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Elevated Soil Temperatures Impact Nematode Reproduction Biology

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Abstract: Plant-parasitic nematodes are one of the economically most important pathogens, and how rising soil temperatures due to climate change impact their ability to damage crops is poorly understood. The current study was conducted to evaluate the reproduction biology (reproduction and virulence) of *Rotylenchulus reniformis* and *Meloidogyne floridensis* on tomato at soil temperatures of 26 °C (control), 32 °C, 34 °C, and 36 °C. The reproduction and virulence of both nematode species were differentially impacted by soil temperature. Relative to the control, the increase in reproduction of *R. reniformis* ranged from 20% to 116% while that of *M. floridensis* ranged from 22% to 133%. The greatest reproduction of *R. reniformis* was observed at 34 °C while that of *M. floridensis* was observed at 32 °C. Across all temperatures, reproduction of *M. floridensis* was 2.9 to 7.8 times greater than the reproduction of *R. reniformis*, suggesting that the former nematode species has a greater fecundity. The rates of change in reproduction relative to the controls were greater in *M. floridensis* than in *R. reniformis*, indicating that the latter nematode species is more resilient to changes in soil temperature. The virulence of both nematode species increased numerically or significantly at 32 °C and 36 °C, but not at 34 °C. The greatest virulence of both nematode species was observed at 36 °C at which 57% and 60% root biomass was lost to *R. reniformis* and *M. floridensis*, respectively, compared to the root biomass of uninoculated plants at that temperature. The results of the current study suggested that crop damage by nematodes will likely increase as global soil temperature continues to increase.

Keywords: biology; climate change; crop losses; nematodes; reproduction; temperature; virulence

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1. Introduction

Climate change reflects a long-term shift in the earth's weather patterns [1,2]. Although climate change is a continuous process, it is accelerated by human activities such as increased burning of fossil fuels and unsustainable land use practices [2–4]. The earth has experienced a temperature increase of 1.1 °C relative to the pre-industrial period, and the temperature is predicted to go up by 4.4 °C by the end of 2100 [4], which is evidence that temperature is the most prominent indicator of climate change. The global rise in soil temperature will likely persist for another three to five decades even if greenhouse gas emissions are halted immediately [5].

Agriculture is hard hit by rising soil temperatures as they result in increased physiological stress on plants and greater pest pressure, thus challenging global food security [6,7]. Previous studies have reported elevated soil temperature as a major contributor

to the shift in microbial communities from beneficial to harmful pathogens—a process that results in increased pathogen virulence, poor crop health, and reduced crop yields [8]. Although a few studies in the past have reported the impacts of elevated soil temperature on virulence of various pathogens [7,9–11], the impacts on nematodes are poorly understood. Nematodes are one of the major agricultural pests that are responsible for an estimated USD 358 billion in annual crop losses worldwide [12], and understanding the impacts of elevated soil temperature on nematodes could help develop better nematode management programs.

The main objective of our study was to understand the impacts of elevated soil temperatures on reproduction biology, collectively referred to as reproduction and virulence, of plant-parasitic nematodes. This study employed two economically important plant-parasitic nematodes: the reniform nematode (*Rotylenchulus reniformis*) and the peach root-knot nematode (*Meloidogyne floridensis*). These nematodes were selected to represent a significant threat to annual and perennial crops in the US due to a lack of effective management methods. The reniform nematode is known to have an increased survival rate, reproduction rate, and virulence at higher soil temperatures [7]. This nematode is an economically important pathogen and has a wide host range comprising 350 plant species in 77 plant families [13,14]. Because of a very low damage threshold of two reniform nematodes/100 cm^3 soil and the lack of highly resistant cotton cultivars, the US cotton belt loses USD 57.2 million to this nematode every year [15]. Similarly, the high level of virulence of *M. floridensis*, its ability to overcome root-knot nematode resistance genes, and its expanding distribution make this a species of serious concern for many vegetable and fruit crops [16–18].

2. Results

2.1. Impact of Soil Temperature on Reproduction of Nematodes

Reproduction of *R. reniformis* was significantly impacted by soil temperatures as presented in Figure 1A ($p = 0.012$). The number of eggs/g of roots ranged from 13,727 to 29,919, with the greatest reproduction occurring at 34 °C and the least reproduction occurring at 36 °C. Nematode reproduction increased numerically at 32 °C and significantly at 34 °C, thereby declining again at 36 °C in a statistically similar level relative to that of the control temperature. The increments in reproductions were 20% at 32 °C and 116% at 34 °C, while the reproduction was decreased by 1% at 36 °C relative to that of the control temperature.

