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Growth and reproduction of *Aphelenchus avenae*, *Aphelenchoides saprophilus* and *Aphelenchoides besseyi* in mono- and mixed cultures cultivated on the fungus *Alternaria tenuis*

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Summary. The biocontrol potential of *Aphelenchoides saprophilus* and *Aphelenchus avenae* has been studied for the control of plant pathogenic fungi since the 1970s. In conditions of accelerating climate change, it is not clear how these nematodes will interact with the parasitic nematode *Aphelenchoides besseyi*, which may rapidly increase in numbers under higher temperature regimes. To prevent harvest losses, we need a complex model that will help to predict the behaviour of each species of nematodes and their mode of interaction. This paper investigates the interactions between the fungivorous nematodes, *Aphelenchus avenae* and *Aphelenchoides saprophilus*, and the plant-parasitic nematode *A. besseyi*. Competitive interactions between the nematodes resulted in decreased numbers of nematodes when they were grown in mixed cultures. *Aphelenchus avenae* was more competitetive than *A. besseyi* and *A. saprophilus* at 15-25°C and 30°C. At 5°C, only *A. saprophilus* increased in numbers. The experiments demonstrated that temperature, reproductive rates and intrinsic characteristics influenced the competitive interactions between the three nematode species.

Keywords: fungivorous nematodes, interspecific competition, plant-parasitic nematodes, temperature regimes.

The fungivorous nematodes *Aphelenchus* and *Aphelenchoides* are the most common genera in soil (Freckman & Caswell, 1985; Yeates *et al.*, 1993; Zolda, 2006; Monokrousos *et al.*, 2021). *Aphelenchus avenae* Bastian, 1865 and *Aphelenchoides* spp. have significant potential as biocontrol agents against plant pathogens and could be used for large-scale field control (Lootsma & Scholte, 1997; Ishibashi *et al.*, 2000; Hasna *et al.*, 2007; Shchukovskaya *et al.*, 2014). *Aphelenchoides saprophilus* can be found in the root systems of clover, even under snow cover, where it successfully develops and reproduces by feeding on soil fungi (Shesteperov, 1985). This species also feeds on mycorrhizal fungi and can influence mycorrhizal development and affect competition between the species of soil fungi (Ruess & Dighton, 1996). *Aphelenchoides besseyi* Christie, 1942 is a plant-parasitic nematode that can cause devastating plant damage and crop losses (Fortuner & Orton Williams, 1975; Rahman & Miah, 1989; Ni *et al.*, 2020; ISC, 2021). *Aphelenchoides besseyi* can be found in soils (Terry, 1972; Nguyen-thi, 1982) and it can also feed on fungi (Jamali *et al.*, 2008). Knowledge of the interspecific interactions between nematodes and the effects of the factors influencing these interactions are important for the prediction of nematode abundance and resistance of plants to parasitic nematodes, and for application of biological and chemical methods of control. Interspecific interactions between nematodes may be complicated due to complex multispecies nematode communities inhabiting any substrate, such as soil, plant tissues or organic materials (compost, mushroom spawn, rotting root, *etc.*) where more than 30 species of nematodes of different ecological groups can be present (Yeates, 1979; Yeates & Bongers, 1999). The occurrence of more than one species in a restricted area where many species use common sources of food can result in several types of interactions. However, little is known about density-dependent population

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interactions in multi-species nematode assemblages. Interactions between species can influence the size of nematode populations in three ways: the population of one or the other or both may increase (+), decrease (–), or have neutral effects (0) (Odum, 1971). The different outcomes of interspecific interactions between nematodes are often determined by trophic relations. Reproductive strategies tend to correlate with pulses of food availability (Yeates, 1987) and fungivorous nematodes can migrate to locations in the soil where reproduction is stimulated by food available in large quantities (Bae & Knudsen, 2001). An example of negative interspecific interactions in the same ecological group may be *Steinernema feltiae* and *Heterorhabditis bacteriophora*, *Bursaphelenchus xylophilus* and *B. mucronatus* as a result of competition for food resources (Aydin & Susurluk, 2005; Vincent *et al.*, 2008). Interspecific competition may occur and be strong at the border of a biotope in the period of simultaneous increase in population numbers and under the changes in ecological factors favourable for both species (Shesteperov, 1985).

