

Article

Population Development of Alien Gall-Forming Aphid *Tetraneura nigriabdominalis* on *Ulmus minor* and *Ulmus glabra*

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Abstract: *Tetraneura (Tetraneurella) nigriabdominalis* (Sasaki, 1899) is a holocyclic and heteroecious species widely distributed throughout the world. Its primary hosts are various elm species, on which it forms galls. The results of this study complement those of previous research on the development of *T. nigriabdominalis* on primary hosts. Our research was conducted on two elm species, *Ulmus minor* and *Ulmus glabra*, at three locations and for three successive seasons between 2017 and 2019. Fundatrices hatched between 27 April and 12 May. The first galls were observed 6–8 days after the hatching date of the fundatrices. On average, there were 1–7.5 galls on one leaf. The highest abundances of *T. nigriabdominalis* galls were found in the medial and basal parts of the leaf blades. The fundatrices matured within 12–21 days after hatching and produced nymphs within 2–3 weeks. The fecundity of the fundatrices was influenced by the temperature in April, the size of the laminae, and the size of the galls. The females developing on *U. glabra* were more fecund (2–58 nymphs), whereas those developing on *U. minor* produced 1–29 nymphs. The winged migrants of the second generation appeared between late May and late June, when the first cracks on the galls were also observed. The entire development of two aphid generations on the primary host was temperature-dependent and lasted from four to almost six weeks. Our results show that *U. glabra* and *U. minor* are suitable hosts for *T. nigriabdominalis*. The development of aphids proceeded similarly on both tree species. Temperature, especially in April, significantly influenced the duration of individual developmental phases and the fecundity of fundatrices.

Keywords: *Tetraneura nigriabdominalis*; elm; gall development; bionomy



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1. Introduction

Tetraneura (Tetraneurella) nigriabdominalis (Sasaki, 1899) is widely distributed throughout the world and can be found in Southwest Asia, Southern Europe, Africa, Australia, and in North and South America ([1], <https://www.cabi.org>, accessed on 17 May 2022). In Europe, its presence has been documented in Italy, Greece, Bulgaria, France, Spain, Portugal, the Czech Republic, Slovakia, and the British Isles [2–4]. In 2015, the presence of this species on elm trees was documented for the first time in Poland [5]. Morphologically, the winged morphs of *T. nigriabdominalis* are similar to *Tetraneura ulmi* (L.), the dominant species on elm trees in Europe [6]. The diagnostic features differentiating the two species can be found on the last segment of the rostrum and on the antennae [5].

T. nigriabdominalis is a holocyclic and heteroecious species. However, it may also be an anholocyclic species in the regions where *Ulmus* is unavailable [7]. Its primary hosts are various elm species, including *Ulmus canescens* Melville, *U. davidiana* var. *japonica* Rehder,

U. parvifolia Jacq, and *U. minor* Mill. [1]. In Poland, this species has also been found on *Ulmus* 'Wredei' (the hybrid elm cultivar of *U. × hollandica*) [5]. *T. nigriabdominalis* forms galls on elm leaves, which are pinkish red and elongated or pouch-shaped, usually with a pointed apex. Galls are stalked, hairy, and located on the upper side of the leaf [5]. The formation of galls is induced by instar fundatrices, which affect the phytohormone balance of the host. In spring, the larvae of fundatrices start feeding on phloem sap from young leaves. The feeding site on the leaf soon begins to cave to the opposite side of the aphid. The gall grows by surrounding and enclosing the aphid inside [8]. Fundatrices moult in the gall four times before producing the winged second generation. According to Takei, et al., 2015, the second generation is not involved in gall induction.

