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Bionomics of wheat seed gall nematode *Anguina tritici*

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Abstract: The wheat seed gall nematode *Anguina tritici* is a scientifically interesting nematode due to its aerial parasitic behaviour and ability to survive for years under desiccated conditions in seed galls. However, *Anguina*'s life cycle and its correlation with host-plant growth and environment are poorly understood. Here, we conducted a microplot study at IARI, New Delhi, India, to examine the effects of early and late sowing dates on the life cycle of the wheat seed gall nematode using growing degree days (GDD). The study confirmed the presence of juvenile stages in the soft, undifferentiated floral mass and the upper one-third part of the stem. During the early stage of floral differentiation, the plant ovary develops into milky grains, while the galls (false ovules) become fully green. An increase in size and gonad cell development was observed when nematode J2S entered the floral tissue. The count of adult females in galls marginally surpasses that of adult males, and the female: male ratio ranged from 1.46 : 1.00 to 1.48 : 1.00. After GDD and cGDD (cumulative growing degree days) calculation, we found that the nematode completed its life cycle in 90 to 140 days, depending on the wheat sowing dates and change in temperature. The study also showed that nematode development was in sync with wheat plant growth and development. The information developed from the study such as the cumulative GDD and it's correlation with *Anguina*'s life cycle, presence of nematode in stem, flower and gall, it's migration from collar to flower, presence of various stages of nematode in different plant tissues, and it's undergoing the anhydrobiotic process in seed galls may be used to determine the best time to intervene and manage nematode infestations.

Keywords: plant-parasitic nematodes; life cycle; parasitism; anhydrobiosis; growing degree days

Plant-parasitic nematodes (PPNs) pose a significant and formidable threat to agricultural production worldwide. The earliest reported nematode pest of the wheat crop is the wheat seed gall nematode (WSGN), *Anguina tritici*. It was the first PPN identified in the literature, discovered in 1743 by T. Needham. Among the five developmental stages (egg, J2, J3, J4, and adults) of *A. tritici*, the second-stage juveniles (J2) serve as the primary source of inoculum for causing disease in plants. J2S are known to survive for 250 days in soil without a host and are reported to infect plants and produce galls after 225 days of survival in soil (Marcinowski 1909). In India, these seed galls are known

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by the common names "Sehun, Tundu, Mammi, and Gegla" (Singh et al. 1953). The average number of adults (female and male) in these immature ear cockles ranges from 10 to 80, but the numbers may reach 283 (Midha & Swarup 1974). In contrast, the average number of J2S in mature galls ranges from 8 415 to 12 773, but may reach 15 112 in larger galls (Ami et al. 2015).

The life cycle of *A. tritici* can take 113 to 164 days to complete (Swarup & Gupta 1971). Other studies suggest that the life cycle (from J2 to J2) completes in 103 days (Gokte & Swarup 1987), to 135–165 days in Semel-Duhok, Iraq (Ami & Taher 2013). *A. tritici* infects wheat, rye, and barley; however, barley plants are not commonly affected in India (Paruthi & Gupta 1987). In India, two distinct physiological populations were identified: the Haryana, U.P., Rajasthan, and Delhi populations representing the first, and the Bihar population. Compared to populations from Delhi, Haryana, Rajasthan, and U.P., the Bihar population was significantly more aggressive in causing infection (Gokte & Swarup 1988). The occurrence of this nematode has also been documented in several parts of Eastern Europe, Iraq, Turkey, China, North Africa, Western Asia, and the Indo-Pak subcontinent. In Iraq and Syria, this nematode causes huge losses in wheat and barley (Khatib et al. 2000; Ami & Taher 2013). *A. tritici* has also been reported from the United States of America, Australia, Brazil, Egypt, New Zealand, and Serbia. Slovenia and Russia (CABI/ EPPO 2002, Skanter et al 2018; Urek et al. 2003; Mackesy & Sullivan 2016). Recently, the nematode was also reported throughout the Sargodha division in Pakistan, though infection was low (Mukhtar et al. 2018).

The nematodes' ectoparasitic feeding causes twisting and crinkling of the leaves. Nematodes feed on the plant as ectoparasites and endoparasites, making the plant susceptible to secondary pathogen attacks. Several researchers have described the disease symptoms on wheat, including stem thickening in the collar region, crinkling and twisting of leaves, stunted growth, and poor or no seed set (Byars 1920; Filipjev & Schuurmans Stekhoven 1941; Christie 1959; Thorne 1961; Swarup & Gupta 1971; Southey 1972, 1978).

The wheat seed gall nematode remains a problem in several underdeveloped countries. The Genome (Singh et al. 2023) and transcriptome (Kumar et al. 2024) of this nematode have been previously published. However, there is still a serious gap in the information and documentation regarding WSGN's infection and parasitic behaviour on wheat, its location and movement within plant tissues, life cycle, and survival. Therefore, we sought to investigate and document *A. tritici's* developmental biology and behaviour during infection in wheat in microplot conditions.

MATERIAL AND METHODS

Nematode Culture. *A. tritici*-infected wheat seed galls were obtained from Dr Ramanna Koulagi, Plant Nematologist at Punjab Agricultural University in Ludhiana. The nematode culture was multiplied and maintained on the wheat cultivar HD2967 in microplots (28.64047 N, 77.16327 E; 228.6 m a.s.l.) at the ICAR-Indian Agricultural Research Institute, New Delhi, India.