Reproduction of *M. floridensis* was significantly impacted by soil temperature as presented in Figure 1B ($p = 0.009$). The number of eggs/g of roots ranged from 48,723 to 113,593, with the greatest reproduction occurring at 32 °C and the least reproduction occurring at 26 °C. Nematode reproduction was significantly higher at 32 °C, the increment being 133% relative to that at the control. Nematode reproduction at 34 °C was 79% greater relative to that of the control, although the increment was not statistically significant. Interestingly, the reproduction of nematodes at 36 °C was increased by 22% relative to that at 34 °C, although the reproductions were statistically similar. The reproduction at 36 °C was 119% greater than that of the control, with the reproductions being significantly different.

2.2. Impact of Soil Temperature and Nematode Species on Root Biomass

Soil temperature significantly impacted the root biomass of tomatoes infested with *R. reniformis* as presented in Figure 2A ($p = 0.002$). The dry root biomasses of tomatoes across all temperatures ranged from 0.08 g to 0.17 g, with the least biomass occurring at 36 °C. The plants at the control temperature had the greatest root biomass. The root biomass was significantly lower at 32 °C compared to the control. At 34 °C, the root biomass was

lower than that of the control, although not at a statistically significant level. The root biomass decreased significantly at 32 °C, numerically at 34 °C, and declined significantly at 36 °C relative to the control temperature. The decrements in root biomasses were 41% at 32 °C, 29% at 34 °C, and 53% at 36 °C relative to the control temperature.