The secondary hosts of *T. nigriabdominalis* are numerous grass species from the Poaceae family, belonging to the following genera: *Agropyron*, *Cenchrus*, *Chloris*, *Cynodon*, *Digitaria*, *Echinochloa*, *Eragrostis*, *Panicum*, *Paspalum*, *Saccharum*, and *Setaria* [3]. In Europe, the vast majority of host plants are crop weeds or ruderal plants. *T. nigriabdominalis* feeds on the roots of grasses. The species is mentioned as a significant pest of rice. It sucks sap from roots, causes leaves to yellow, and reduces the yield of plants and even causes their death [9]. In Japan, *T. nigriabdominalis* has been found to decrease rice yield by an estimated 50% [10]. *T. nigriabdominalis* inhabits numerous graminaceous weeds, such as *Eleusine indica* (L.), *Pennisetum subangustum* Stapf and Hubb., *Ischaemum rugosum* Salisb., and *Paspalum commersonii scrobiculatum* L., which serve as alternate hosts for the root aphid in Sierra Leone [11]. Because these weeds are a source of food for aphids, they can multiply freely and colonise crops. Aphids can also be a pest of important crops, such as *Zea mays* L. and *Sorghum bicolor* (L.) Moench [3]. Root-feeding aphids are accompanied by ants, which transport and protect them in exchange for honeydew [12].

According to the literature, the eggs of this species overwinter on the trunks of elm trees. Fundatrices hatch in April, move to young leaves, and begin to induce galls [8]. The females are parthenogenetic and produce the second generation in the galls. The females of the second generation are winged and move to the secondary host after the galls have burst. According to Heinrichs and Barrion [10], several generations develop on rice. Females produce 35–45 nymphs in a lifetime of 2–3 weeks. Kuo, et al. [13] found that temperature was one of the most important physical factors influencing the rate of development, reproduction, and survival of aphids on roots. The researchers found that 30 °C was the optimal temperature for the development of nymphs. The highest demographic parameters and the highest fecundity of the aphids were observed at 25–30 °C. On the secondary host, the development of aphids was inhibited, and their fecundity decreased at 10 °C and 35 °C, whereas mortality increased at these temperatures [13]. In autumn, the sexupara returned to the primary host and gave birth to a sexual generation. There were more males than females, and more than three males at a time have been observed crowding around a single female in attempts to copulate. The female lays a single egg on the elm bark. Oviposition ends with the extrusion from the oviduct of a dark liquid that covers the egg, fixing it to the remains of the mother [12].

Information on the biology of *T. nigriabdominalis* is lacking. The literature usually focuses on the development of aphids on secondary hosts. This is because some gramineous host plants, such as rice, maize, and sorghum, are economically important. In Europe, this species is heteroecious and requires two hosts to develop. The results of our research complement the information on selected elements of the *T. nigriabdominalis* bionomy on the primary host. The aim of our study was to determine the date of fundatrix hatching, the date of the appearance of galls on leaves, the number of aphids depending on the size of the galls, the fecundity of the fundatrices, and the duration of subsequent developmental phases on two hosts: the field elm *Ulmus minor* and the wych elm *Ulmus glabra* Huds. Additionally, we assessed the effect of temperature on the population development of the aphid.

2. Materials and Methods

2.1. Study Area

This study was conducted in three different locations in Poland between 2017 and 2019. In midwestern (Poznań, UTM: XU31) and southeastern (Rzeszów, UTM: EA74) Poland, observations were made on *Ulmus minor*, whereas in eastern Poland (Lublin, UTM: FB 07), observations were made on *Ulmus glabra*. The trees in all locations grew in green areas.

2.2. Field Study

2.2.1. The Development of Fundatrices

For the study, 5 trees were selected and numbered in all three locations in 2017 ($n = 15$). In 2017–2018, observations were made at weekly intervals, from the moment the fundatrices hatched until the galls burst and the migrants left them. From each tree, 10 leaves with galls of *T. nigriabdominalis* were collected within arm's reach. The first samples were taken when the first galls appeared on the leaves. Depending on the rate of gall development, 4–6 samples were collected from each tree per year. The leaves were placed in plastic bags and took to the laboratory. Each leaf was numbered, while its length and width were measured with a calliper to an accuracy of 0.1 mm. Next, each leaf was divided into 3 equal parts: apical, medial, and basal. The *T. nigriabdominalis* galls on the surface of each leaf were counted. Each gall was numbered, and their heights and widths were measured before they were opened with a scalpel. The aphids inside the galls were rinsed with 65% alcohol and placed in Petri dishes. The numbers of fundatrices and nymphs were recorded. A total of 1400 leaves were collected.