Experimental setup. To study the nematode's life cycle and its correlation with host development, wheat was sown on seven dates at bi-weekly intervals: October 15, November 4, November 18, December 8, December 20, January 3, and January 12 during the agricultural season 2022–2023. Two microplots (1 m × 1 m) in open-field conditions were used for each sowing date. In each microplot, seed sowing was done in three rows, and the nematode inoculation in soil at the collar region was done thrice, i.e., three galls per seed at sowing; and by adding 1 000 active J2S one week after sowing, and at two weeks after sowing, respectively. The active J2S were collected by soaking the dry wheat galls in water for 2 days, then teasing them with forceps. Microplots were observed daily to note any changes in plant morphology. Every week, three plants were uprooted from microplots and brought to the lab. These plants were thoroughly examined for nematode presence, infection, symptoms, and location. Plant samples were collected for observation of nematode infection and parasitism at several stages of the crop's growth, including at the beginning of the emergence of leaves, spikelets, and florets, as well as active culm and spike growth, floret death, grain set, and grain filling. Samples were brought to the lab and kept at 10 °C for further investigations to check nematode presence and infection. Photomicrographs of plants, symptoms and galls were taken using a microscope (Olympus BX51, Japan) with a camera attached.

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Nematodes found in plant tissues were extracted and examined for morphology and developmental stage. Roots and stems were methodically washed to check for nematodes on the outside or inside of the leaf whorl. Floral primordia in top-folded leaves, early-stage minute galls, immature dark-green galls, and mature galls were cut and studied individually in Petri dishes to determine nematode location and developmental stage. Horizontal cuts were made using razor blades on floral primordia, early-stage minute galls, immature dark green galls and mature galls. The cuts helped extract nematodes from within these tissues/parts. The extracted nematodes were counted using a counting dish. After killing and fixing, the nematodes were mounted temporarily in distilled water, and observations of their development and photographs were taken under the microscope. Observations of plant symptoms and nematode location were also recorded.

The days required to complete the life cycle of the nematode were calculated by collecting nematode

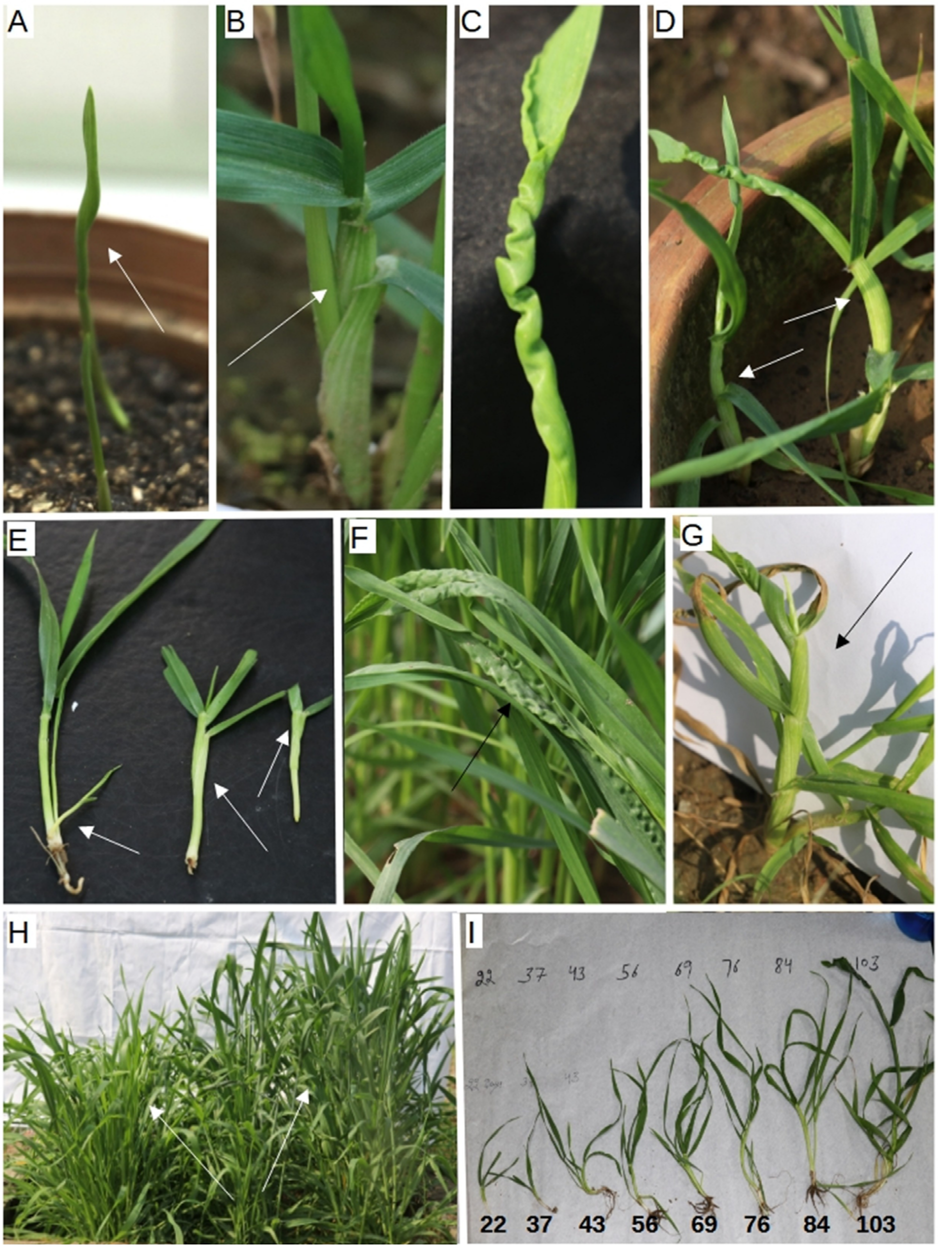

Figure 1. Symptomatology of wheat plant infected by *Anguina tritici*

A – plant after 1 week of sowing; B – thick collar region; C – leaf twisting; D – stunted plant with thick collar region and twisted leaf; E – collar, mid and upper region selected for nematode extraction; F – crinkling of leaves; G – severe infested plant; H – stunted and normal plants; I – wheat growth stages after infection