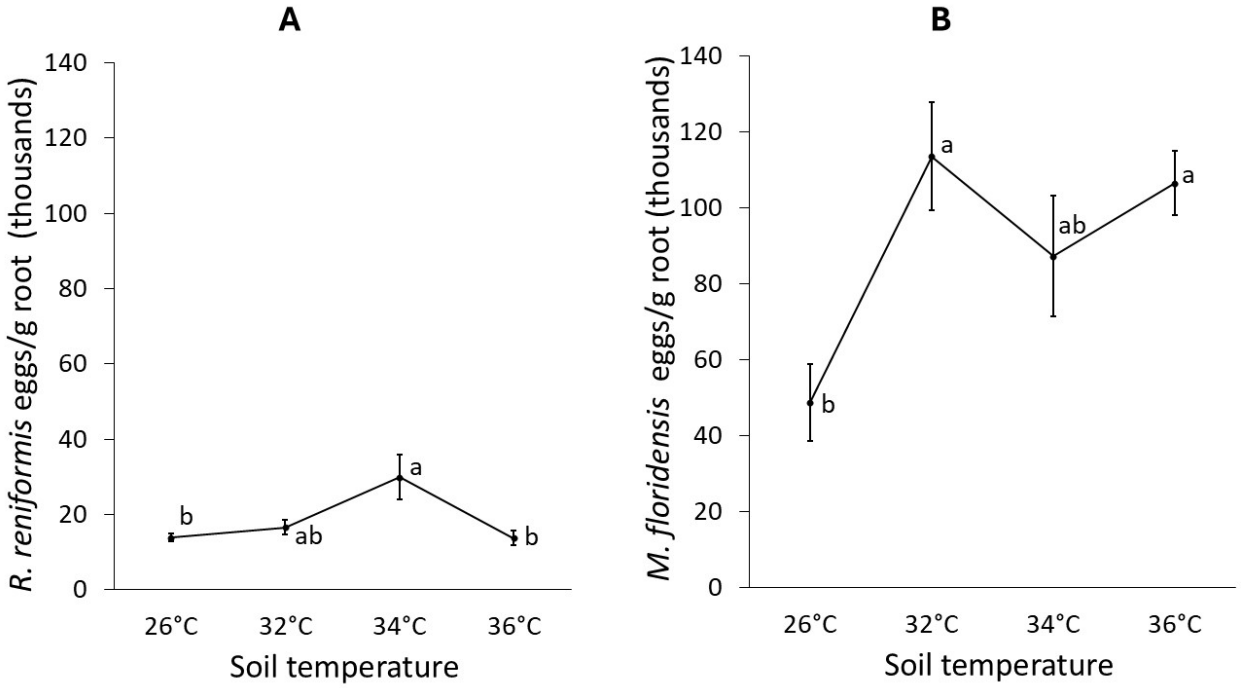

Figure 1. The reproduction of *R. reniformis* (**A**) and *M. floridensis* (**B**) on tomatoes as influenced by various soil temperatures at 30 days post-inoculation. Data were combined over two experiments and are means of eight replications. Treatment means followed by a common letter are not significantly different according to Tukey's HSD test ($p < 0.05$).

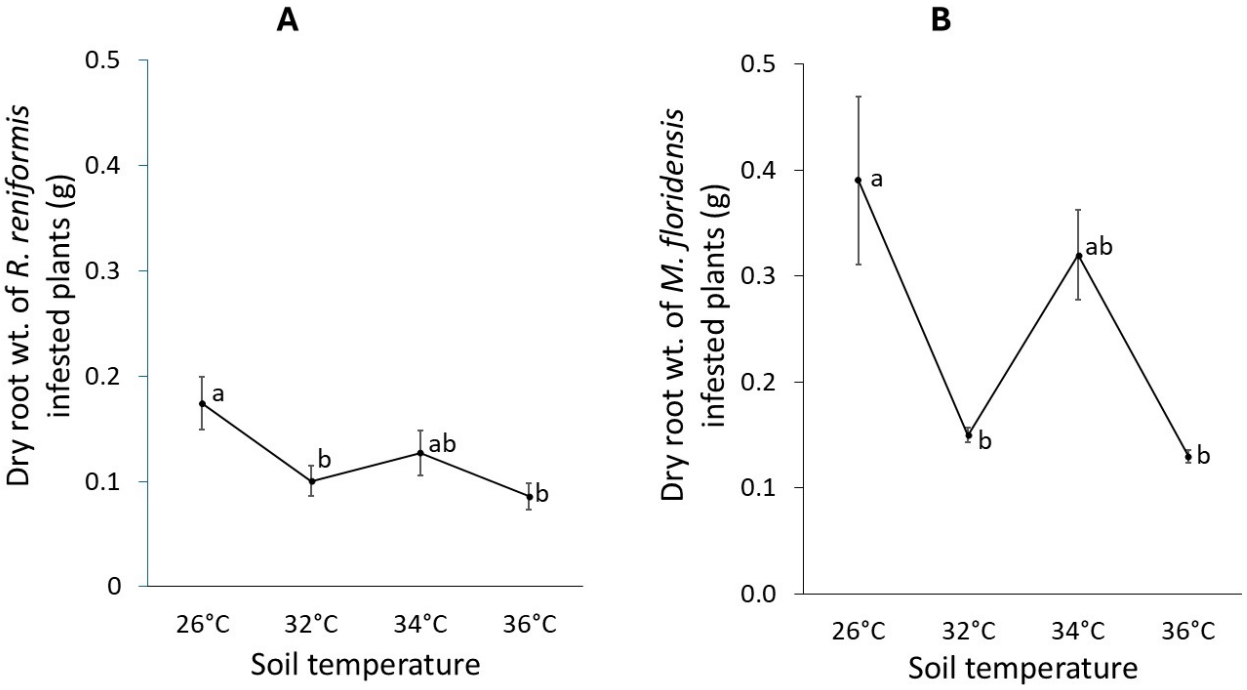

Figure 2. The root biomasses of tomatoes infested with *R. reniformis* (**A**) and *M. floridensis* (**B**) as influenced by various soil temperatures at 30 days post-inoculation. Data were combined over two experiments and are means of eight replications. Treatment means followed by a common letter are not significantly different according to Tukey's HSD test ($p < 0.05$).

Soil temperature significantly impacted the root biomass of tomatoes infested with *M. floridensis* as presented in Figure 2B ($p = 0.004$). The dry root biomass of tomatoes across all temperatures ranged from 0.13 g to 0.39 g, with the least biomass occurring at 36 °C and the greatest biomass occurring at the control temperature. The statistical trend in the impacts of soil temperatures on root biomass of *M. floridensis*-infested plants was the same as that displayed on the plants infested with *R. reniformis*. However, the rates of changes in root biomasses were greater for the plants infested with *M. floridensis* compared to those infested with *R. reniformis*. Additionally, the root biomasses of tomatoes infested with *M. floridensis* were consistently higher at each soil temperature relative to those infested with *R. reniformis*. The reduction in root biomass of *M. floridensis* plants was 62% at 32 °C, 18% at 34 °C, and 67% at 36 °C relative to that of the control temperature.