2.2.2. Maximum Fecundity of Fundatrices

To assess the maximum fecundity of the fundatrices, 100 mature galls were collected in 2017–2019 just before they burst open. The galls were collected from the same trees as those used for the observations of fundatrix development. The galls were collected in late May or early June, depending on the rate of their development. The height and width (in mm) of individual galls were measured with a DIN863 Digital Micrometer (MIB, Messzeuge, Germany) to an accuracy of 0.1 mm. Next, the galls were opened, and the nymphs inside were counted.

2.3. Meteorological Data

Meteorological data were collected from the following weather stations: Poznań–Ławica Airport, Rzeszów–Jasionka Airport, and Lublin–Radawiec Airport (<https://www.weatheronline.pl/weather/maps/city>, accessed on 30 August 2021) (Table 1).

Table 1. The average monthly temperature in 2017–2018 at individual research areas.

Month	Poznań		Lublin		Rzeszów	
	2017	2018	2017	2018	2017	2018
January	−2.1	2.3	−5.6	1.6	−5.8	0.8
February	0.8	−2.4	−1.7	−4.1	−0.2	−3.6
March	6.9	1.0	5.4	−0.5	6.4	0.3
April	7.9	13.5	7.0	13.0	8.1	13.9
May	14.1	17.4	13.5	16.7	13.7	17.0
June	18.1	19.8	17.7	18.3	19.0	18.5
July	18.6	20.6	18.1	19.9	19.0	20.1
August	19.3	21.8	19.1	20.2	20.0	20.3
September	13.9	16.6	13.6	15.3	14.0	15.3
October	11.4	11.2	8.8	9.8	9.9	10.5
November	5.6	7.8	3.7	3.5	4.4	5.7
December	2.9	2.6	1.6	0.1	2.1	0.8

2.4. Statistical Analyses

The Kruskal–Wallis test was used to determine the significance of the differences in gall height and width and nymph numbers, depending on the tree species. Spearman rank correlation tests were used to determine the relationships between the average temperature and the length of the pre-reproductive period, reproduction period, and number of nymphs per gall. Spearman rank correlation tests were also used to determine the relationships between gall height and width and the number of nymphs. In order to reveal links between tree species, gall parameters, and nymph numbers, we used principal component analysis. All statistical analyses were conducted using the Statistica version 13 programme (TIBCO Soft-ware Inc. Palo Alto, CA, USA, 2017, <http://statistica.io>; accessed on 5 May 2022) and PAST 3 software (PAleontological STatistic version 4.0; Øyvind Hammer, Natural History Museum, University of Oslo, Oslo, Norway).

3. Results

3.1. The Development of Fundatrices

The first fundatrices hatched in late April or early May (Table 2). In 2018, *T. nigriabdominalis* fundatrices hatched earlier than in 2017 due to higher temperatures in April (Table 1). The nymphs hatched during the elm budburst period. After the first leaves unfolded, the nymphs settled on leaves' abaxial faces between the veins. The first galls were observed within 6–8 days after the fundatrices hatched (Table 2). In 2017, there were on average 1–7.5 galls on each collected leaf for both elm species. In 2018, there were much fewer galls observed on the elm leaves, and the average number of galls on one leaf ranged from 1 to 1.66 (Table 3).

Table 2. Timetable of fundatrix hatching and appearance of the galls and nymphs of *T. nigriabdominalis* on *U. minor* and *U. glabra* (day/month).

Term	<i>Ulmus minor</i> 1 *		<i>Ulmus minor</i> 2 **		<i>Ulmus glabra</i>	
	2017	2018	2017	2018	2017	2018
First hatching of fundatrices	12/05	2/05	6/05	27/04/	8/05	29/04
Appearance of first galls	19/05	8/05	14/05	6/05	16/05	7/05
Appearance of first nymphs	2/06	15/05	24/05	9/05	29/05	15/05
Gall cracks	21/06	2/06	16/06	25/05	12/06	8/06

* 1 (study area in Poznań). ** 2 (study area in Rzeszów).

Table 3. Number of *T. nigriabdominalis* galls on *U. minor* and *U. glabra* (mean ± SE (standard error)).

Year	<i>Ulmus minor</i> 1 *		<i>Ulmus minor</i> 2 **		<i>Ulmus glabra</i>	
	Min–Max	Mean (±SE)	Min–Max	Mean (±SE)	Min–Max	Mean (±SE)
2017	1–8	2.5 ± 0.24	1–7	1.47 ± 0.19	1–12	3.14 ± 0.25
2018	1–2	1.08 ± 0.04	1–3	1.58 ± 0.26	1–2	1.33 ± 0.06

* 1 (study area in Poznań). ** 2 (study area in Rzeszów).

