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Giant willow aphid (*Tuberolachnus salignus* Gmelin, 1790) – a literature review

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Abstract. *Tuberolachnus salignus* is a cosmopolitan aphid that predominantly feeds on the willow. It can be an economically important pest of this plant. The aim of the study was to present the thematic scope of the literature on this species in Poland and in the world. The typical issues related to aphid biology (life cycle, nutrition, distribution) and its potential harmfulness are considered. Additionally, aphid genetics, dyes, natural enemies, indirect influence on the soil environment as well as the use of this insect species in research on plant physiology are taken into account.

It was found that in recent years, the studies on giant willow aphid have been mainly motivated by the potential utilisation of the results in the protection of willow against this aphid. Despite a wide range of topics, the publications collected in the SCOPUS and Web of Science databases are not sufficient sources of information about this species. The available data must be supplemented and updated using modern research methods. The experiments and observations should consider the direct and indirect relationships of *T. salignus* with other organisms and the environment.

Keywords: Lachnidae, *Salix*, pest, insect, invasive species

INTRODUCTION

Tuberolachnus salignus (Gmelin, 1790) is a very large aphid. It predominantly feeds on the willow. It is an anholocyclic species, i.e. it does not change its host plant, and reproduces only parthenogenetically (Heie, 1995; Szelegiewicz, 1962). The large body size, availability and easy reproduction of the food plant, genetic homogeneity of the population and simple rearing make this species a good subject of biological research. The economic importance of the willow additionally broadens the scope of interest in this aphid species by matters concerning the impact of its feeding on the host plant.

The aim of this work is to present the thematic scope of research on *T. salignus* conducted in the world and in Poland as well as to review the literature on the species.

Records from the Scopus and Web of Science databases (no time limits, keyword: Tuberolachnus, access to the full text or extensive abstract; in References marked in blue font) as well as additional source items expanding on the studied topics were used for review the world literature. The websites of institutions and people, whose activities are related to this subject, were also taken into account. Polish literature came from the AGRO and SIGŻ databases (no time limits, keywords: Tuberolachnus, aphids, willow – in Polish: Tuberolachnus, mszyce, wierzba) as well as the BioMap database, which integrates data on the distribution of insect species in Poland from archival and contemporary collections and publications. Information from handbooks of willow production was also included. The article contains photographs from the production and experimental plantations located in the Lubelskie voivodeship.

The number of publications on the giant willow aphid in the databases mentioned before is small, which results from the low importance of *T. salignus* in the economy. Three periods of increased interest in this species can be observed in the world literature (Fig. 1). In the 1960s and 1970s of the 20th century, this was associated with the research on plant physiology, at the beginning of the 21st century, with the cultivation of willow for energy purposes, whereas in recent years, with the arrival of *T. salignus* as an invasive species in Australia and New Zealand. The world literature covers various topics, including the biology and economic importance of the species. In the Polish literature, *T. salignus* predominantly appears in faunal studies on aphids as well as in publications on the occurrence of pests in plantations. One original article concerns the assessment of its effect on willow plants.

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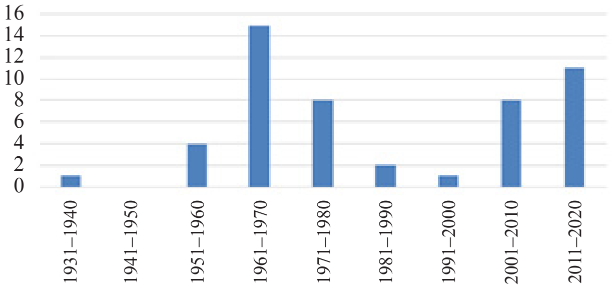

Figure 1. SCOPUS query results for „Tuberolachnus".

TAXONOMY AND MORPHOLOGY

The *T. salignus* aphid (J.F. Gmelin, 1790) belongs to the suborder Sternorrhyncha and the Lachnidae family. In Poland, it is the only representative of the genus (Biodiversity Map).

