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The impact of anhydrobiosis on the persistence of *Scottinema lindsayae* (Nematoda): a modeling analysis of population stability thresholds

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Abstract The nematode (*Scottinema lindsayae*) is one of the most common soil invertebrates in the soils of the McMurdo Dry Valleys, Antarctica. A stage-structured population model developed for *S. lindsayae* was modified to include the effects of anhydrobiosis resulting from soil moisture limitations. Model results indicated that anhydrobiosis lowered temperature requirements needed to establish stable populations by buffering mortality at low temperatures. Moisture conditions producing anhydrobiosis in about 5% of the population had the lowest temperature requirements; fully active populations required 50% more cumulative annual degree-days to persist. Hence, transfer between active and anhydrobiotic states enhanced the persistence of *S. lindsayae* in these extreme cold desert soils.

Introduction

Soil biota in the McMurdo Dry Valleys survive some of the most extreme conditions on earth. Annual mean temperature averages -21°C and total annual precipitation is less than 10 cm, with most of that falling as snow during winter (Campbell et al. 1987; Freckman and Virginia 1997; Fountain et al. 1999). The soils have low nutrient content, little to no organic matter, brief and erratic periods of $>0^{\circ}\text{C}$, low precipitation, high salinity, soil moisture usually $<1\%$ and sporadic, aberrantly warm years (Freckman and Virginia 1997). Not surprisingly, soil communities are simple. Primary production is largely limited to algae and fauna are almost exclusively microbial grazers, i.e., mostly proto-

zoa, rotifers, tardigrades and nematodes (Freckman and Virginia 1997; Treonis et al. 1999). Of these organisms, the nematode *Scottinema lindsayae* Timm 1971 is most common and widespread. This species is found in about 60% of the soils and is the only invertebrate in soils $<2.5\%$ moisture content (Freckman and Virginia 1997). However, it is absent from saturated soils or sites with electrical conductivity $\geq 3,000 \mu\text{mhos cm}^{-1}$ (Treonis et al. 1999). Clearly, even *S. lindsayae* faces frequent environmental limitations in the Dry Valleys.

Moisture availability is one of the most important determinants of species distributions in Antarctica (Kennedy 1993). Indeed, moisture is one of the most important controls on soil nematode distributions in any environment (Ettema et al. 2000). Cephalobidae, like *S. lindsayae*, are often a dominant family in soils that have extended periods of low matric potentials (Griffiths et al. 1995; Neher et al. 1999; Yeates et al. 2002). For example, Yeates et al. (2002) observed growth of *Cephalobus* sp. in soils containing water restricted to pores 1–5 μm in diameter. As for *S. lindsayae*, Treonis et al. (2000) showed that this species changes rapidly between active and inactive states (anhydrobiosis) in response to small, diurnal changes in relative humidity. The species appears able to survive frequent and prolonged desiccation that is a characteristic of Dry Valley soils.

Nematodes may survive desiccating or freezing conditions by entering the quiescent, cryptobiotic states of anhydrobiosis or cryobiosis, respectively (Womersley et al. 1998; Wharton 2002). Both mechanisms involve the biosynthesis of low molecular weight carbohydrates, proteins, and glycerol (Wharton 2003), verifying early speculation by Grime (1974, 1988) that tolerance to one environmental stress may impart tolerance for other stressors. More recently, Convey (1996, 1997) extended this rationale to Antarctic faunal communities, suggesting that pre-adaptations to stress were instrumental to colonizing Antarctic sites by invertebrates. Sustr and Block (1998) and Convey (2000) further suggested that such pre-adaptations explain higher investment in cryoprotectants and greater metabolism at cold tem-

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peratures in Antarctic invertebrates. Perhaps *S. lindsayae* is one of the most common and widely distributed terrestrial animals in the Dry Valleys because it can persist at low matric potentials and low temperatures (Overhoff et al. 1993), and responds rapidly to soil moisture fluctuations (Treonis et al. 2000). Cryptobiosis not only enhances survival of this species, but may also facilitate dispersal when katabatic winds erode soils in the Dry Valleys (Doran et al. 2002; Lancaster 2002).