In 2017, the samples of *U. glabra* leaves had 6.3 times more galls than did the samples collected in 2018. The *U. minor* samples had 3 (study area in Rzeszów) to 8 times (study area in Poznań) more galls.

In both years of the study, aphids most often colonised the medial and basal parts of the leaf surface on both elm species. The share of galls in the medial part of the *U. minor* lamina amounted to 40.2%–60% of all galls recorded in the sample. On *U. glabra*, however, the share of galls was about 57%. The share of the galls in the basal part of *U. minor* and *U. glabra* lamina ranged from 22.8 to 54.4% and 29.1 to 36%, respectively. The fewest galls were found on the apical part of the leaves (2.8%–17% of all galls on *U. minor* and 7%–14% on *U. glabra*).

Only one fundatrix developed in one gall. The study seasons differed considerably in the length of the pre-reproductive period of *T. nigriabdominalis* (Figure 1). These differences were significantly influenced by temperatures in April. The higher the temperature was in April, the shorter the pre-reproductive period of the fundatrices was (Spearman's rank correlation coefficient values were $\rho = -0.98$; $p < 0.05$). In 2018, the females matured in early (study area in Rzeszów) or mid-May, which was on average two weeks earlier than in 2017. In 2017, the pre-productive period of the fundatrices lasted 18–21 days, whereas it lasted 12–16 days in 2018. The length of the reproductive period of the fundatrices lasted 2–3 or more weeks and was affected by the temperature in April (Figures 1 and 2). The mean temperature in April was negatively correlated with the average number of larvae per gall ($\rho = -0.43$, $p < 0.05$). The fecundity of the *T. nigriabdominalis* fundatrices was also influenced by the size of the laminae. The leaf length and width were positively correlated with the number of nymphs per gall ($\rho = 0.64$, $p < 0.05$ and $\rho = 0.46$, $p < 0.05$, respectively). The average fecundity of the fundatrices developing on the *U. minor* trees was 6.44 nymphs in 2017 and 8.25 nymphs in 2018 (study area in Rzeszów). In Poznań, these values were 23.58 and 9.43 nymphs, respectively (Figure 2b,c). The average fecundity of the fundatrices on the *U. glabra* trees in 2017 amounted to 11.96 nymphs, whereas in 2018 it was 16.35 nymphs (Figure 2a). The winged migrants of the second generation appeared between late May and late June when the galls began to crack open (Table 2). Predacious syrphid larvae were occasionally observed in the opened galls. The entire development of two aphid generations on the primary host was temperature-dependent and lasted from 4 (in 2018) to almost 6 weeks (in 2017) (Figures 1 and 2).

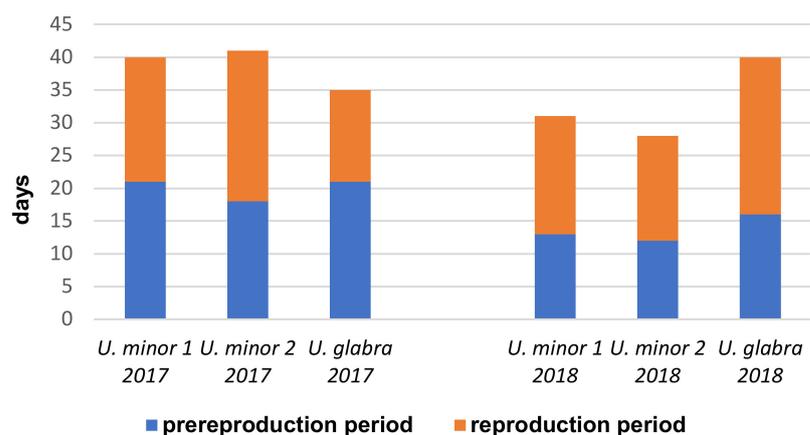


Figure 1. The duration of subsequent developmental stages of *T. nigriabdominalis* fundatrices on *U. minor* and *U. glabra* (*U. minor* 1, study area in Poznań; *U. minor* 2, study area in Rzeszów).