Interactions between soil nematode populations are influenced by a number of environmental factors (Hasna *et al.*, 2007) with temperature being one of the most important in the case of direct or indirect competition for food resources (Kurt *et al.*, 1996). Changes in temperature play an important role in nematode growth and development (Pudasaini *et al.*, 2008). Environmental conditions may also influence sex ratio of nematode populations (Yeates, 1987). The previous study showed that optimal temperature for development of one nematode species might cause elimination of the other species (Shesteperov, 1985). However, when the temperature changed, thus creating better conditions for the reproduction of these other species, the one that had previously been thriving suffered decreases in its population.

This study examined competitive interactions between the two species of fungivorous nematodes *A. avenae*, *A.saprophilus* and one species of plant-parasitic nematode *A.besseyi* growing on the fungus *A.tenuis* at different temperatures. The following hypotheses were tested: *i*) reproductive rates of all three species are related to temperature; *ii)* in mixed culture of nematodes a species advantage in competitive interactions is determined by its competitive capacity and higher reproduction rate at certain temperatures; and *iii)* temperature and population interactions affect the sex structure of nematode populations.

MATERIAL AND METHODS

Nematodes. *Aphelenchoides besseyi* was isolated from the seeds of rice 'Dubovsky' (from Astrakhan region, Kamyzyaksky district). *Aphelenchus avenae* and *A. saprophilus* were isolated from plants of winter wheat (Moscow region, Podolsky district). The nematode cultures were maintained on fungus *Alternaria tenuis*. These nematode species were used because they have good growth and reproduction rates on this fungus, they differ in their optimum temperatures for growth, and they naturally occur together in seeds and soils (Shesteperov & Savotikov, 1995).

The choice of biological characteristics of the species is shown in Table 1.

Effect of temperature on growth rate and reproduction of nematodes. Populations of *A. avenae*, *A. saprophilus*, *A. besseyi* were cultured on fungus *A. tenuis* grown on potato dextrose agar (PDA, Difco). Ten ml of melted agar medium were poured in 50 ml glass tubes at an angle 15° forming 15 cm^2 agar surface. The fungus was grown for 7 days at 27°C. The tubes showing equal amount of mycelium covering the surface of medium were selected for the experiment. Volumes of 0.5 ml of the nematode suspensions (100 ± 6 nematodes) in sterile tap water were inoculated in each tube according to the treatments shown in Table 2. The volume of water in the tubes was adjusted to 1.5 ml. There were five replicates for each variant at each temperature. One set of tubes (mono- and mixed cultures) was kept 140 days in refrigerator at 5°C; the second set for 22 days at 15-25°C; the third set for 14 days at 30°C. Each treatment was analysed after the mycelium had been fully grazed by the nematodes.

Estimation of nematode numbers. One part of nematodes was flushed by water from the walls of tubes; the nematodes from agar medium were isolated by Baermann funnel method putting all the agar mass on milk filters. Nematodes were counted in 0.1 ml subvolume with 4 replications for every tube. Five tubes for one variant were used in the experiment. The experiment was repeated twice.

Statistical analysis. Standard deviation of the mean values were calculated for all data at $P < 0.05$. One-way analysis of variance (ANOVA) was performed using STATISTICA 6.0 (StatSoft Inc., www.statsoft.com) to determine effects of temperature on the population density of nematodes. The means were compared by Turkey's test ($P = 0.05$).

Table 1. Biological characteristics of nematodes.

Biological characteristic	Nematode species		
	Aphelenchus avenae	***Aphelenchoides saprophilus***	***Aphelenchoides besseyi***
Feeding strategy	fungivorous	fungivorous	parasite of plants
Life cycle (days)	10[1]	8-15[1]	10[2]
Mean lifetime (days)	25[1]	10[1]	35-50[1]
Number of laid eggs by one female	128[1]	up to 43[1]	43[1]
Number of laid eggs in 24 h	5[1]	5[1]	2[1]
Number of laid eggs in 24 h without feeding (in water)	up to 12[1]	8-12[1]	0[1]
Embryonic development (days)	2[3]	2-3[1]	2[1]
Survival at desiccation	yes[3]	n.i.	yes[4]
Presence of male	no[6]	present[6]	present[5]
Optimum temperature for population increase	+29°C[7]	+5°C[6]	+28-30°C[5, 6]

n.i. – not identified, [1]Turlygina & Chizhov (1991), [2]ISC (2021), [3]Kostuk (1971), [4]Chen (2017), [5]Sudakova (1968), [6]Shesteperov (1985), [7]Okada &Ferris (2001).