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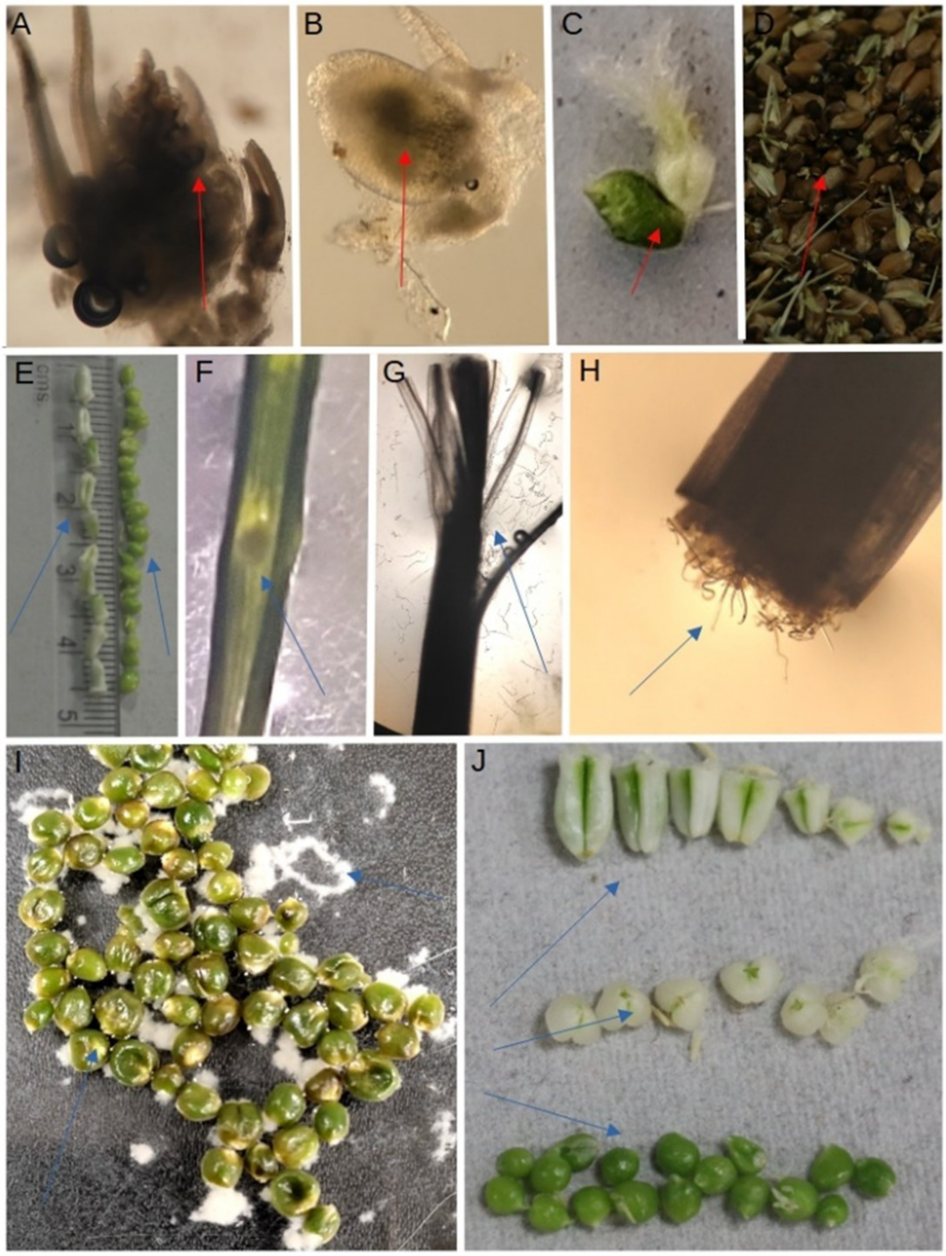

Figure 2. Wheat seed gall nematode location in different parts of the wheat plant
A – floral primordia; B – ovary; C – gall and grain in single floret; D – mature seed galls and grains; E – immature seed galls and grain; F – longitudinal cut in stem and bunch of J2s; G – unwhorling stem and presence of J2s; H – J2s in cortex and stem pith, I – green galls and anhydrobiotic white mass of J2s; J – milky grains, immature infected grains and green galls

life stages on alternate days to observe nematode life stages, along with the plant tissue in which they were present, and wheat crop growth stages. Graphs were drawn from collected data to depict the nematode stage and the wheat plant's growth stage.