2.3. Impact of Soil Temperature on Nematode Virulence

Soil temperature had a significant impact on the virulence of *R. reniformis* as presented in Figure 3A ($p = 0.003$). The level of nematode virulence (loss of root biomass due to nematode infestation) differed across the soil temperatures. The nematode was responsible for a loss of 24% root biomass at the control temperature, 49% at 32 °C, and 57% at 36 °C. There was a gain of 15% root biomass by the plants infested with the nematode at 34 °C relative to the uninoculated plants at that temperature, although the gain was not statistically significant. The virulence was significantly higher at 32 °C and 36 °C, and it remained statistically similar at 34 °C and at the control temperature.

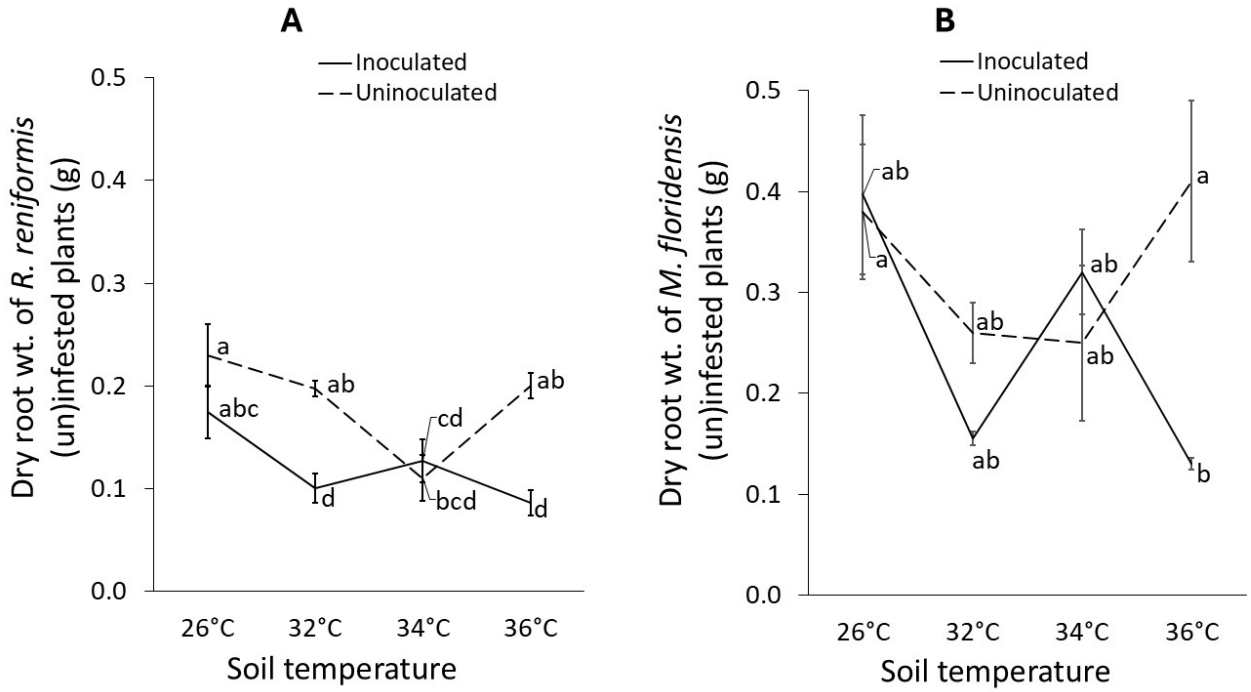

Figure 3. The root biomasses of tomatoes inoculated with *R. reniformis* and uninoculated controls (**A**) and *M. floridensis* and uninoculated controls (**B**) as influenced by various soil temperatures at 30 days post-inoculation. Data were combined over two experiments, and are means of eight replications. Treatment means followed by a common letter are not significantly different according to Tukey's HSD test ($p < 0.05$).