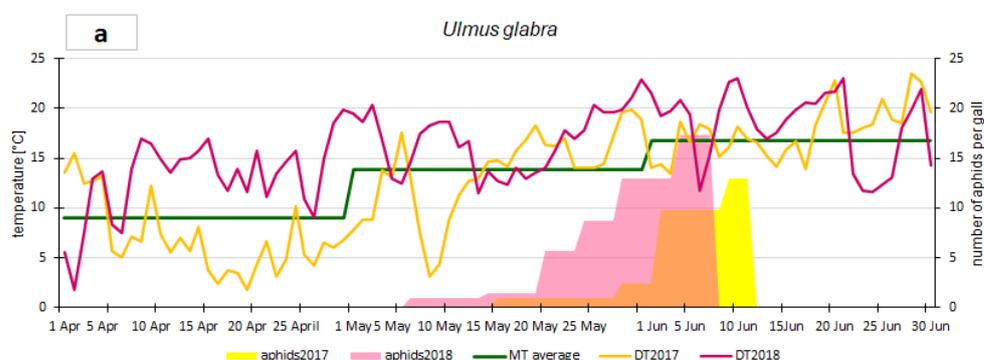


Figure 2. Cont.

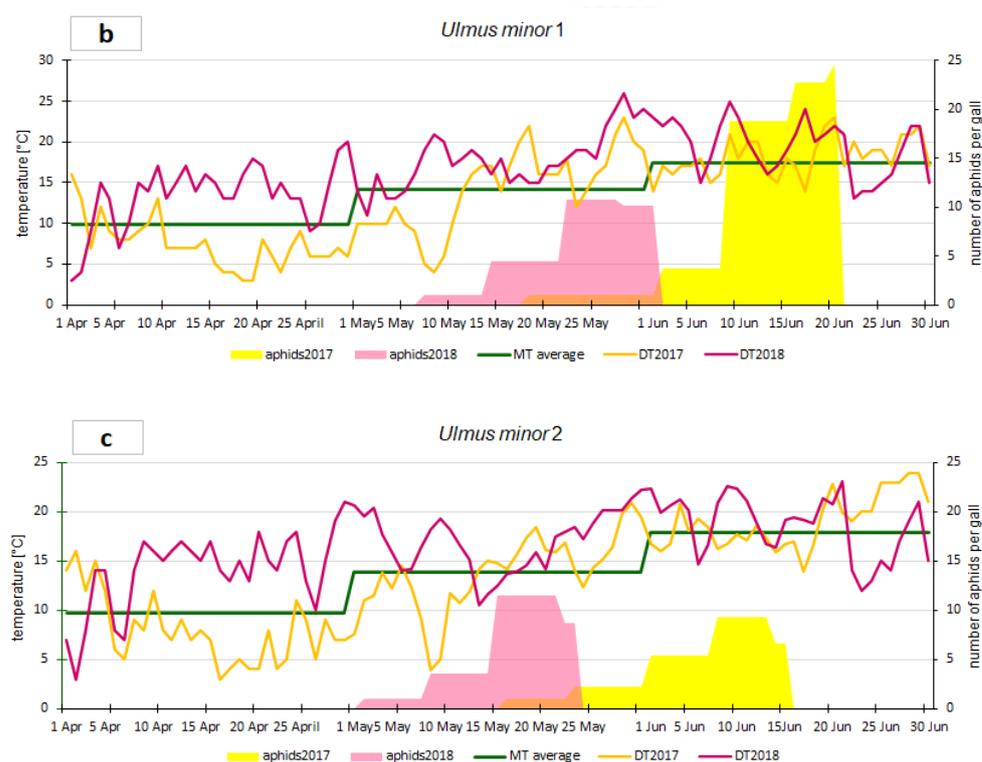


Figure 2. The dynamics of *T. nigriabdominalis* abundance on *U. glabra* (a) and *U. minor* (b), and (c) in relation to temperature. *U. minor* 1 (study area in Poznań), *U. minor* 2 (study area in Rzeszów); aphids: average number of aphids per gall. MT: average monthly air temperature; DT: average daily air temperature.