Calculation of growing degree days and cumulative growing degree days. Cumulative growing degree days *(*cGDDs*)* are the total degree days required by a crop till physiological maturity. Wheat growth phases can be accurately estimated using growing degree days (GDD) (Ghosh et al. 2000). A specific number of heat units or GDD is required for a specific stage of plant growth to complete. As the nematode life cycle coincides with plant growth, a relationship between wheat plant GDD helps count nematode life-cycle days, as GDD is directly influenced by temperature, which in turn affects the wheat life cycle and, by extension, the nematode

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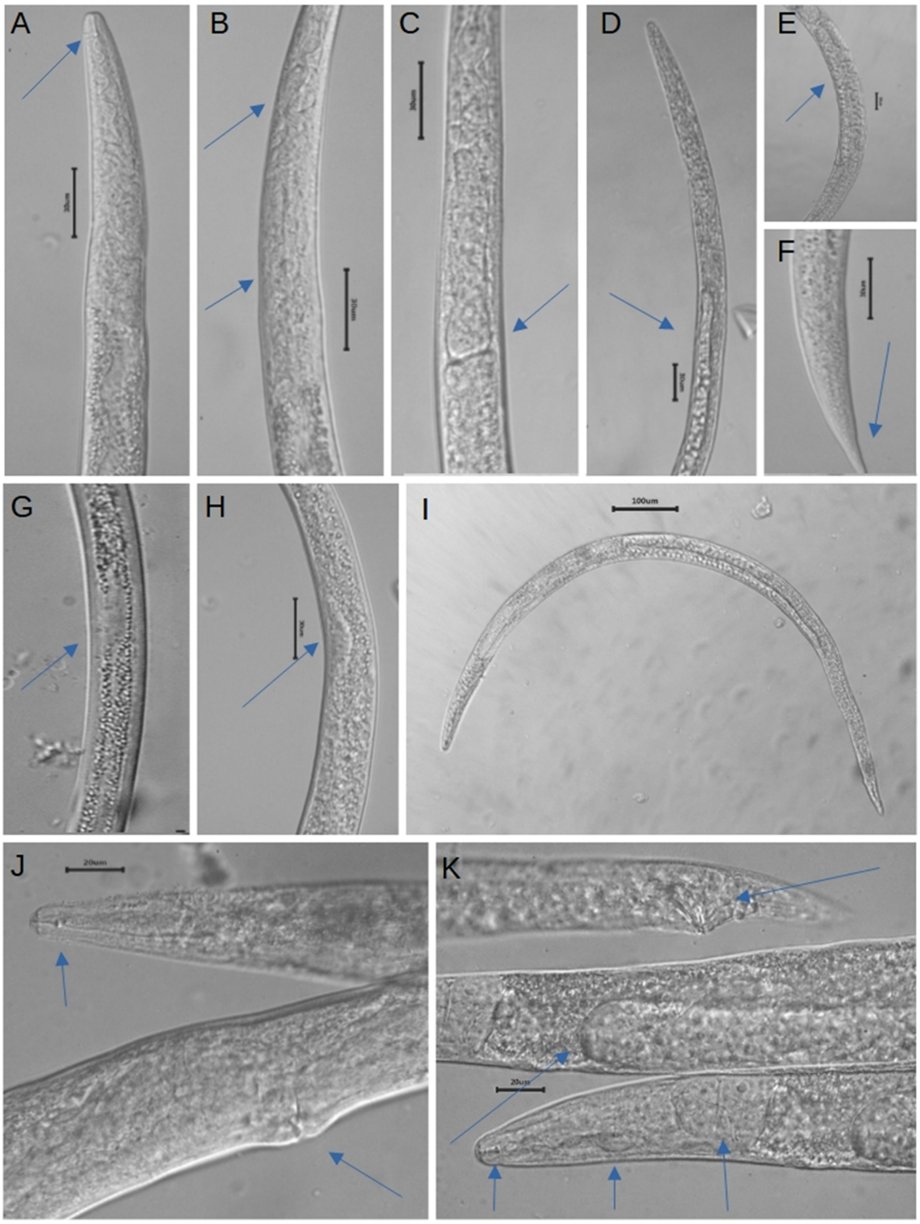

Figure 3. Different stages of nematode

J2 (A – stylet, B – median bulb and post corpus, C – J2 oesophageal-intestinal region, F – tail); D, E – J3, gonad development; G, H – J2, (G – pre parasitic J2 gonad, H – post parasitic J2 gonad cells); I – J4 stage; J – female, anterior and vulval region; K – male, posterior, median and anterior (stylet, median bulb and basal bulb) region; scale bars: A–H = 30 µm; I = 100 µm; J, K = 20 µm

stage. So GDDs were calculated by simple arithmetic accumulation of daily mean temperatures above the base temperature of 4.5 °C for the wheat crop (Nuttonson 1955).

$$\text{Growing degree days (°C)} = \frac{T_{max} + T_{min}}{2} - T_b \qquad (1)$$

Where: T_{max} – daily maximum temperature (°C); T_{min} – daily minimum temperature (°C); T_b – base temperature (4.5 °C).

Temperature data for growing degree days was obtained from the weather-based Agromet Advisory, IARI, New Delhi. (https://www.iari.res.in/bms/agromet/index.php).

RESULTS

The nematode life cycle was observed to be synchronised with the wheat plant growth and develop-

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Figure 4. Different types of abnormal growth of panicles after infection

A – empty panicle; B, C, D, E – undeveloped panicles; F, G, H – deformed panicles; I – panicles having galls; J, K – maturing galls

ment. Wheat seeds take six to nine days to germinate, which is similar to the time taken by the nematodes to emerge from the anhydrobiotic stage within the galls and reach the coleoptile for infection.

