Prolonged diapause of earthworms as an adaptation to semiarid environments. A case study

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SUMMARY. An extremely long diapause period of *Bimastos syriacus* specimens is reported. Since there is a positive significant correlation between the length of the diapause period and length of the drought period in the Levant the possibility that this is an adaptation to the semiarid conditions in the Levant is discussed.

INTRODUCTION

The presence of autochthonous earthworm species in the semiarid regions along the Levantine borders of the Saharo-Syrian desert belt (Pavlíček et al., 2003) raises the question whether these earthworms have been adapted to this environment or they are relicts of this species, their populations being survivors of a past humid climate in these areas, without adapting themselves to the progressively growing aridization. It is well established that earthworm activity is significantly correlated with the soil moisture (Garsney, 1994; Wever et al., 2001) but genetic, ecological, morphological and behavioural adaptations present in certain species might help them to survive in the semiarid regions characterized by prolonged drought periods and low-soil humidity. Such adaptations may include e.g., retention of urine in nephridium and re-absorption of part of water if the earthworm is exposed to low hydration in *Apporectodea caliginosa* (Ghabbour, 1999), the cocoons diapause during summer drought in *Microscolex dubius* (Doube and Auhl, 1998), and adult diapause or aestivation (Vejdovský, 1892; Omodeo, 1948). We suggest that the extended diapause allowing earthworms to survive the prolonged periods of drought might be the macroscopic adaptation to the semiarid environments. In this article we use the term adaptation in its broad sense (see for more details Gould and Vrba, 1982).

MATERIAL AND METHODS

The adult specimens of *Bimastos syriacus* were collected in January 2004 in Nahal Tabor, lower Galilee, Israel. They were kept alive in plastic bags (2 l volume) in the laboratory conditions (temperature 18-20 °C, little light intensity during daytime).

Earthworm specimens were fed with lettuce leaves and soil was watered (according to visual inspection) from January till April. They were left without any disturbance from the beginning of May, when they entered into diapause till the end of November. The number of present specimens in diapause was checked at the end of November and after that soil was watered again to see if they revive.

RESULTS

At least four specimens of *B. syriacus* have been in diapause from the beginning of May till the end of November, i.e. for seven months. Four specimens became active again after water was applied, but an additional six specimens did not survive (60% mortality). Which factor(s) triggered the beginning of diapause is not clear in *B. syriacus*. However, our findings indicate that diapause in this species might be obligatory and genetically-based, since specimens enter into it even if the soil was wet and the temperature about 18-20 °C. Specimens of *B. syriacus* enter diapause by tying themselves up into a knot inside a little hole, lined with slimy substances to avoid moisture loss, similar to the way described by Omodeo (1948) and Zicsi (1958).

DISCUSSION

Climatic background

Undoubtedly, progressive aridization, starting in the middle Miocene, has been a threat to earthworm survival in the area of the Sahara-Syrian desert belt. In fact, no "true" desert earthworms exist. However, earthworms actually live in desert "wet" localities such as oases, temporary pools, sweet water springs, and banks of streams (e.g. Pavlíček et al., 1997; Omer-Cooper, 1947). In contrast to the desert interiors, the desert borders, i.e., areas with 200 mm or more of annual rainfall, are frequently inhabited by a unique earthworm fauna with some species apparently endemic to those regions (e.g. *Dendrobaena negevis* Csuzdi et Pavlíček, 1999; *Perelia shamsi* Csuzdi et Pavlíček, 2005; *B. jordanis* Csuzdi et Pavlíček, 1999). Certainly, the earthworms (with an exception of semi-aquatic species) of the semiarid regions are exposed to low annual rainfall but, e.g., in the Levant, they also face a prolonged (6 to 7 months) summer drought usually with no rain (Fig. 1), as well as to dramatically spatiotemporally, fluctuating soil moisture during the rainy period (Fig. 2).

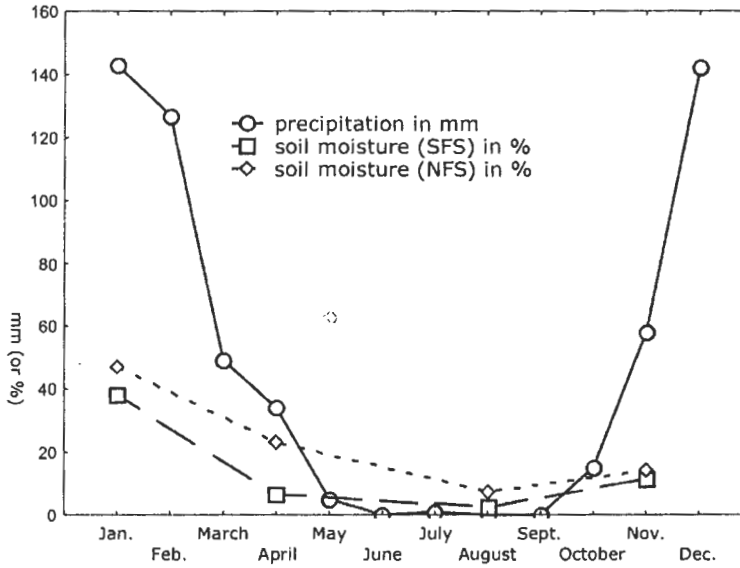

Fig. 1. Diagram of the average monthly precipitation in the Mediterranean regions in Israel in millimeters (from: Bodenheimer, 1935) and the soil moisture (in %) at the south- and north-facing slope, lower Nahal Oren, Mt. Carmel, Israel (From: Grishkan et al., 2000)