The virulence of *M. floridensis* was significantly influenced by soil temperatures as presented in Figure 3B ($p = 0.03$). Root biomass losses of 40% and 60% were observed at 32 °C and 36 °C compared to the root biomass of uninoculated plants at their respective temperatures. The root biomasses of nematode-inoculated plants were 4% higher at the

control temperature relative to those of uninoculated plants, although not at a significant level. Similarly, a 28% gain in root biomass was observed in plants inoculated with the nematode at 34 °C relative to the uninoculated plants at that temperature, although the gain was not statistically significant.

3. Discussion

As global soil temperature continues to increase, changes in the biology of pathogens are essential for their successful adaptation and continued invasion of plants. Nematodes are one of the most important plant pathogens [12]; however, a knowledge gap exists on how nematode reproduction and virulence, collectively referred to as reproduction biology, is influenced by rising soil temperature. The current study employing two economically important nematode species found that changes in soil temperature led to changes in nematode reproduction biology, consequently impacting plant growth and development. Under the circumstances of the current study, we noticed that two nematodes have their own unique temperature regimes: the tipping point for *R. reniformis* reproduction was at 34 °C, while that point for *M. floridensis* was at 32 °C. Although the reproduction of *R. reniformis* declined at 36 °C relative to 34 °C, the reproduction at 36 °C remained at a statistically similar level to that of the control temperature, suggesting that this nematode may develop adaptability at soil temperatures beyond 36 °C. The reproduction of *M. floridensis* at 36 °C being at a statistically similar level to that at 32 °C suggests that this nematode may continue to increase its reproduction beyond 36 °C. While the soil temperature beyond 36 °C may not be suitable for crop growth, further studies are needed to confirm the reproductive ability of *R. reniformis* and *M. floridensis* beyond that temperature.

The high reproduction of *R. reniformis* at 34 °C and reduced reproduction beyond that temperature is not surprising as the nematode is of subtropical origin. It also seems reasonable that *M. floridensis* may be able to adapt to increasing soil temperatures by increasing the level of reproduction as the nematode is of tropical origin. Nematodes are highly adaptive to abiotic stresses due to their ability to survive at very low oxygen concentrations (<1.44 μM), halt or slow down biological functions, and cross-tolerate detoxification [19]. These characteristics have enabled nematodes to co-evolve with earth's changing environment for the past several million years [20]. Warmer climates can also influence the rate of reproduction, sex ratio, abundance, diversity, development, and period of transmission [21,22]. The greater or statistically similar reproductions of *M. floridensis* and *R. reniformis* at higher soil temperatures relative to the control temperature suggest that nematode reproduction will likely be favored as global soil warming continues.

A marked difference in the level of reproduction as well as the rate of reproduction was observed between *R. reniformis* and *M. floridensis*. The reproduction of *M. floridensis* was 2.9 to 7.8 times greater than the reproduction of *R. reniformis* suggesting that the former nematode species reproduces in a greater capacity. Furthermore, the rates of change in reproduction relative to the controls were greater in *M. floridensis* than in *R. reniformis*. The slower and relatively less fluctuating reproduction of *R.* reniformis is an indication that this nematode is probably more resilient to soil temperature changes. A previous study also reported a similar trend in the level and rate of reproduction of *R. reniformis* and *M. floridensis*: the reproduction of the former species decreased at a decreasing rate as the soil temperature increased while that of the latter species decreased at an increasing rate [7]. While *R. reniformis* in the current study also seemed to be more resilient to changes in soil temperature than *M. floridensis*, the reproduction of both nematodes fluctuated as the soil temperatures increased. A possible reason for the slight differences in results between the current study and the previous study could be due to the environmental conditions, the

range of temperatures, and the duration of the study. The current study employed heat 24 h a day throughout the study period while the previous study employed heat for 7 h a day, which might have affected the level and the rate of nematode reproduction. However, a study conducted in the mid-1980s reported that uniform or fluctuating day and night temperatures had a similar impact on the egg hatching of a different nematode species, *Longidorus elongates* [23]. The duration of the current study was one month while that of the previous one was 45 days. While a month is the average time for most plant-parasitic nematodes to complete their life cycle, conducting nematological research for 60 and 45 days is very common. Collecting data at the time when nematodes complete their life cycle would provide a better estimation of nematode reproduction. The current study employed a wider range of temperatures than the previous one, providing a better insight into the impacts of lower and higher temperatures on nematode reproduction. The literature also suggests that the extent of the impacts of soil temperature on nematode reproduction biology is dependent upon the temperature and the nematode species [24]. However, it is unclear what percentage of the eggs hatch into the infective stages—the stage that subsequently infests the crop and undergoes reproduction. Because nematodes go through multiple life cycles in a single crop growing season, longer-duration studies are needed to determine the impacts of soil temperatures on the reproduction biology of subsequent generations of nematodes.