The first symptom of nematode infection appeared 22 days after sowing, when second-stage juveniles (J2) began living between the whorls of the stem (the pith and cortical-vascular region) and feeding there. The thickening of the collar region of the stem was the first symptom of wheat seed gall nematode (Figures 1B, 1D). Such plants were also stunted (Figures 1D, 1G, 1H). Highly mobile juveniles congregated at the meristem (Figures 2F–H). After 45–50 days of sowing, when the wheat panicle starts forming in the folded flag leaf, the post-J2S enter the soft, undifferentiated floral mass (Figures 2A, 2B), moult into the J3 stage (Figures 3D, 3E), and live for 10–15 days. The J3 stage juveniles showed increased size

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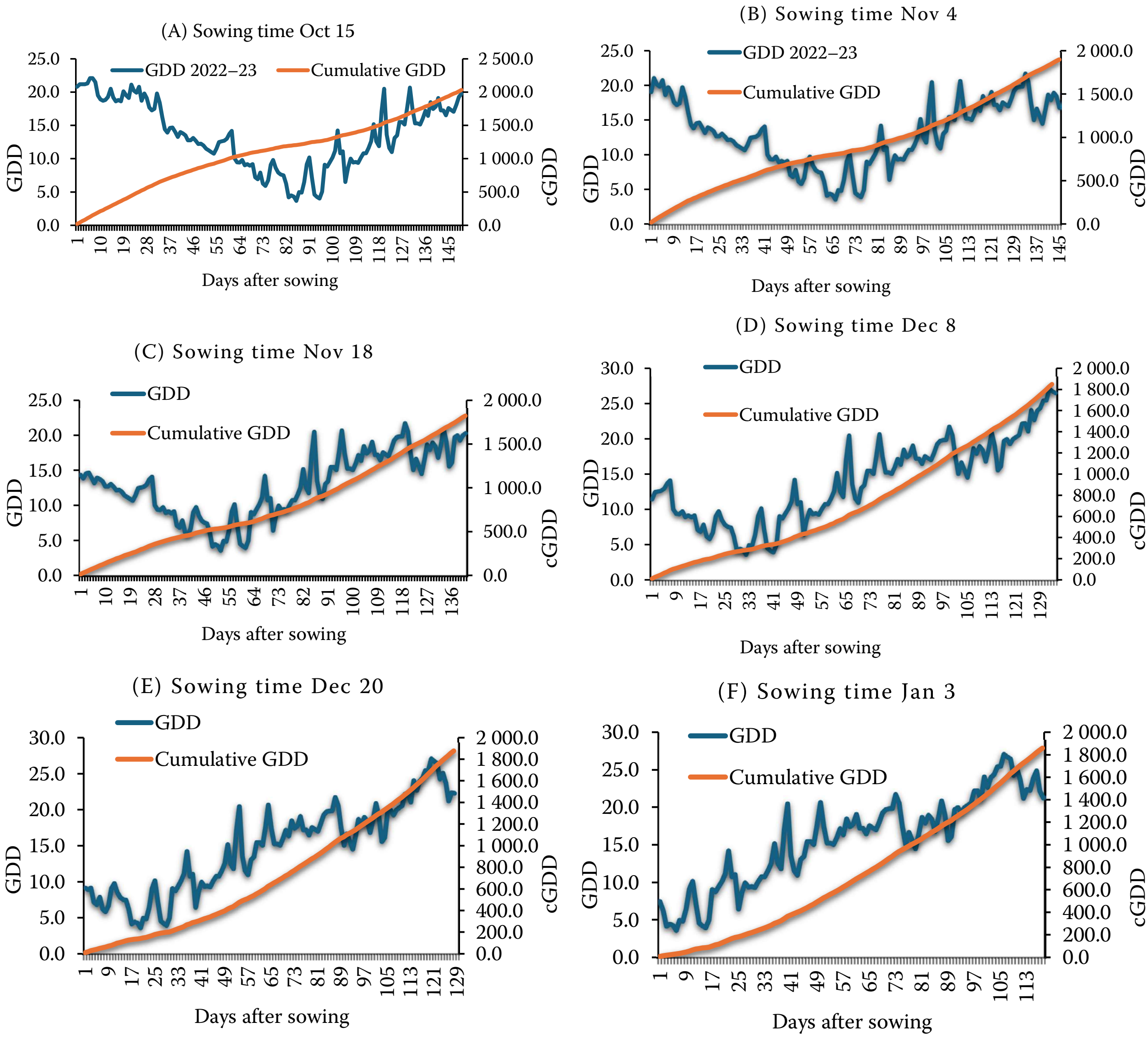

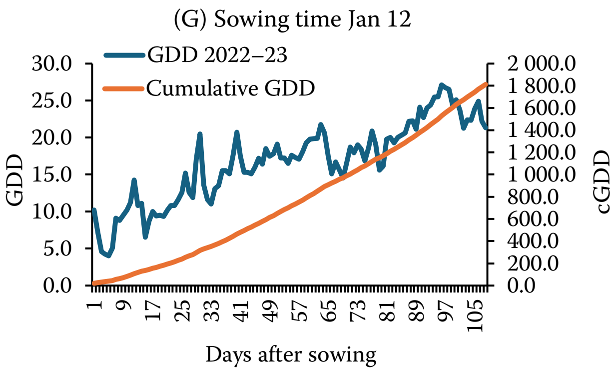

Figure 5. Growing degree days (GDD) and cumulative growing degree days (cGDD) of wheat plants on different sowing dates

and gonad cell development. J3 moulted into the J4 stage, which also showed an increased size and lived for 10–15 days (Figures 3H, 3I).