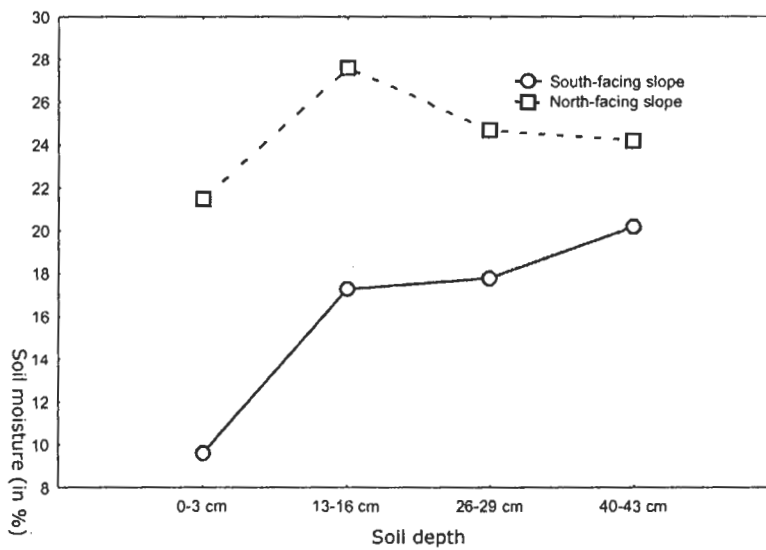

Fig. 2. Spatial fluctuation of soil moisture at different depths in the mid April at lower Nahal Oren, Mt. Carmel, Israel (according to Grishkan I., unpublished)

The Levantine model of earthworm diapause

If we can generalize the test on *B. syriacus* in the laboratory, then our results indicate that earthworms of the semiarid regions can survive at least seven months in diapause. Notably, our data probably represent the longest recorded survival rate of earthworms, e.g., 1.8 times longer as compared to data recorded by Zicsi (1958) in Hungary. Since there is a positive significant correlation between the length of the diapause period and length of the drought period in the Levant, we regard the length of diapause period as an adaptive character to the semiarid conditions in the Levant. Due to our data characteristics, this is not to say that *B. syriacus* cannot survive a longer time in diapause. In spite of the fact that much longer survival is not much probable due to usually high earthworm mortality during diapause or eastivation (e.g., Zicsi, 1958; Garnsey, 1994), in certain years the drought period might be longer than the 6-7 months average recorded in the Levant. Moreover, in certain habitats earthworms face more severe drought than the average rainfall data indicate. For example, native earthworm species are present on xeric slopes in the Levant where higher solar radiation input through increased evapotranspiration contributes dramatically to the water deficit and shortening of the activity period (see Pavlíček et al., 1996 and contrast between south- and north-facing slopes of "Evolution Canyon" at lower Nahal Oren, Mt. Carmel, Israel in Fig. 1). It should be noted that diapause described in *Microscolex dubius* (Fletcher, 1887, when only cocoons survive drought periods (Doube and Auhl, 1998,) might be rather exceptional since the life-span of the majority of the autochthonous species is expected to be more than one year at least in the Levant. Nevertheless, the cocoon diapause probably contributes to *M. du*bius' traits, magnified by human transport, to successfully colonize mesic and desert biotopes in the Levant (Pavlíček et al., 1996, and unpublished). Apart from the long drought period, most earthworms are facing the problem of large soil moisture fluctuations during the 5-6 months prolonged rainy period in the Levant (data in preparation). These fluctuations expose earthworms to two challenges: a) high soil moisture during the rain, and shortly after, sometimes accompanied by floods, b) relatively dry soil in the periods between two consecutive rains. In other words, they must be able to discharge excess water in wet soil (in conditions of 35-45% water moisture in *Ap. caliginosa*: Ghabbour, 1999) and minimize water loss from their bodies if the soil is relatively dry (in conditions of less than 25% water moisture in *Ap. caliginosa*: Ghabbour, 1999). The ability to switch from discharging excess water to water re-absorption is another important adaptation in the semiarid regions (Ghabbour, 1999). The activity during the relatively dry period between the two consecutive rains extends significantly the activity period (that is short, anyhow) that would not be possible if earthworms enter to aestivation due to dryness. Probably, the autochthonous genera *Dendrobaena, Perelia*, and *Bimastos* adaptively radiated to the semi-arid conditions in the Levant (Pavlíček et al., 2003, Csuzdi and Pavlíček, 2005a,b).

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