Table 2. Plan of the experiment. Initial number of nematodes in variants 1-3 – 100 individuals per test-tube and for variant 4 – 300 individuals per test-tube.

№	Variant	Temperature regimes		
1	*Aphelenchus avenae* – 100 ind.	5ºC	15-25ºC	30ºC
2	*Aphelenchoides besseyi* – 100 ind.	5ºC	15-25ºC	30ºC
3	*Aphelenchoides saprophilus* – 100 ind.	5ºC	15-25ºC	30ºC
4	*A. avenae* (100 ind.) + *A. besseyi* (100 ind.) + *A.saprophilus* (100 ind.)	5ºC	15-25ºC	30ºC

RESULTS

Effect of temperature on population growth of nematodes in monocultures. Growth and reproduction of nematodes were significantly different at temperature 5°C (n = 5, F = 6.98, P = 0.013), at 15-25°C (n = 5, F = 32.80, P < 0.00001) and at 30°C (n = 5, F = 12.16, P = 0.001). The numbers of *A. besseyi* and *A. avenae* were found to be 180- and 700-fold higher at the temperature 15-25°C as compared to the initial number of animals. At 30°C the number of animals increased by more than 150- and 700-fold for *A. besseyi* and *A. avenae*, repectively. Complete utilisation of the fungal biomass by the nematodes was recorded after 14 days at 30°C, and after 22 days at 15-25°C. Few individuals of *A. besseyi* survived at 5°C. *Aphelenchus avenae* did not reproduce at 5°C but numbers remained fairly constant during the whole period of observation. At temperature 15-25°C numbers of *A. avenae* were 1.5-fold higher than at 30°C. *Aphelenchoides saprophilus* increased at 5°C and 15-25°C but the numbers were much higher at 15-25°C (108,810 and 138,840 individuals per tube, respectively). It took 140 days for the fungal mycelium to be grazed down by *A. saprophilus* at 5°C. This species did not develop at 30°C (Fig. 1).

The temperature of 5°C only favoured the reproduction of *A. saprophilus* but all three species increased at 15-25°C with the largest increase for *A. saprophilus* of 1.3- and 7-fold greater than *A. avenae* and *A. besseyi* respectively. In monoculture, the population growth of *A. besseyi* was 5- to 7-fold slower than that of the other two species at 15-25°C.

Cultivation of nematodes in mixed culture. Significant effects of temperature on nematode populations were detected for growth in mixed cultures at 5°C (n = 5, F = 6.97, P = 0.013), 15-25°C (n = 5, F = 8.64, P = 0.006) and 30°C (n = 5, F = 7.8, P = 0.009). In mixed culture the final number of *A. besseyi* was 7- and 8-fold smaller than in monoculture at 15-25°C and 30°C, respectively. At 5°C this species did not develop in monoculture (Figs 1 & 2). The population of *A. besseyi* was not significantly different when cultivated with other nematodes at 15-25°C and 30°C (2,520 and 2,050 individuals per tube). The number of *A. avenae* decreased in treatments with other nematodes at 15-25°C and 30°C compared with the growth in monoculture (by 1.3- and 1.5-fold, respectively). In mixed culture, this species reached highest numbers at 15-25°C, 80,890 individuals per tube, which was 1.7-fold greater than its growth at 30°C, 47,740 individuals per tube. *A. avenae* was the best competitor at these temperatures. At 5°C, *A. avenae* slightly increased its population compared with initial number of nematodes, but it was significantly smaller than that of *A. saprophilus*. The numbers of *A. saprophilus* were the same as in the mono- and mixed cultures at 5°C. At 5°C, *A. saprophilus* was the best competitor compared with others species. In the presence of other nematodes it reached the highest density compared with *A. avenae* and *A. besseyi*. It was the only species capable of population growth at 5°C. At 15-25°C, *A. saprophilus* numbers decreased by 40-fold in the mixed treatment compared with its growth in monoculture, and by 34-fold compared to mixed culture at 5°C. Its numbers did not increase at 30°C (Figs 1 & 2).