Teasing the soft, undifferentiated floral mass revealed the presence of post-J2, J3, and J4 stages. During floral primordial development in the grains or galls, juveniles moulted into adult males and females and carried out amphimictic reproduction. Near physiological maturity, when grain filling is completed, nematode females begin egg laying in the

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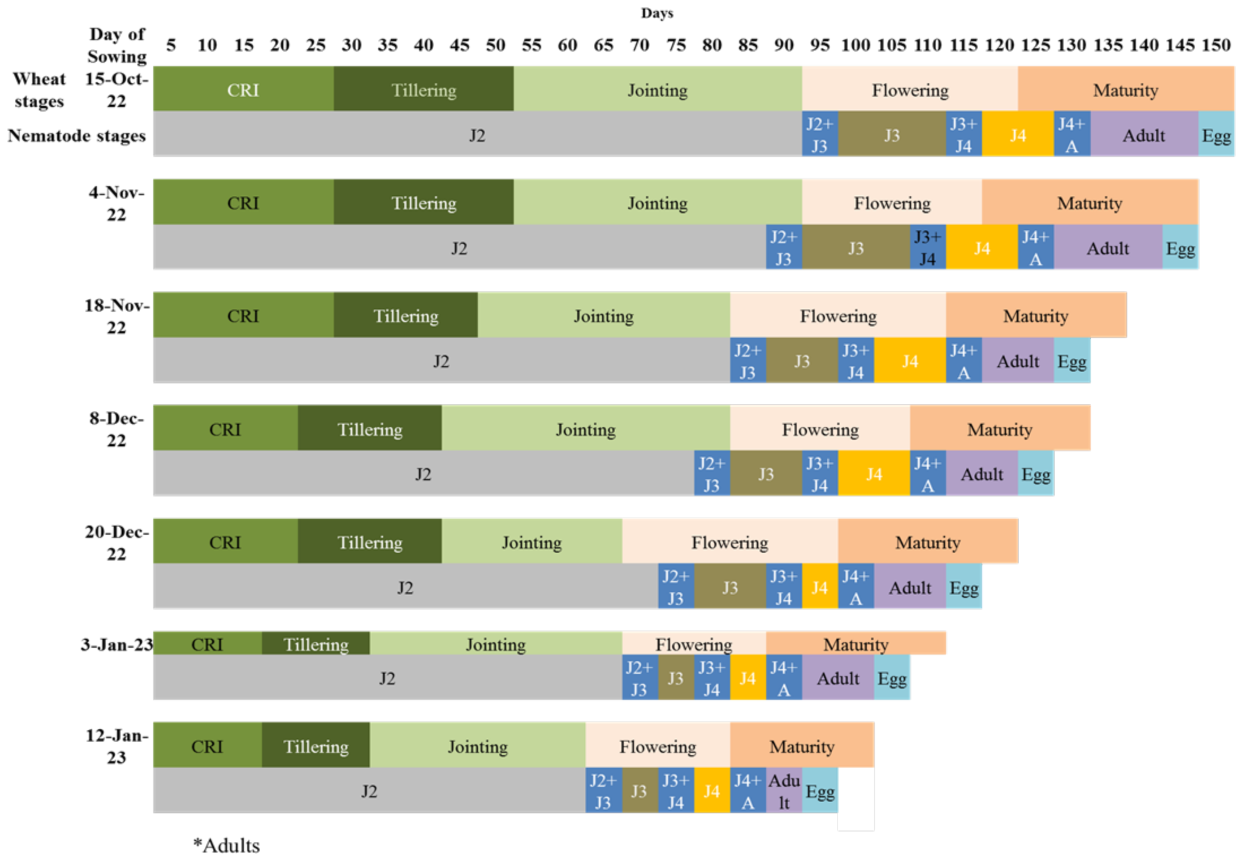

Figure 6. Life cycle of *Anguina tritici* on wheat plants (wheat growth stages and nematode growth stages in figure)

developing galls, and the eggs begin hatching simultaneously. By the time grains and galls attain maturity, J2S developing from freshly laid eggs undergo anhydrobiosis. The entire process of nematode egg laying, hatching, and anhydrobiosis is completed within 15–20 days in the developing seed.

The development of wheat panicles is affected by nematode infection in several ways, including: *(i)* normal, complete grain development without infection (Figure 2D), *(ii)* undeveloped grain-like structures when nematode destroys stamen and carpel, affecting pollination and causing growth to cease (Figure 2J), *(iii)* seed galls containing nematodes; (Figure 2J), and *(iv)* two galls also develop in one floret, which may be the result of one ovule and one anther or two ovary lobes (Figure 2C).