Herein we expand an earlier modeling analysis of the sensitivity of *S. lindsayae* to temperature regimes in Taylor Valley, Antarctica (Moorhead et al. 2002), by adding the effects of soil moisture content on nematode activity (Treonis et al. 2000). A previous modeling analysis showed that anhydrobiosis tended to stabilize population densities of a soil nematode in a warm desert through periods of moisture fluctuation (Moorhead et al. 1987). The purpose of this investigation is to examine interactions between moisture and temperature limitations to the persistence of *S. lindsayae* under typical soil conditions for the McMurdo Dry Valley region.

Methods

A stage-structured model was developed by Moorhead et al. (1987) to simulate the effects of temperature and moisture regime on population dynamics of *Acroboloides* sp., a common nematode, in warm desert soils of the northern Chihuahuan Desert of New Mexico, USA. This model was modified by Moorhead et al. (2002) to simulate the effects of temperature regime on population dynamics of *S. lindsayae* in cold desert soils of the McMurdo Dry Valleys. Herein, we examine the impacts of moisture limitations on *S. lindsayae* by adding the effects of anhydrobiosis to the model of Moorhead et al. (2002), following the approach of Moorhead et al. (1987). In addition, the sex ratio of adult *S. lindsayae* reported from field studies was used in current simulations instead of the equal proportion of sexes assumed by Moorhead et al. (2002).

We simulated anhydrobiosis in *S. lindsayae* based on the observations of Treonis et al. (2000). However,

a number of uncertainties surround the relationship between soil moisture and anhydrobiosis. For example, the high molarity of the solution used to extract nematodes from soil causes ca. 30% mortality (Freckman et al. 1977), and could lead to underestimating anhydrobiosis. In addition, coiling is the primary criterion used to determine if a nematode is anhydrobiotic, but an uncoiled animal is not necessarily alive. This could lead to overestimating anhydrobiosis. These uncertainties add corresponding uncertainty to model interpretation, but the quantification of this uncertainty has not been defined empirically and lies beyond the goals of the present study.

Field observations indicated that 74–91% of the terrestrial nematodes in the Dry Valleys were desiccated (anhydrobiotic) when soils had $\leq 2\%$ water content (Treonis et al. 2000); *S. lindsayae* accounted for 74–100% of these nematodes or about 90% of the total. We assumed that these observations represented *S. lindsayae* responses to soil moisture, and estimated the inactive fraction of the nematode population as a sigmoid function (Fig. 1; after Treonis et al. 2000) of soil water content:

$$F = 1 - A^2 / (A^2 + H_2O^2) \quad (1)$$

where F is the active fraction, H_2O represents gravimetric moisture and A is a best-fit model parameter (Table 1). Soils in the Antarctic Dry Valleys are $>95\%$ sand so that soil water potential varies from -0.6 to -26.9 Mpa at 2% gravimetric moisture (Treonis 1999). The fraction of nematodes that were anhydrobiotic increased rapidly below 2% moisture (Fig. 1). Adjustments were made at each model iteration to maintain the ratio of active: inactive juveniles and adults (F) by shifting individuals between active and inactive states. Each age cohort was adjusted to achieve this ratio (Moorhead et al. 1987).

Temperature regimes used to drive population dynamics were modeled in two ways. First, a cosine function was fit to field data as in the original model formulation (Moorhead et al. 2002):

$$T = B \times \cos(D/365 \times 2\pi) + C \quad (2)$$

Table 1 Definitions and values of model parameters

Parameter	Period above 0°C	Definition	Units	Value
A		Best fit	Unitless	0.65
S	55	Temperature profile shape	Temperature day ⁻²	-0.0032 to -0.0022
	60			-0.0027 to -0.0018
	65			-0.0022 to -0.0016
	75			-0.0016 to -0.0010
	80			-0.0014 to -0.0010
	85			-0.0013 to -0.0009
M	55	Maximum seasonal temperature	Temperature	1.3–2.7
	60			1.3–2.6
	65			1.3–2.5
	75			1.3–2.5
	80			1.3–2.4
	85			1.3–2.4