Sex ratio of nematode populations. The sex ratio of *A. avenae* did not change significantly in monoculture or in mixed culture at 5°C. The populations of this species consisted mainly of females (70-82%) with a clear granular storage structure; many of these females contained eggs. *Aphelenchoides saprophilus* populations at 5°C mostly included juveniles. In the mixed culture, the number of females and males of this species were twofold greater than in monoculture (Table 3). The ratio of females to males (F/M) calculated on absolute number of nematodes decreased in mixed culture by 19-fold. At 15-25°C, the cultures of *A. avenae* were dominated by juveniles. At 15-25°C, there were changes in the sex ratios of *A. saprophilus* and *A. besseyi*. The number of males increased from 3% to 20% in the monoculture for *A. saprophilus*, and from 3% to 14% for *A. besseyi* in the mixed culture. The F/M ratio for *A. besseyi* decreased by three-fold in mixed culture. The percentage of *A. saprophilus* females in the mixed culture increased by three-fold, and the number of juveniles decreased by 2.3-fold compared with the monoculture. Numbers of *A. besseyi* juveniles decreased from 40% in monoculture to 26% in a mixed culture with the other nematodes (Table 4). At 30°C, the numbers of *A. avenae* juveniles in the mixed culture fell from 87% (in monoculture) to 59%, and the number of females rose almost threefold. The numbers of *A. besseyi* males in mixed culture with *A. avenae* and *A. saprophilus* decreased, and that of juveniles also decreased by two-fold compared with monoculture. The F/M ratio for *A. besseyi* in mixed culture increased twofold (Table 5).

DISCUSSION

The population growth of nematodes is affected by temperature, with different optimum temperatures for population development of *A. avenae* and the genus *Aphelenchoides* (Hasna *et al.*, 2007). This study has shown that reproduction rates of the three nematode species in mixed cultures affected their interspecific interactions.

The temperature regime of 15-25°C was favourable for growth and reproduction of all the three nematode species in monoculture. The temperature 30°C was favourable for *A. avenae* and *A. besseyi*. At 5°C, only *A. saprophilus* developed and multiplied. These results are generally in agreement with previous studies by Okada & Ferris

Table 3. Population structure (%) in mono- and mixed culture of *Aphelenchus avenae* and *Aphelenchoides saprophilus* at 5°C from initial concentration (100 individuals).

Variant	Species checked	Population structure (%)			
		Females	Males	Juveniles	F/M
monoculture					
A. avenae 100 ind.	*A. avenae*	82 ± 9 (11)[1]	–	18 ± 3 (17)	–
A. saprophilus 100 ind.	*A. saprophilus*	9 ± 3 (33)	2 ± 0.5 (25)	89 ± 25 (28)	3.8 ± 1.1[b](29)
mixed culture					
A. besseyi 100 ind. + *A. saprophilus* 100 ind. + *A. avenae* 100 ind.	*A. saprophilus* (100 ind.)	18 ± 4 (22)	4 ± 3 (75)	78 ± 27 (35)	0.2 ± 0.04[a](20)
	A. avenae (100 ind.)	70 ± 16 (23)	–	30 ± 4 (13)	–

[1]Mean number ± SD (Coefficient of variation, %), n = 5; means with different letters are significantly different at $P < 0.05$. F/M is a ratio of females to males calculated on absolute number of nematodes.