The first symptoms of infection were observed in three-leaf-stage plants (22 days after sowing). Plants also showed symptoms such as stem thickening, leaf twisting and curling, stunted growth, twisted panicles, the absence of awns, and, in severe cases, no panicle formation (Figures 2 and 4). Terminal growth of the crop decreased as the nematode fed on the stem's apical region. No nematodes were recorded from the roots of wheat plants. Highly active nematodes were observed in the upper one-third region of the stem (Figure 1G). The nematode-infected plants were dark green, stunted, and had more tillers. (Figure 2H). Awns were observed to be short and twisted after a week of pollination, when the panicle colour began to change from light green to dark green (Figures 4B–E). Sometimes, stigma was not present where gall formation occurred, but a yellow detached anther was present, while in seed grain florets, hairy stigma and dehiscent anther were both present. In the early stage of differentiation, the ovary develops into milky grains, whereas the galls (false ovules) are green. The average number of nematodes collected from three different infected wheat stems was approximately 1 240, 3 260, and 2 400 (Figure 2E). No major changes were found in the nematode juvenile parasitic stage when compared with the revived juvenile stage, except for gonad cell development (Figures 3G, 3H). Parasitic juveniles were much more mobile than revived ones. In the microscopic studies of these nematodes, we observed that tail shape varied from conoid to mucronate. The number of adult females slightly exceeded the number of adult males in a ratio

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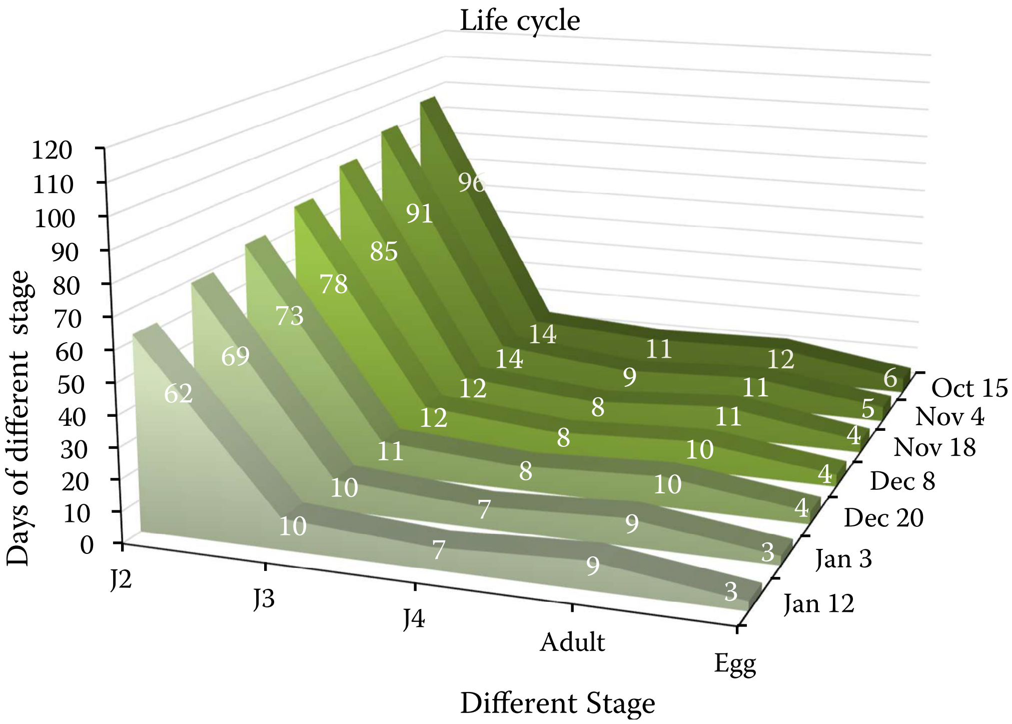

Figure 7. Survival period of different stages of nematode at different sowing dates of host plant

of 1.48 : 1.00 in early green galls and 1.46 : 1.00 in late mature galls (Table 1). Large females were C-shaped or ring-shaped, with the ends not fused, an obese centre, and tapering towards both ends. [Electronic Supplementary Material (ESM) Figure 1G). Reflexed ovaries can be seen in females. Males were less obese than females and remained ventrally curved (ESM Figure 1F). Both males and females were visible and distinguishable by the naked eye, whereas J2, J3, and J4 were not. Since nematode juvenile development and infection are synchronised with the development of the wheat crop (mid-October to mid-January), these nematodes survive over a wide range of temperatures, from 5 °C to 35 °C.

The calculated GDD and cumulative GDD for different wheat sowing dates to physiological maturity are shown in Figure 5. It shows that early-sown plants on 15th October complete their required growing degree days around 140 days. Late-sown plants complete their required heat units around 90 days due to a rapid increase in temperature, and the wheat life cycle shortens, which directly affects nematode life cycles. Plants reached physiological maturity between 100 and 150 days after sowing, depending on the sowing date from October to January. Nematodes living inside plants complete their life cycle in 90 to 140 days, which can vary according to environmental factors and long- or short-duration varieties. The different stages of nematode variation with plant stages are shown in Figure 6. For every date given in Figure 6, two strips are shown: the upper strip is for wheat growth stages, and the lower strip is for nematode growth stages. It depicts that from the invading plant's seedling stage, CRI stage, and Tillering stage, to floral primordial formation (J2 stage), J2, J3, and J4 stages live in floral primordia; adults live in green galls and Hatching eggs; J2S live in maturing galls. When the galls started maturing, the females laid eggs, which hatched into J2 and entered an anhydrobiotic phase for an indefinite time. The comparison of days count for different developmental stages of nematodes in Figure 7 showed that J2 spanned the longest time and Eggs the shortest. The primary inoculum stage, anhydrobiotic stage, and the longest-living stage are the second-stage juvenile stage, which is of utmost importance in seed gall nematodes.