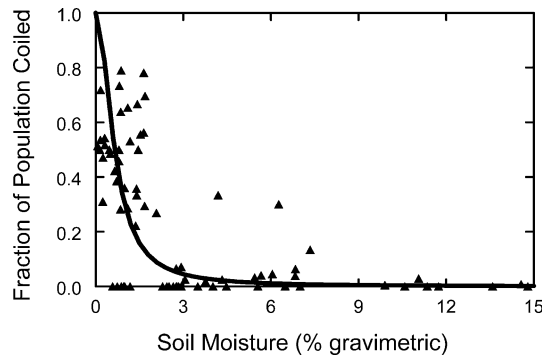


Fig. 1 Observed relationship between anhydrobiosis and gravimetric soil moisture (*solid triangles*) (Treonis et al. 2000) and model predictions (*solid line*).

where D is Julian day, and B and C are best fit model parameters. We made small adjustments to the values of B reported by Moorhead et al. (2002), to more closely match field observations of cumulative degree-days during the summer season (Table 2).

Initial simulations revealed differences in model results for sites that had similar values of cumulative, annual degree-days, but differed with respect to maximum temperatures and duration above 0°C . We next

Table 2 Values of model parameter B , resulting field temperature regimes, and results of simulations with various levels of soil moisture

Site (lake basin)	Depth (cm)	Slope (B)	Model degree-days	Lambda (λ) at 100% activity	Percent stable moisture simulations (out of 50)
Bonney ^a	0	18.37	261.1	1.18	100
	5	21.29	272.4	1.19	100
	10	20.70	193.5	1.04	100
Brownsworth ^a	0	15.13	100.4	0.81	26
	5	17.11	64.6	0.77	0
	10	15.86	27.5	0.63	0
Fryxell ^a	0	12.53	93.8	0.76	14
	5	16.93	85.4	0.77	0
	10	14.43	42.8	0.69	0
Vanda ^a	0	17.76	166.5	1.00	100
	5 ^b	—	—	—	—
	10	15.21	36.8	0.61	0
Vida ^a	0	13.37	98.3	0.75	12
	5	13.31	25.9	0.64	0
	10	12.78	9.6	0.65	0
Hoare ^a	0	22.94	98.4	0.82	18
	5 ^b	—	—	—	—
	10	11.53	15.0	0.56	0
Hoare ^c	0	21.83	311.1	1.27	100
	5	23.25	279.3	1.27	100
	10	21.94	215.2	1.04	100
Hoare ^d	0	28.42	601.2	1.66	100
	5	24.56	442.7	1.54	100
	10	23.39	377.7	1.40	100

^aPermanent meteorological stations (McMurdo LTER website <http://huey.colorado.edu/LTER/>)

^bInsufficient data for analysis

^cLong-term soil warming experiments control plots

^dLong-term soil warming experiments treatment plots

explored the impacts of these differences in temperature regime on model behavior by using a quadratic equation to define seasonal temperature pattern:

$$T = S \times (P - I)^2 + M \quad (3)$$

where P is time in days and I shifts the temperature curve so that the season with temperatures above 0°C begins on the first day of simulation, S defines the shape of the temperature profile, and M is the maximum seasonal temperature (Table 1).

All simulations were started with 100 eggs and ran until a stable population was obtained or the population declined to zero. We define stability in the same manner as Moorhead et al. (2002), i.e., when $\lambda \geq 1$ (the coefficient of population increase) and λ fluctuated $< 5\%$ between successive years. Lambda was calculated for each simulation by dividing the total population (N) at the end of a given year (t) by the population at the end of the preceding year ($t-1$).

$$\lambda = N_t / N_{t-1} \quad (4)$$

Simulations were terminated after 365,000 days, even if a stable population was not achieved.

Three sets of simulations were performed. First, the original suite of simulations conducted by Moorhead et al. (2002) was repeated with the sex ratio of the nematode population changed from 50 to 63% female, as reported for field populations ($\text{SD} = 0.24$, $n = 27$; McMurdo LTER website <http://huey.colorado.edu/LTER/>). We next examined the interaction of soil moisture and temperature on *S. lindsayae* population dynamics with two sets of simulations. The first set investigated the impact of varying soil moisture content (Eq. 1) on population stability, given observed field temperature regimes (Eq. 2). Moisture was varied from 0.5 to 25% (by weight) by increments of 0.5%, for a total of 50 moisture levels at each of 22 temperature regimes (Table 2), yielding 1,100 simulations for this analysis. This moisture range (0.5–25%) corresponds to field conditions ranging from wet soils adjacent to streams, where *S. lindsayae* is rarely found, to drier soils where this nematode usually is the only soil invertebrate present.