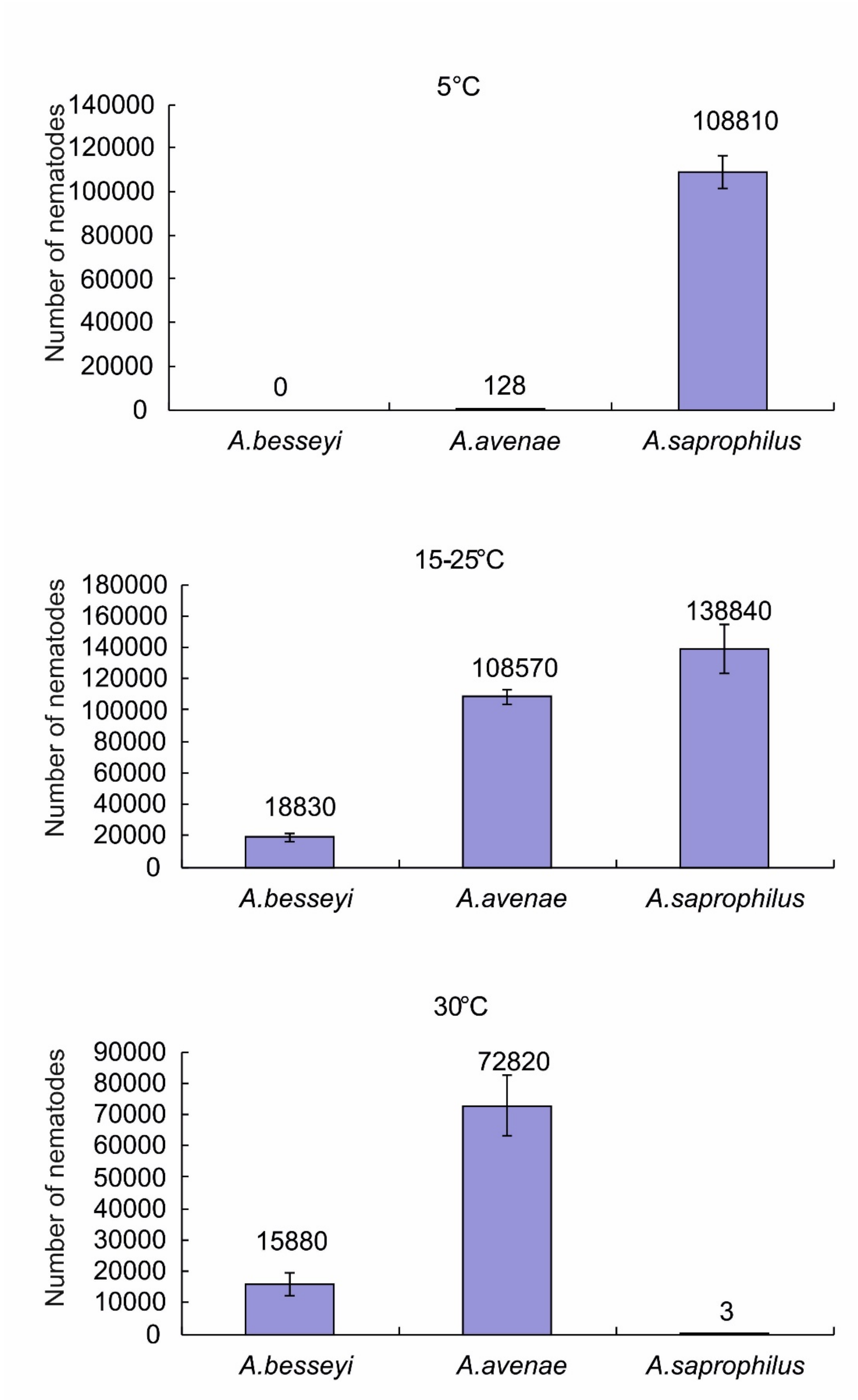

Fig. 1. Mean number ± SD of *Aphelenchus avenae*, *Aphelenchoides saprophilus* and *Aphelenchoides besseyi* at 5°C, 15-25ºC and 30ºC in monocultures from initial concentration (100 individuals). Each bar is the mean of five replications (n = 5).