Table 1. Number of males and females in galls

	Early–stage galls		Matured galls	
	male	female	male	female
Mean ± SE	2.50 ± 0.34	3.70 ± 1.64	12.70 ± 1.79	18.60 ± 2.22
SD	1.08	1.95	5.66	7.03
Range	1.00–4.00	1.00–7.00	7.00–24.00	10.00–32.00
N	10.00	10.00	10.00	10.00

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DISCUSSION

Anguina tritici is the first plant-parasitic, seed-borne nematode with a limited host range that causes ear cockle disease in wheat, oats, and barley. This nematode attack is frequent in some countries, such as Bulgaria (Mohamedova & Piperkova 2013), Pakistan (Mukhtar et al. 2018), and Turkey (Tülek et al. 2021), where old seed lots are used for sowing. In Iraq, this nematode causes an estimated 30% of crop losses in wheat-growing areas (Ami & Taher 2013). In India, wheat seed gall nematode caused heavy losses in wheat cultivation in Haryana and Rajasthan in the 19th and 20th centuries (Gaur 2010). Our study correlated all three factors (sowing time, GDD, temperature) to examine the effects of early and late wheat sowing on the life cycle of the wheat seed gall nematode. The results showed that an early-sown wheat crop was associated with a longer Anguina life cycle (more than 135 days), whereas a late-sown crop (till January) had a shorter life cycle. The normal life cycle of *A. tritici* ranges between 103 and 164 days (Swarup & Gupta 1971; Gokte & Swarup 1987). A wide range of temperature tolerance benefits the nematode by promoting reproductive stability (Aleuy & Kutz 2020). In both early- and late-sowing conditions, nematodes survived and infected the plant over a broad temperature range (5–35 °C).

In our study, the nematode life cycle varies from 92 to 140 days. The wheat plant requires 1 800–2 200 growing degree days (GDDs) to reach physiological maturity. Upon changing the sowing date, the degree-day or heat-unit requirements of the plant change. Plant growth is slow due to the low temperatures associated with late-sown wheat in December and January. Thereafter, the heat unit requirement is met in March and April, when temperatures are high; therefore, the plant receives the required GDDs and reaches maturity. Depending on plant growth, the nematode's life cycle can be shorter or longer. The process of egg laying, hatching, and anhydrobiosis takes 15–20 days to complete, and this duration can be influenced by factors such as irrigation, temperature, wheat cultivar, sowing date, and crop maturity.

A. tritici infects the plant by seed gall formation (Khan et al. 2023). However, sometimes seed galls form without symptoms, and *vice versa*. Therefore, it is necessary to study changes in nematode growth phases associated with the wheat plant's growth throughout the season.

We detected this nematode in stem whorls, below the epidermis, the cortical region, and the stem pith, where it lived in the hundreds and fed ectoparasitically. J2 is the infective stage that invades seedlings (Ami & Taher 2013). J2 starts living between the whorls of the stem, i.e., the pith and the cortical-vascular region, and feeds there. We found that post-J2 stages, i.e., J3 and J4, feed on floral, soft, undifferentiated mass, and that adults feed in galls for 10–15 days. We observed increased size and gonad cell development from post-J2 stages onward in the nematode, from the invading collar region to floral primordia. The changes in body shape and gland size during nematode growth stages may be due to differences in feeding behaviour across plant tissues.

Further, our study confirmed the presence of highly active nematodes (juvenile stages) in the upper one-third region of the stem. The first symptoms of infection were visible at three-leaf stage plants (22 days after sowing). Plants show symptoms such as stem thickening, leaf twisting and curling, stunted growth, twisted panicles, the absence of awns, and, in severe cases, no panicle formation. Further, we found that in nematode-infected florets, no pollination occurs, so only false ovaries or anthers develop. Moreover, there were a few underdeveloped ovaries (neither galls nor grains) without nematodes. Usually, seed gall development occurs by infection of the reproductive parts of plants (Mobasseri et al. 2017). The formation of two galls at the same time in a single floret confirms that gall formation originates from either the ovary, the anther, or both. This indicates that nematodes invade at a very early, soft, undifferentiated floral primordial stage in folded top leaves. The number of adult females slightly exceeded that of adult males, with ratios of 1.48 : 1.00 in early green galls and 1.46 : 1.00 in late mature galls, which differed from the 1.7 : 1.0 ratio reported by Gokte and Swarup (1987).

CONCLUSION

The GDD and cGDD concepts show that the nematode can align its development and life cycle with the wheat plant's growth stages and adapt to different temperatures. The timing of crop sowing and temperature directly impact its proliferation. Additionally, the presence of juvenile stages within the floral tissue and their mobility in the stem highlight the nematode's resilience, further underscoring its impact as a significant pest in wheat cul-

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tivation. Nematodes have been shown to survive across a wide range of temperatures (5–35 °C). Living of hundreds of J2 as a bundle in the stem and approaching to flower; variation in the duration of life stages according to environment and sowing dates; J3 and J4 in flower and adult in seed; feeding of all stage on stem, flower and ovary; the fast anhydrobiosis after hatching; these findings demonstrate the versatility of the nematode and its dessicated survival.

We knew that management of this nematode could be achieved through saline-water flotation of galls and sowing certified seeds. But we aimed to provide well-documented, high-quality photographs of the ecto- and endoparasitic behaviour of nematodes, their locations, and feeding in different parts of plants. This study can be useful for a better understanding of above-ground parasitism.

Because *A. tritici* shows good anhydrobiosis, and our lab is working on the molecular aspects of anhydrobiosis survival, which, in combination with bionomic information, will help determine how these features can be used to induce anhydrobiosis in Entomopathogenic nematodes (EPNs) to increase the shelf life of formulations.

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