large area *Deschampsia cespitosa* and the mofettophilous *Eriophorum vaginatum* were stand building, mofettophilous accessory species were *Aulacomnium palustre* and *Festuca ovina*. The average carbon dioxide concentration of the investigated plots amounted 0.2% to 51.4%.

2.1.3. Cotton Grass-Mofette (pitfall traps C1–C7)

This mofette field has an elongated shape of about 60 m length and only few meters width. It is situated between moist meadows, but bordered by a grove in the North and some willow bushes in the West (50.1461°N, 12.4514°E, 433 m a.s.l.). According to Saßmannshausen (2010), it is classified as *Eriophorum-Deschampsia* type with the mofettophilous *Eriophorum vaginatum* as peat-building dominant plant species. The traps were placed between tussocks of *Eriophorum* at spots with average CO_2 concentrations between 0.3% and 48.0%.

2.2. Spider sampling

Epigeic spiders were sampled using pitfall traps between 26 March and 26 June 2013. The first series of traps were exposed for three weeks (due to difficulties resulting from sub-zero temperatures) and the following six trap series for two weeks. Seven glass jars of 5.5 cm diameter and 14.5 cm depth, filled with a preserving agent according to Renner (1980) (40% ethanol, 30% water, 20% glycerin, 10% acetic acid and some detergent) were placed at each of the three sites, the distance between traps varying between 3 and 5 m depending upon the CO_2 concentration of the specific spot. Each trap was provided with a transparent roof as protection against rain and snow and to prevent interference by birds or mammals (Woodcock, 2005).

The nomenclature of the species is according to the World Spider Catalog by Platnick (2014). We applied the habitat preferences given by Blick and Scheidler (1991), Martin (1991), Hänggi et al. (1995), Platen and von Broen (2005) and the Czech Arachnological Society (2015). Reference specimens are preserved in the Arachnological Collection of the Senckenberg Museum of Natural History Görlitz.

2.3. Vegetation analysis

The distribution of spider species is to a large part depending upon habitat conditions, in particular of vegetation cover and structure, temperature and moisture (see Section 4). In contrast to singular or few measurements of these parameters by instruments plant species are tightly constrained by the climatic regime and soil conditions and are useful indicators for long term influences (ter Braak and Gremmen, 1987).Therefore, vegetation surveys were conducted within 1 m^2 plots around each pitfall trap at 10 July, 2013. We used the percentaged coverage of plant species because a detailed gradation of vegetation is useful for the comparison with the accuracy measurement of CO_2 and O_2. The indicator plant system of Ellenberg et al. (1992) was applied to assess temperature and soil moisture conditions at each plot. Simple arithmetic means of indicator plant figures and the cover percentage of vegetation were used for CCA.

2.4. CO_2 and O_2 analysis

Atmospheric carbon dioxide and oxygen concentration were measured close to the soil surface at four points around the pitfall traps on each of the six pitfall exchange dates. The investigations