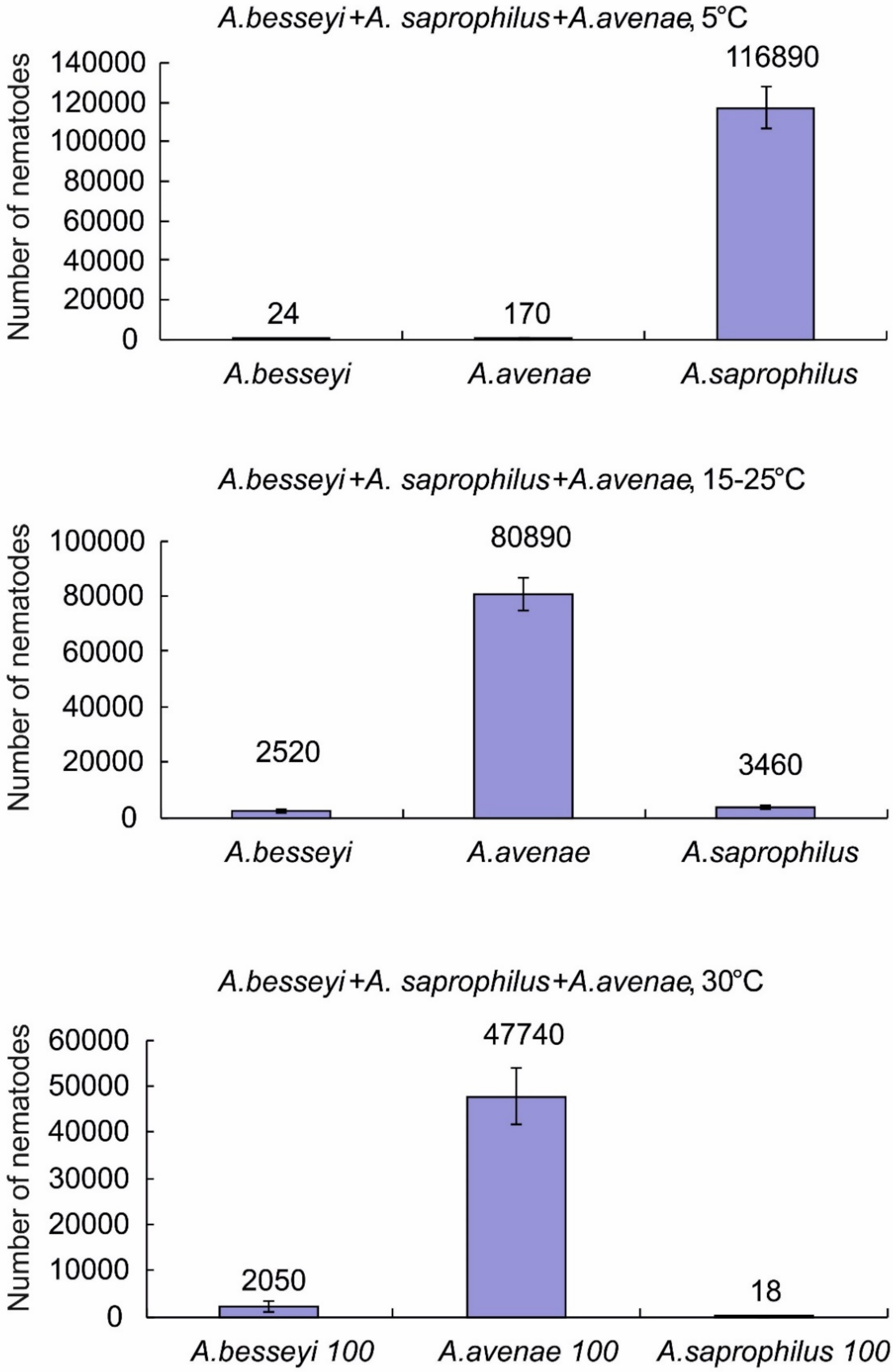

Fig. 2. Mean number ± SD of of *Aphelenchus avenae*, *Aphelenchoides saprophilus* and *Aphelenchoides besseyi* at 5°C, 15-25°C and 30°C in mixed culture from initial concentration (100 individuals). Each bar is the mean of five replications (n = 5).

Table 4. Population structure (%) in mono- and mixed culture of *Aphelenchus avenae* and *Aphelenchoides saprophilus* at 15-25°C from initial concentration (100 individuals).