Relative to the controls, root biomasses of nematode-infested plants were reduced as the soil temperatures increased. The rate of losses, however, differed between the two nematode species. The root biomass losses to *R. reniformis* increased at a decreasing rate while the losses to *M. floridensis* increased at an increasing rate. While a soil temperature of 34 °C seemed to be a favorable temperature when crop losses to nematodes became statistically similar to that of the control temperature, the crop suffered greater losses at other soil temperatures. Our results are in agreement with previous reports of increased crop losses due to climate-change-induced soil warming [6,7], suggesting a need for the development of climate-change-resilient crop management programs.

Comparisons of plant root biomasses between nematode inoculated and uninoculated plants provided a better indication of nematode virulence. The greatest root biomass losses of 49% to *R. reniformis* and 40% to *M. floridensis* at 32 °C compared to those of uninoculated plants suggested the virulence of both nematodes was greater at that temperature. Furthermore, 57% and 68% of root biomasses lost to *R. reniformis* and *M. floridensis*, respectively, relative to the uninoculated plants at 36 °C suggested that the greatest nematode virulence occurred at that temperature. Nematode virulence was not observed at 34 °C despite an increase in nematode reproduction at that temperature. To the best of our knowledge, there are no published studies on the impacts of soil temperatures on these nematode species, other than the one published by Khanal and Land in 2023. As stated earlier, further studies are needed to determine the reasons behind statistically similar root biomasses of nematode-infested and uninfested plants at 34 °C. Nevertheless, our study indicates that nematode virulence will increase as the soil temperature increases, suggesting that agriculture will be hard hit by climate change-induced soil warming.

Current nematode management methods are heavily reliant on fumigants that are harmful to human health and the environment, making this practice highly unsustainable. Fumigants are applied as pre-plant applications, and they do not suppress nematode reproduction throughout the crop growing season [25,26]. Thus far, neither alternatives such as non-fumigant and biological nematicides nor crop rotations have provided effective nematode management as fumigants. A safer and more sustainable method would be the use of host plant resistance. Ironically, a handful of root-knot nematode resistance genes currently known become unstable at soil temperatures above 27 °C [27–31]. The activity

of pathogenesis-related proteins, such as superoxide dismutase, peroxidase, chitinases, and beta 1-3 glucanase, is decreased at higher soil temperatures leading to reduced nematode resistance [32]. Some *R. reniformis*-resistant cotton breeding lines developed in the past displayed severe stunting when nematode pressures were higher [33,34]. Increased reproduction and virulence of nematodes coupled with the inefficacy of resistance genes at higher soil temperatures will likely lead to greater crop damage in the future. Identification of nematode resistance genes that are stable at higher soil temperatures is necessary for protecting our crops from the wrath of climate change.

The development of effective and durable nematode management programs requires a deeper understanding of the relationship between nematode and soil environment complex. Our study helped understand how nematode reproduction biology is impacted by soil temperature which is one piece of the soil complex puzzle. Previous studies have also emphasized temperature as a key component to determine embryogenic and other biological processes [35–38]. Long-term studies are required to fully understand the impacts of climate change on the soil environment complex that includes nematodes, other soil microbiomes, moisture, texture, nutrient content, and electrical conductivity, to mention a few.

4. Materials and Methods

4.1. Preparation of Nematode Inoculum

Populations of *R. reniformis* and *M. floridensis* were maintained in a growth room environment on soybean (*Glycine max* L., cv. Braxton, Asgrow Seed Company, Kalamazoo, MI, USA) and tomato (*Solanum lycopersicum* L. cv. Rutgers, Seedway, New York, NY, USA) plants, respectively. Nematode eggs were extracted by agitating the plant roots in 10% commercial bleach for four minutes according to the method of Hussey and Barker [39]. The root agitation was conducted at 150 revolutions per minute in a New Brunswick™ Innova shaker (VWR, Radnor, PA, USA). Extracted eggs were collected in a beaker using a 500 µm USDA Standard sieve.