In the final set of simulations, we used the quadratic expression to generate temperature regimes (Eq. 3) that were combined with varying levels of nematode activity to assess the impacts of anhydrobiosis on population dynamics. We set the active fraction of the nematode population at a constant value within a simulation, which was varied between simulations from 10 to 100% by increments of 5%. We chose periods $> 0^{\circ}\text{C}$ that generated seasonal, cumulative degree-day values near the threshold for persistence (90–100 degree-days; $\lambda \approx 1$). The parameter S (Eq. 3) was varied to generate temperature regimes bracketing minimum periods of $> 0^{\circ}\text{C}$ observed for Lake Fryell (55- to 65-day seasons) and Lake Hoare (75- to 85-day seasons) (Table 1). For each combination of nematode activity and temperature

regime, M (Eq. 3) was varied until a stable population was achieved. Occasionally, a declining population would experience a short period of $\lambda > 1$, which would erroneously terminate the simulation and identify the population as being stable. For this reason, a final population of < 80 individuals was not considered stable, regardless of λ , because it was smaller than the smallest, truly stable population.

Results and discussion

Simulations generated stable populations ($\lambda \geq 1$) for 10 of the 22 microsites examined in field studies (Table 2); temperature regimes for 12 microsites did not produce stable populations. Six fewer stable simulations resulted from this study than from Moorhead et al. (2002), and our values of λ were lower under equivalent field conditions (Table 2). This difference occurred because mortality of the oldest adult age cohort was underexpressed in the original model (Moorhead et al. 2002), permitting very old adults to accumulate over long simulations. The current model precludes this accumulation.

Although the ancestral reproductive state of nematodes is amphimictic (Hope 2002), sex determination occurs late in development and may be linked to environmental conditions (Hodgkin 1988). In any case, increasing the female fraction of the *S. lindsayae* population from 50 to 63% in simulations increased values of λ at all temperatures. Moreover, the linear relationship between λ and cumulative, annual degree-days had higher intercept (0.61 vs 0.58) and greater slope (0.0020 vs 0.0018) when the female fraction was increased, respectively (Fig. 2; $n = 22$ and $r^2 = 0.97$ for both cases). Thus a higher proportion of females in the population lowered the minimum threshold of temperature at which a population could exist.

Simulations exploring the effects of soil moisture under field temperature regimes produced a range of nematode activity from $< 0.1\%$ of the total population

being anhydrobiotic at 25% gravimetric moisture to 62.8% being anhydrobiotic at 0.5% moisture (Fig. 1). Of 1,100 simulations comprising this suite of analyses, 535 generated stable populations (Table 2). Ten temperature regimes had > 166 cumulative annual degree-days, which generated stable populations for all moisture conditions (500/500 simulations). Four temperature regimes had 93–100 cumulative degree-days and generated stable populations for a subset of moisture conditions (35/200 simulations). Eight temperature regimes had < 93 cumulative degree-days and failed to generate stable populations at any moisture level (0/400 simulations).

These model results are curious because they suggest that *S. lindsayae* would not survive the temperature regime at 5-cm soil depth at Lake Fryxell (data was inadequate for simulation at this depth for Lake Hoare), regardless of moisture conditions, although population densities reported at these sites ranged from 2,000 to 9,000 nematodes/kg soil (McMurdo LTER website <http://huey.colorado.edu/LTER/>). Nonetheless, Porazinska et al. (2002) noted that *S. lindsayae* populations have declined from 1993 to 1999 on the south side of Lake Hoare, which corresponds to the period of time during which the field temperature regimes used in our simulations were obtained. Perhaps these temperature conditions truly are unsuitable for the nematode and simulation results correctly illustrate the observed decline in population density. In contrast, Lake Bonney soils are too saline to support *S. lindsayae* populations although simulations suggest that temperature regimes are suitable (McMurdo LTER website <http://huey.colorado.edu/LTER/>).