3.2. Maximum Fecundity of Fundatrices

The fundatrices developing on *U. glabra* trees were more fecund than those developing on *U. minor* (Table 4). Their fecundity ranged from 2 to 58 nymphs, whereas the fecundity of the fundatrices found on the *U. minor* trees ranged from 1 to 29 nymphs. The size of the galls significantly influenced the number of nymphs. Gall height and width were positively correlated with the number of nymphs ($\rho = 0.48$, $p < 0.001$ and $\rho = 0.11$, $p < 0.001$, respectively) (Figure 3). The galls found on the *U. glabra* trees were significantly higher than those found on the *U. minor* trees (Table 4) (Kruskal–Wallis test $H = 257.08$). During the three consecutive seasons, 5467 nymphs were found in the 300 galls collected from the *U. glabra* trees. The maximum fecundity of the fundatrices was lower by 25% (study area in Poznań) to 62% (study area in Rzeszów) on *U. minor* than on *U. glabra*. The fecundity of the fundatrices depended significantly on the average daily temperature in April and the heights and widths of the galls ($\rho = -3.44$, $p < 0.001$; $\rho = -4.11$, $p < 0.001$; $\rho = -9.71$, $p < 0.001$, respectively). The lower the temperature was in April, the taller and wider the galls were, consequently making fundatrices more fecund.

Table 4. Maximum fecundity of *T. nigriabdominalis* fundatrices, gall widths and heights in *U. minor* and *U. glabra* in 2017–2019 (mean \pm SE (standard error)); values marked with different letters differ significantly at $p < 0.05$ for each parameter (Kruskal–Wallis test)).

	<i>U. minor</i> 1 *	<i>U. minor</i> 2 **	<i>U. glabra</i>
Mean no. of nymphs/gall/year			
2017	23.13 \pm 0.29	4.34 \pm 0.44	15.94 \pm 1.04
2018	7.45 \pm 0.42	7.6 \pm 0.33	21.25 \pm 1.23
2019	10.71 \pm 0.47	9.01 \pm 0.59	17.48 \pm 1.17
Mean max fecundity of the fundatrices 2017–2019	13.76 \pm 3.9a	6.98 \pm 1.13a	18.22 \pm 1.29b

Table 4. Cont.

	<i>U. minor</i> 1 *	<i>U. minor</i> 2 **	<i>U. glabra</i>
Average gall width/year			
2017	5.28 ± 0.53	5.63 ± 0.2	4.53 ± 0.11
2018	4.45 ± 0.16	4.26 ± 0.07	4.54 ± 0.11
2019	5.84 ± 0.15	4.08 ± 0.11	4.76 ± 0.11
Average gall width in 2017–2019	5.19 ± 0.33a	4.65 ± 0.4a	4.61 ± 0.06a
Average gall height/year			
2017	17.6 ± 0.45	11.8 ± 0.47	21.4 ± 0.42
2018	12.6 ± 0.5	13.3 ± 0.4	21.1 ± 0.37
2019	16.2 ± 0.4	18.1 ± 0.49	21.2 ± 0.43
Average gall height in 2017–2019	15.46 ± 1.21a	14.39 ± 1.55a	21.23 ± 0.07b

* 1 (study area in Poznań). ** 2 (study area in Rzeszów).