Variant	Species checked	Population structure (%)			
		Females	**Males**	**Juveniles**	**F/M**
monoculture					
A. besseyi 100 ind.	*A. besseyi*	57 ± 20 (35)[1]	3 ± 1 (33)	40 ± 16 (40)	22 ± 12^b(54)
A. avenae 100 ind.	*A. avenae*	15 ± 14 (93)	–	85 ± 4 (5)	–
A. saprophilus 100 ind.	*A. saprophilus*	15 ± 5 (33)	3 ± 2 (67)	82 ± 25 (30)	4.6 ± 2^a(43)
mixed culture					
A. besseyi 100 ind. + *A. saprophilus* 100 ind. + *A. avenae* 100 ind.	*A. besseyi* (100 ind.)	60 ± 22 (37)	14 ± 5 (36)	26 ± 9 (35)	6.8 ± 4.7^a(69)
	A. avenae (100 ind.)	20 ± 5 (25)	–	80 ± 13 (16)	–
	A. saprophilus (100 ind.)	44 ± 29 (66)	20 ± 5 (25)	36 ± 19 (53)	3.5 ± 1.3^a (37)

[1]Mean number ± SD (coefficient of variation, %), n = 5; means with different letters are significantly different at $P < 0.05$. F/M is a ratio of females to males calculated on absolute number of nematodes.

Table 5. Population structure (%) in mono- and mixed culture of *Aphelenchus avenae* and *Aphelenchoides saprophilus* at 30°C from initial concentration (100 individuals).

Variant	Species checked	Population structure (%)			
		Females	**Males**	**Juveniles**	**F/M**
A. besseyi 100 ind.	*A. besseyi*	54 ± 41 (76)[1]	32 ± 22 (69)	14 ± 10 (71)	1.74 ± 0.6^a(34)
A. avenae 100 ind.	*A. avenae*	13 ± 6 (46)	–	87 ± 47 (54)	–
A. saprophilus 100 ind.	*A. saprophilus*	80 ± 9 (11)	0	20 ± 3 (15)	–
A. besseyi 100 ind. + *A. saprophilus* 100 ind. + *A. avenae* 100 ind.	*A. besseyi* (100 ind.)	70 ± 54 (77)	23 ± 9 (39)	7 ± 5 (71)	3.3 ± 1.3^b(39)
	A. avenae (100 ind.)	41 ± 4 (10)	–	59 ± 11 (19)	–
	A. saprophilus (100 ind.)	88 ± 7 (8)	0	12 ± 3 (25)	–

[1]Mean number ± SD (coefficient of variation, %), n = 5; means with different letters are significantly different at $P < 0.05$. F/M is a ratio of females to males calculated on absolute number of nematodes.

(2001). In our study, the largest numbers of negative interspecific interactions were recorded under the 15-25°C regime. All species of nematodes developed well in the monoculture. A significant decrease of nematode numbers in mixed cultures was a consequence of the competition for fungal food resources.

There is an overall trend for nematode populations to increase the proportion of males when they are subjected to some form of stress including temperature and crowding (Yeates, 1987). Our results have shown that in mixed cultures the proportion of *A. besseyi* and *A. saprophilus* males increased from 3% to 14-20% at 15-25°C. The temperature regime of 15-25°C was favourable for all the nematode species and we suggest that interspecific competition between nematodes is a major cause of the increase in the number of males in the populations. The analysis of the population structure of competitors is important because the species with the highest rate of reproduction will have a competitive advantage (Odum, 1971).

Aphelenchus avenae showed the best competitive capacity compared with the other nematode species at 15-25°C and 30°C. This species can be found in different structures and in the rhizosphere of higher plants in various combinations with fungivorous and other trophic groups of nematodes (Ishibashi *et al.*, 2000; Taher *et al.*, 2017; Javed & Khan, 2021). *Aphelenchus avenae* has a set of adaptations for the occupation of different ecological niches and resistance to interspecific competition. It consumes a variety of fungal species and is characterised by high fecundity (more than 200 eggs at a time, laying eggs without feeding), parthenogenesis and survival of desiccation (Kostuk, 1971; Turlygina & Chizhov, 1971; Huang *et al.*, 1972; Ishibashi *et al.*, 2000, Okada & Ferris, 2001; Chen *et al.*, 2017; Javed & Khan, 2021). All these features enable the species rapidly to achieve high numbers under favourable conditions. Moreover, this species can attack other nematodes (Decker, 1962; Zhang *et al.*, 2020). In our experiments, population numbers of *A. besseyi* and *A. saprophilus* at 15-25°C in the cultures with *A. avenae* decreased drastically, particularly the numbers of juveniles. We speculate that the stylet-bearing nematode *A. avenae* may have predated the eggs and/or slow-moving juveniles. Haraguchi & Yoshiga (2020) also demonstrated the suppression of plant parasitic nematode *Ditylenchus destructor* by *A. avenae* at 20°C on nutrient medium and in soil.