The body of adult aphids is dark, almost black in colour, and its length varies between 3.3 and 5.8 mm. The abdomen is covered with numerous thin hairs, which are responsible for its grey shade. The proboscis is long and reaches the hind coxae. In general, the morphology is characteristic of the Lachninae subfamily. A detailed description can be found in keys for identification of aphids (e.g. Heie, 1995; Szelegiewicz, 1962). A characteristic feature is the black dorsal tubercule on the abdomen, 0.2–0.3 mm high, particularly well visible at apterous adults (Heie, 1995).

No oviparous females, eggs and males have been found for *T. salignus* (Dhatwalia, Gautam, 2009; Fang et al., 2016; Llewellyn et al., 1974). Only larvae and adult parthenogenetic females are present in the colonies. The larvae go through four developmental stages, the youngest being light brown (Llewellyn et al., 1974). Viviparous aphids occur in two forms, i.e. winged and wingless. The wing pads of larvae are clearly visible from the third developmental stage (Mittler, 1958b). Aphids form large, dense colonies on plants, located on trunks and branches. From a distance they look black. Since they abundantly excrete honeydew, shiny spots on the surfaces of plants and soil are visible near the colonies. A honeydew may be a substrate for black sooty mould development (Martin, 2017; Tun et al., 2020a).

DISTRIBUTION

T. salignus is thought to be native to Asia; however, it is currently found in all areas where willow occurs (Charles et al., 2014; Szelegiewicz, 1962). In December 2013, the first aphids were found in New Zealand, and in early 2014, in Australia (Sopow et al., 2017). Heie (1995) claims that *T. salignus* cannot overwinter in the far north of Europe and is transferred to these areas from warmer regions. Based on the results of phylogeographic studies, Fang et al. (2016) suspect that the range of the species was limited by the last glaciation and began to expand later.

In the BioMap database, the earliest report from Poland dates back to 1868. *T. salignus* appears in faunal reviews from natural sites and parks (e.g. Krzywiec, 1982; Osiadacz, Wieczorek, 2003). Its presence was also noted at production plantations (Czerniakowski, 2007, 2010; Styszko, Pałosz, 2008).

Publications emphasise the large diversity of the population size of the giant willow aphid over the years. Very high plant colonisation may occur immediately after the seasons, in which the willow aphids were not found (Jurekova, Drazic, 2011; Styszko, Pałosz, 2008).

It is assumed that the winged forms can reach new areas by actively flying or are passively transported with air masses (Heie, 1995; Plant Biosecurity..., 2016; Sopow et al., 2017), even over long distances (Hill et al., 2020). Aphids can also be carried by water if they accidentally fall into it. In autumn or when the colonies are overcrowded, some individuals wander in search of a new host (Hill et al., 2020; Plant Biosecurity..., 2016). Aradottir et al. (2012) suggest that *T. salignus* is a very mobile species. Fang et al. (2016) suspect that human activities (trade, transport) also contribute to the spread of the species.

In Europe, *T. salignus* most often appears on plants in late summer or autumn and can be observed even in the winter, after which it disappears until the next season (Czerniakowski, 2007; Molnár, 2003).

Since the presence of eggs was not found, it is assumed that the viviparous females overwinter and begin to appear the following year (Aradottir et al., 2012). Martin (2017) believes that only the winged form is capable of this, while according to Szelegiewicz (1962), larvae of earlier developmental stages can also survive over winter. Fang et al. (2016) observed aphids hidden in the cracks in the trunk bark of willow, which according to the researchers, allows them to survive in harsh winter conditions.

HOST PLANTS AND FEEDING

T. salignus predominantly feeds on the willow. Sopow et al. (2017) listed 50 species/hybrids, including both woody and shrub forms, on which the presence of this aphid was confirmed (Tun et al., 2020c). Incidentally, the occurrence of *T. salignus* on the black poplar (*Populus nigra* L.) was noted (Charles et al., 2014). In New Zealand, it was observed that aphids in different stages of development fed on the *Coprosma macrocarpa* shrub (cited after Sopow et al., 2017).

Similarly to other aphids, *T. salignus* has piercing-sucking mouthparts. The main element is the stylet, with food and salivary canals. It has been found that *T. salignus* aphids use sap from newly differentiated phloem sieve tubes adjacent to the cambium (Mittler, 1957).