4.2. Establishment of Experiment

Experiments were established in a growth room on the main campus at Clemson University in Clemson. The treatments included a factorial structure of two nematode species (*R. reniformis* and *M. floridensis*) and four soil temperatures (26, 32, 34, and 36 °C). The lowest temperature of 26 °C represented the soil temperature during the experiment establishment in April of the previous year (2022), and it served as a control temperature. Similarly, 32 °C was selected to represent the maximum soil temperature recorded from April to June 2022 by the Midwestern Regional Climate Center (https://mrcc.purdue.edu/RMP/historical#, accessed on 20 March 2023). Finally, temperatures of 34 °C and 36 °C were selected to represent the IPPC-predicted 4 °C rise in soil temperature by 2100 from the base of the current maximum temperature [4].

Three-week-old tomato seedlings were transplanted into 15 cm top-diameter plastic pots filled with 1.5 kg sandy loam soil. Prior to pot filling, the soil was autoclaved in three cycles of 45 min at 123 °C and was left for a week in open plastic bins to allow for the release of possible toxic gases formed during sterilization. On the day of transplanting, a 1 mL water suspension containing 10,000 freshly extracted eggs of *R. reniformis* or *M. floridensis* were inoculated to each pot using a pipette and by making three 5 cm depressions 2 cm away from the crown region [40]. Pots were placed on 53 cm long and 51 cm wide commercial heat mats (iPower, Model No. GLHTMTCTRLV2HTMTMX2, China) immediately after inoculation. Four sets of heat mats were laid on a table in the growth room with temperature settings of 26, 32, 34, and 36 °C. Heat mats were turned on throughout the study period.

Soil temperatures were monitored daily at 2 pm. Pots that did not receive any nematode inoculum served as uninoculated controls for each temperature. Each treatment was replicated four times in a randomized complete block design. The ambient temperature of the growth room during the study period was 25 ± 1 °C and relative humidity was 46 ± 11%. The four metal halide bulbs (1000 W) hanging approximately 3 m above the table provided a 14 h photo period. Plants were watered daily and fertilized weekly using Miracle Grow Plant Food (N-P-K 20-20-20). Standard insect management practices that are not known to impact nematodes (Imidacloprid, Bifenthrin, Pyridaben, etc.) were conducted. The entire experiment was repeated once.

Each experiment was terminated a month after inoculation and nematode reproduction and plant biomass data were collected. Nematode eggs were extracted from each nematode inoculated root system by gently washing the roots with tap water to remove soils and subsequently agitating them in 10% commercial bleach solution, as described above. Eggs from each root system were enumerated under a compound microscope (Martin Microscope Company, Easley, SC, USA) at 40× magnification to represent the nematode reproduction. Roots after egg extraction were dried at 55 °C for 2 weeks. At any temperature and for each nematode species, a decrease in root biomass of plants inoculated with nematodes relative to the root biomass of those that did not receive nematodes was assessed as a measure of increased nematode virulence.

4.3. Data Analysis

The data from two experiments were combined for analysis because of the absence of experiment by treatment interactions. Nematode reproduction and root biomass data were subjected to one-way analysis of variance (ANOVA) using R stat version 4.2.2 [41]. The data were assessed for normality, and any non-normal data were transformed to fulfill the assumptions of ANOVA, as suggested by the R package BestNormalize function. Soil temperature, nematode reproduction, and root biomass were considered fixed effects, while replication was considered a random effect. For the assessment of nematode virulence, root biomasses of nematode inoculated and uninoculated plants were subjected to two-way ANOVA using JMP PRO [42]. Nematode inoculation (inoculated and uninoculated) and soil temperature were considered fixed effects while replication was considered a random effect. Tukey's HSD ($p \leq 0.05$) was used for *post-hoc* mean comparisons. Nematode reproduction is the number of eggs per gram root system, and virulence is the loss of the root biomass due to nematode infection.

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Data Availability Statement: The datasets used and/or analyzed during the current study will be made available from the corresponding author upon reasonable request.

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Conflicts of Interest: The authors declare no conflicts of interest.

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