Simulations using the quadratic temperature function produced similar trends in moisture response of nematode populations (Fig. 3). However, this set of simulations revealed that temperature regime exerts more subtle controls on population dynamics than captured by simple degree-day sums. In essence, sites with different season lengths and maximum temperatures produced different values of λ despite having comparable sums of cumulative annual degree-days (Table 1). This difference resulted from the periods of low temperature that existed at either end of the season, because egg and juvenile mortality are particularly sensitive to low temperatures (Moorhead et al. 2002). Therefore, the shape of the quadratic curve generated stable age distributions at lower degree-day sums than the cosine function, because it has a shorter period of lower temperatures. Moreover, quadratic temperature regimes of shorter duration and higher maximum temperature generated greater values for λ than longer periods of lower temperature despite both regimes producing the same number of degree-days for the season. This observation corroborates the speculation of Moorhead et al. (2002) that sensitivities in egg and juvenile survivorship to temperature may explain some of the variability in the relationship between λ and annual degree-day sums (Fig. 2).

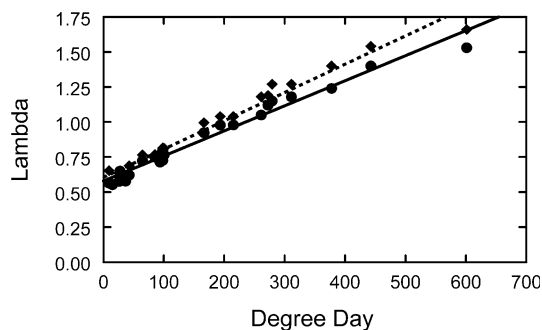


Fig. 2 The relationship between predicted growth rate coefficient (λ) and cumulative degree-day sums for simulations with 50% female populations (solid circles, solid line) ($y = 0.0018x + 0.58$, $n = 22$, $r^2 = 0.97$) and 63% female populations (solid diamonds, dashed line) ($y = 0.0020x + 0.61$, $n = 22$, $r^2 = 0.97$)

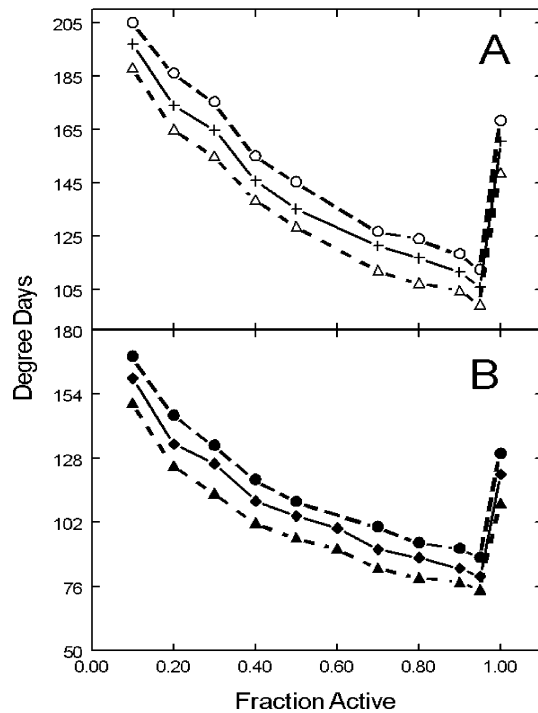


Fig. 3 Relationship between cumulative annual degree-days and the active fraction of the population generating minimum population stability ($\lambda=1$); Simulation results for seasonal durations reported at Lake Hoare (graph A: open circles 85 days, crosses 80 days, open triangles 75 days) and Lake Fryxell (graph B: solid circles 65 days, solid diamonds 60 days, solid triangles 55 days)