The course taken by the stylet can be determined thanks to saliva traces or callose deposited in places of cell wall damage (Lawton, 1977; Mittler, 1957). The proboscis is flexible and typically passes between cells without penetrating their contents. The proboscis marks are often branched. Mittler (1957) believes that this is a result of searching for a better site in different parts of the phloem sieve tube in the event of local exhaustion of the phloem sap or a drop in its pressure without having to change the feeding place. Saliva plays an important role in the piercing activity, creating a protective salivary sheath around stylet. Sometimes it is also visible on bark as a small cone around the proboscis. In the cells, the salivary sheath is smooth, with a non-uniform structure between the cells. Saliva can accumulate in places, where the stylet meets obstacles and changes direction (Mittler, 1957). The cited sources do not provide data on the composition of the *T. salignus* saliva; however, studies on other species indicate that apart from a gel fraction facilitating tissue penetration, the saliva of aphids contains a watery fraction, the task of which is i.a. to counteract the plant's defenses (Will, Vilcinskas, 2015).

It has been found that the pressure in the sieve tubes is a factor, which ensures sap flow in the food canal in the proboscis. Thus, *T. salignus* does not suck, but actively swallows food (Mittler, 1957). Aphids anaesthetised with CO_2 did not become distended and excrete honeydew, which indicated the presence of a mechanism that controls the flow of fluid through the proboscis. Taking into account the phloem sap viscosity, it was calculated that to ensure its flow through the stylet food canal in the amount of 1–2 mm^3/h, a pressure of 20–40 atmospheres was needed (Mittler, 1957).

A single *T. salignus* aphid ingests 10–40 mm^3 of phloem sap per day. Mittler (1957) observed that when plants wilt, aphid colonies disperse and the insects seek alternative places to feed. They readily accumulate over incisions, which block the outflow of assimilates.

Feeding is inextricably linked with the production of honeydew. The food is low in nitrogen-containing substances; therefore, the aphid must take up a lot of phloem sap to meet its nitrogen demand. The excess of sap components is excreted in the form of honeydew. The volume of honeydew drops increases with the size of the insect (Mittler, 1958b). Cameron et al. (2019) estimated it to be between 3 and 5 µl.

In terms of the type of nitrogen-containing compounds, the composition of honeydew is similar to that of phloem sap. It contains aspartic acid, glutamic acid, serine, threonine, alanine, valine, leucine and/or isoleucine, asparagine, glutamine and possibly gamma-aminobutyric acid. However, the concentration of each of these compounds is lower because the aphids absorb approximately 55% of the nitrogen from the ingested sap. No ammonia, uric acid, proteins, peptides or their degradation products were detected in honeydew (Mittler, 1958a).

In terms of carbohydrates, the *T. salignus* honeydew was composed of saccharose, glucose, fructose and the melezitose trisaccharide in similar proportions (Mittler, 1958a). The concentration of sugars in honeydew did not differ by more than 5% from that determined in phloem sap (Mittler, 1958a). Hexoses are not transported in the phloem sieve tubes; thus, both monosaccharides originate from the decomposition of saccharose by the aphid. The presence of melezitose in fresh honeydew and its absence in the phloem sap indicates that this trisaccharide is synthesised in the body of the insect (Mittler, 1958a). The calorific value of honeydew was estimated to be 3.9 cal/mg (Llewellyn et al., 1974). *T. salignus* produces very large amounts of honeydew. It was calculated that adult aphids excrete 750–2048.4 µg of honeydew per hour (Moir et al., 2018). For this reason, this species was excluded from the modelling studies on honeydew excretion as an atypical representative of aphids. The abundance of honeydew even gave rise to the idea of using it to make candies (Charles et al., 2014).