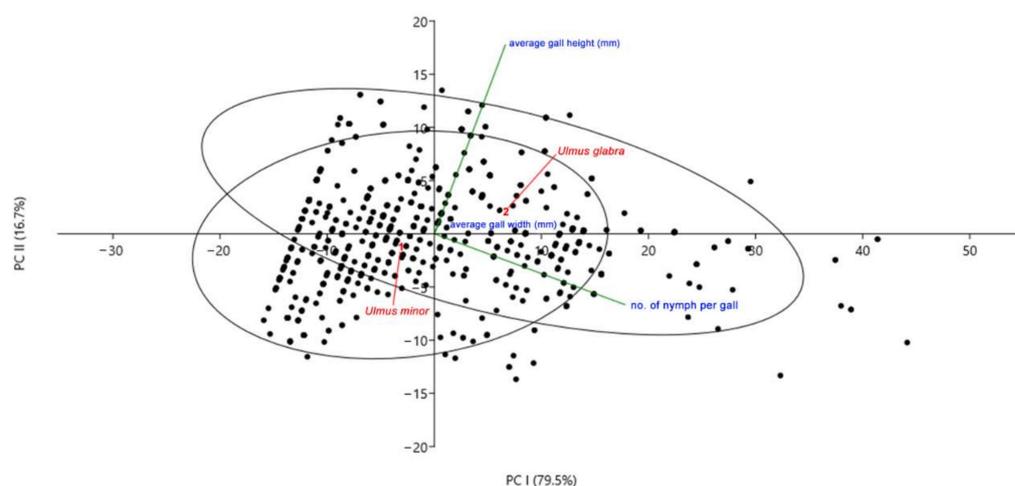


Figure 3. Principal component analysis (PCA) of the gall height and width, number of aphids per gall, and tree species.

4. Discussion

We studied the population development of *T. nigriabdominalis* on *U. glabra* and *U. minor* and assessed how temperature affects its development. The results of our study show that both elm species are suitable hosts for *T. nigriabdominalis*. The aphids developed similarly on both host plants. The temperature, especially in April, significantly influenced the duration of the individual stages of development and the fecundity of the fundatrices.

The distribution and abundance of aphids are affected by the phenology of the host plant according to temporal variation in the host's quality. Life cycle synchronisation with the developmental stages of the host plant is particularly important for gall-forming species [14]. The key stages of gall development include initiation, increments in mass and qualitative differentiation, maturation, and senescence [15,16]. Fundatrices require the host tissue in a relatively undifferentiated stage to form a gall [17]. Aphid galls are formed mostly on young, growing plant tissues; consequently, aphid hatching is usually timed with budburst [18,19]. In our study, the *T. nigriabdominalis* fundatrices hatched during bud break on the elm trees in each study area, whereas the first galls in the initial phase of development appeared about 6–9 days later. It is known that there may be considerable differences in bud break between years and even between trees [20]. Temperature and photoperiod are assumed to be the main factors controlling the timing of bud swelling and leaf emergence on deciduous trees in spring [21]. The spring phenology of trees is generally defined as a response to effective heat sums [20]. Being ectothermic animals, aphids are strongly affected by thermal conditions [22,23]. Temperature mainly affects the

life activities of these insects, influencing the rate of their development, the phenology of appearance, spring and autumn migrations, and the survival of the species [24–27].

In 2017, the average daily temperature in April and early May was well below the long-term average, which spanned the years 2000–2016. On the contrary, in 2018, the average daily temperature at this time of year was significantly higher than the long-term average. During our study, in 2018, the fundatrices hatched, and gall initiation happened up to 11 days earlier than in 2017. Similar observations were made for *Hormaphis hamamelidis* (Fitch) inducing galls on *Hamamelis virginiana* L., where the date of gall initiation differed between years by at least 12 days [17]. The larvae of fundatrices need to find suitable places for gall formation on ‘reactive’ plant tissue, which may be available for a short period of time and may change from year to year, even on individual trees [17]. Vitasse, et al. [20] found that the microclimatic conditions of the bud (e.g., shadowing) had significant effects on budburst timing. It has also been found that the non-migratory, gall-forming aphid *Kaltenbachiella japonica* Matsumura has achieved genetic differentiation in hatching time between tree-associated populations [22].

Gall-forming aphids are commonly considered to benefit from the manipulation of host plant development. They can redirect the growth and physiology of host plant tissue [18]. During our study, the young galls of *T. nigriabdominalis* grew very quickly, especially in 2018. The length of the gall growth and formation period was synchronised with the length of the pre-reproductive period of the fundatrices. When the adult fundatrices began to produce the first larvae of the second generation, the gall volume stopped increasing. This observation is in line with the research findings conducted on a Japanese population of *T. nigriabdominalis* [8]. Takei, et al. [8] detected a high level of endogenous indoleacetic acid only in the first- and second-instar fundatrices, which may prove their exclusive gall induction ability and the important role of phytohormones in gall formation.