Degree-day requirements for stable populations declined as moisture increased, to a minimum degree-day requirement at 95% activity (Fig. 3). Surprisingly, degree-day requirements sharply increased when the population became 100% active, but these apparently counterintuitive results are easily explained. The inverse relationship between degree-day and soil moisture resulted from replacing dead nematodes with those from the inactive, but living anhydrobiotic pool to maintain the active fraction of the population defined by soil moisture content (Eq. 4). Thus high mortality during periods of low temperature in spring and autumn was buffered by activation of anhydrobiotic individuals. It seems unlikely that such a simple mechanism operates under field conditions, but Treonis et al. (2000) found that the activity level of *S. lindsayae* was directly linked to small changes in soil humidity caused by diurnal changes in temperature. In short, Treonis et al. (2000) found that nematode activity was greater during warmer periods of the day, suggesting a rapid response of the population to changes in soil humidity. Perhaps the rapid activation of anhydrobiotic nematodes in our model is a reasonable approximation of this process.

In contrast to dry soils, moist soils maintain an insufficient pool of anhydrobiotic nematodes to compensate for periods of high mortality. Thus warmer temperatures were needed at high soil moisture content to achieve a stable population. Soil moisture conditions for sites that were reported to contain only *S. lindsayae*

ranged from 0.9 to 2.5% water content (Treonis et al. 2000), which corresponds to 66 and 94% of the population being active, respectively (Eq. 1; Treonis et al. 2000). Simulations suggest that this range of activities is near the optimum for achieving a stable population at the lowest temperatures (Fig. 3).

Conclusions

Results of this study suggest that *S. lindsayae* can persist at sites with as little as 93–100 cumulative degree-days per year, and that the interaction of temperature and soil moisture plays an important role in determining the presence and persistence of the species. Anhydrobiosis and growth at low matric potentials are characteristics that are pre-adaptive in Cephelobidae (Freckman 1978; Yeates et al. 2002) although the sensitivity and magnitude of these responses in *S. lindsayae* may represent novel adaptations to Antarctic conditions, as speculated by Convey (2000) for soil arthropods. Mechanisms underlying interactions between temperature and moisture controls on *S. lindsayae* used in this study do not specifically address the rapid responses to diurnal changes in soil humidity reported by Treonis et al. (2000). However, the constant balance between active and anhydrobiotic fractions of the population maintained in simulations may approximate this response.

At this time, data are insufficient to determine the effects of cryptobiosis or conductive freezing on mortality of *S. lindsayae*. Studies of temperate nematodes suggest that mortality is low while in a quiescent state (Womersley et al. 1998). Moreover, studies of arthropod physiology for Antarctic species suggest that mortality rates might be higher for temperate species under comparable conditions (Worland and Convey 2001). Survival of conductive ice nucleation has been demonstrated for *Panagrolaimus davidii*, another Antarctic nematode (Wharton 2002). However, soil water potentials related to *S. lindsayae* distributions combine matric and solute potentials (Treonis 1999), adding to the uncertainty of extrapolating freezing resistance to *S. lindsayae*. Finally, populations of *S. lindsayae* decline as soil moisture increases (Treonis et al. 2000), suggesting that the species may be sensitive to conductive ice nucleation.

In a larger context, although Grime's (1974, 1988) model of life history strategies has seldom been applied to animals, Convey (1996, 1997) suggests the suitability of this model to Antarctic fauna. The idea that tolerance to one environmental stress may enhance tolerance to other stressors seems particularly relevant for mechanisms of anhydrobiosis and cryobiosis in *S. lindsayae*. Convey (1997) noted that some adversity/stress-selected organisms had characteristics often associated with ruderal lifestyles (Grime 1988). Indeed, stress-selected ruderals would be expected to tolerate conditions that combine high stress with high disturbance, which are typical features of Dry Valley ecosystems. By analogy,

mosses represent forms of plant life that best meet the criteria for stress-tolerant ruderals, are the highest form of plant life found in the McMurdo Dry Valleys, and yet exist only in the most favorable microsites (Dale et al. 1999). Indeed, mosses share some key attributes with *S. lindsayae* in that they can survive frequent, prolonged, and unpredictable periods of desiccation and freezing, as well as being dispersed by wind while in a cryptobiotic state (Dale et al. 1999). Perhaps Grime's (1974, 1988) model of life history strategies is consistent among both plant and animal kingdoms.

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