At 5°C, *A. saprophilus* exhibited a higher reproductive rate than *A. besseyi* and *A. avenae*. This growth at low temperatures is consistent with *A. saprophilus* being a soil-living species. The previous experiments showed that this species developed and reproduced under snow cover and reached 10,000 individuals (25 g roots)$^{-1}$ (Shesteperov, 1985).

Aphelenchoides besseyi and *A. avenae* did not reproduce and compete for food at 5°C; *A. saprophilus* did not compete at 30°C, which can be explained by its inability to develop rapidly at high temperatures. Although in monoculture the population numbers of this species were the highest at 5°C and 15-25°C, in the presence of other species of nematodes it was unable to compete and its population numbers fell dramatically at 15-25°C.

As a parasite of higher plants, *A. besseyi* was unable to compete with the fungivorous nematodes *A. avenae* and *A. saprophilus* because of its slower growth rate. In all treatments other than at 30°C where *A. saprophilus* could not develop, the numbers of *A. besseyi* were considerably lower than those of the other nematode species. This suggests that in the course of its evolution *A. besseyi* became parasite of higher plants and lost its competitive ability as mycophagous organism. Negative effects of temperature on the growth and development of *A. besseyi* at 5°C may be used to develop a biotechnological approach for suppressing this plant parasite.

The awareness of temperature dependent interaction effects as documented in the present study is essential if we are to understand the patterns of nematode population dynamics, to predict and assess the plant's resistance to parasitic nematodes and to develop the strategy of biological and chemical control of pathogenic microorganisms in conditions of rapid climate change. The chosen model takes account of biological characteristics of nematodes under different temperature regimes using the data obtained in the course of experiments. The study has demonstrated that population dynamics of the investigated species of nematodes are related to temperature and there are temperature optimums for each of the species, with clearly visible patterns of highly competitive interactions between them. These patterns are characterised by changing sex ratios dependent on temperature regimes: unfavourable conditions caused increases in the number of males in the population.

The results of these experiments may contribute to a better understanding of the mechanisms of competition between different species of nematodes. The observed patterns of population growth of rare species of nematodes in plants and soil have led us to suppose that dominant species prevail in competitive interactions with other species owing to their competitive capacity in these conditions but without the elimination of rare species. Under environmental conditions unfavourable for the dominant species, they are displaced by the species possessing ecological attributes that enable them to reproduce and survive in this biotope. Permanent changes in environmental conditions and original biological properties of nematodes may allow co-existence of different nematodes in natural ecosystems.

The results of the present study are particularly relevant to the production of rice; further research is needed to examine the behaviour of nematodes living in other terrestrial ecosystems.

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А.А. Шестеперов и В.Д. Мигунова. Рост и размножение *Aphelenchus avenae*, *Aphelenchoides saprophilus* и *Aphelenchoides besseyi* в чистых и смешанных культурах при культививировании на грибе *Alternaria tenuis*.

Резюме. *Aphelenchoides saprophilus* и *Aphelenchus avenae* используются для биологической борьбы с патогенными грибами растений с 1970-х годов. При изменении климатических условий не совсем очевидно, как эти нематоды будут взаимодействовать с фитопаразитом *Aphelenchoides besseyi*, который может быстро увеличивать свою численность при высоких температурах. Для предотвращения потерь урожая необходима модель, которая поможет предсказать поведение каждого вида нематод при их взаимодействии. В статье исследуются взаимодействия между грибоядными нематодами *Aphelenchus avenae* и *Aphelenchoides saprophilus* а также фитопаразитической нематодой *A. besseyi*. Конкурентные взаимодействия между нематодами привели к снижению численности животных при их совместном содержании в смешанных культурах. *A. avenae* оказался более конкурентноспособным, чем *A. besseyi* и *A. saprophilus* в интервалах 15-25°C и 30°C. При 5°C только *A. saprophilus* значительно увеличил свою численность. Эксперименты показали, что температура, репродуктивный потенциал, а также биологические характеристики вида влияют на конкурентные взаимодействия между тремя видами нематод.