Our study showed that the fecundity of *T. nigriabdominalis* was positively correlated with gall volume. The fundatrices produced the most offspring in the galls formed on *U. glabra* trees, whose galls and leaves were larger than those on the *U. minor* trees. Our findings corroborate the observations made on other aphid species: *H. hamamelidis* [28], *Tetraneura ulmi* L. [6], *Kaltenbachiella japonica* [29], *Pemphigus spyrothecae* Pass. [30], *Pemphigus bursarius* (L.), and *Pemphigus phenax* Börner and Blunck [31]. Gall-inducing aphids benefit from the manipulation of plant development to correct the nutritive value in the feeding place through a local increase in the content of amino acids, sugars, and other plant nutrients [18,31,32]. Being phloem feeders, aphids can modify the organisation of a plant’s vascular system to increase food supply [33]. According to Larson and Whitham [34], *Pemphigus betae* Doane galls absorb nutrients from the whole leaf and adjacent leaves. Finding the right galling site appears to enable the stem mother to induce a large gall, which has a marked effect on her fitness and fecundity and benefits her offspring [6,28,29]. There is contradictory information regarding the relationship between gall and leaf size in scientific publications. In our study, gall volume was positively correlated with leaf blade area. Similar results were found in studies conducted on four *Pemphigus* species [30,31,35]. However, the fecundity of *H. hamamelidis* [28] and *K. japonica* [29] was not influenced by leaf area.

Regardless of the host plant species, most of the *T. nigriabdominalis* galls were found in the medial and basal parts of the leaf blades. The reproductive success of *P. betae* was achieved by fundatrices inducing their galls at the base of the largest poplar leaves, where the lateral veins were the longest [35]. The galls located in this region acquired more photosynthetic products than the ones located in other sites of the leaf surface [29]. However, in our opinion, the site where aphids form galls may be influenced by competition between aphids, adaptation, and weather conditions, as well as other factors [8,36–38].

In our study, there were many more galls on the leaves in 2017 than in 2018. Warm weather may have accelerated leaf development, and some aphids (e.g., those that hatched later) may not have found a suitable feeding site, or they could have moved more slowly.

Due to the short ‘window of opportunity’, there may have been increased competition between fundatrices [17,36].

The first occurrence and the first migration of various aphid species are now taking place earlier in the year than previously observed due to global warming and other factors of climate change. Likewise, the end of the occurrence and the last migration of aphids take place at later dates than they did previously [39]. Global warming may accelerate the development rate of insects and increase the number of their generations produced in each year [40,41]. Higher temperatures promote parthenogenetic development. *T. nigriabdominalis* is a pest of economically important crops, such as rice, maize, and sorghum. These insects cause large crop losses in West Africa. The host plant species significantly affects the performance of this aphid. It was observed that *T. nigriabdominalis* that fed on corn had the longest nymphal developmental time, whereas those that fed on rice had the shortest nymphal developmental time [13].

Spring and autumn temperatures have been increasing in recent years. Consequently, heteroecious aphid species return to their winter hosts later and lay eggs later. At the same time, male aphid species numbers have been decreasing over the course of the last decade [42]. Rising temperatures have prevented a subset of the parthenogenetic population of *Cinara juniperi* De Geer from transitioning to a sexual generation [43]. *T. nigriabdominalis* can develop only parthenogenetically in warm regions. Therefore, higher temperatures may extend the development of parthenogenetic generations. The return to the winter host may be delayed, which can reduce the population of this species on elm trees.

Being ecologically adaptable, aphids have already begun to respond quickly to global warming. Research has shown that an increase in temperature by 2 °C generates 1–5 additional generations [44]. However, not all aphid species benefit from higher temperatures. For most insects, the rate of development increases with temperature until a certain threshold, after which it decreases. The research conducted by Durak, et al. [43] showed that *C. juniperi* did not benefit from global warming despite the elongation of their entire life cycle. This species developed faster at 20 °C than at 25 °C. The results of our study correspond with this conclusion. Temperatures in April significantly influenced the developmental parameters of *T. nigriabdominalis*. Lower temperatures in April corresponded with a longer pre-reproductive period for fundatrices, wider and higher galls, and greater fecundity.

Temperature and the quality of nourishment determine the physiological states of insects. These are key variables that regulate the survival rate and density of insect populations. Higher temperatures promote insects to migrate and colonise new plants.

T. nigriabdominalis is an alien species that is relatively new to the fauna of Central and Eastern Europe, but its range is expanding. It is important to investigate the biology of this species and learn how temperature influences its life cycle in order to monitor and control its populations.

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