The production of honeydew depends on many factors. It increases with the body size and sap absorption capacity at successive development stages of the insect from 0.45 to 2.08 mm^3 per hour (Mittler, 1957). Mittler (1958b) determined that when the nitrogen content of the phloem sap decreased, the excretion of honeydew increased. Llewellyn et al. (1974) observed such a correlation only in the case of larvae, but found that aphids showing lower growth rates excreted more honeydew than those exhibiting better development. In most larvae, the honeydew excretion decreased by more than 40% in the day before moulting, and increased immediately after moulting (Llewellyn et al., 1974). The amount of honeydew excreted by the aphids did not depend on the position of the colony on the plant and the light intensity (in the range of 3000 to 6000 lux). Nevertheless, the influence of the seasons on this process was noted. The production increased from May to August. By October, this trend was maintained only for the last larval stage and adult aphids (Llewellyn et al., 1974).

LIFE CYCLE

T. salignus is an aphid, which reproduces only parthenogenetically (Aradottir et al., 2012; Judenko, 1930; Szelegiewicz, 1962), i.e. embryos development occurs without fertilisation. The advantage of parthenogenesis is the possibility of a rapid population growth under good conditions and in the presence of abundant food. The disadvantage is mainly the lack of genetic variation enabling adaptation to environmental changes. This form of reproduction in aphids is also associated with the lack of change of the host plant, i.e. anholocyclic development. Szelegiewicz (1962) states that the genesis of *T. salignus* anholocyclic development is unknown. According to Mordowiłka (cited after Judenko, 1930), such a cycle in aphids is secondary to the holocyclic development and occurs as a result of the lack of access to host plants of the sexual generation. The studies of Fang et al. (2016) indicating the possibility of survival of *T. salignus* in isolated mountain enclaves during the ice age may confirm this hypothesis.

Female *T. salignus* breed larvae, which undergo four developmental stages. In the studies of Llewellyn et al. (1974), the total length of the larval development averaged 14 days. Collins and Leather (2001) found that aphids required 196 degreedays to mature, with a threshold temperature of 5.5°C. In the studies of Özder et al. (2007) and Özder and Sağlam (2008), the first stage was the longest, whereas Collins and Leather (2001) showed no such relationship. The last larval stage, which precedes the transition into an adult aphid, was longer than the second and third stages (Collins, Leather, 2001; Özder et al., 2007; Özder, Sağlam, 2008).

Mittler (1958b) found that alate 3rd and 4th stage nymphs moulted 1 and 2–3 days later than larvae of apterous morphs, respectively.

The impulse for the formation of winged aphids may be the insufficient nutritional value of food (Mittler, 1958b). The increase in temperature shortened the larval development. At 10°C, it lasted as many as 40 days (Collins, Leather, 2001), while at 25°C, only 10–13 days (Collins, Leather, 2001; Özder et al., 2007; Özder, Sağlam, 2008). This trend was similar for all larval stages. At 27.5°C, the larvae in the 4th stage of development did not survive (Özder et al., 2007). The reproductive period lasted an average of 12 days (Llewellyn et al., 1974).

Mittler (1958b) emphasises the differences in the biological parameters and behaviour between the winged and wingless forms. The reproductive period of winged individuals was more than 30% shorter than that of the wingless individuals (Collins, Leather, 2001; Mittler, 1958b). Wingless females started eat quickly and bred larvae 2–3 days after the last moult. Their abdomens contained 70–80 embryos at all stages of development, many ready for birth (Mittler, 1958b). In contrast, winged individuals did not feed for the first 3–4 days and developed only approx. 30 small embryos. Then they started eating and the amount of honeydew excreted by them matched that of the wingless females. After 2–3 days of feeding, they began to breed the first larvae. Collins and Leather (2001) also observed that at 20°C, the pre-reproductive period in the winged forms was longer than that in the wingless morphs, while at 10°C, such a difference was not noted. The aphid aggregation did not have a large effect on the development of the larvae and the number of embryos in the pre-reproductive period (Hargreaves, Llewellyn, 1978).

The average fecundity reached 42–52 larvae (Özder et al., 2007; Özder, Sağlam, 2008), and under the most favourable conditions, even 100 larvae (Collins et al., 2001a). The total number of larvae born by a winged aphid ranged from 34 (Collins, Leather, 2001) to 42 (Mittler, 1958b). For the wingless form, it ranged from 70 (Collins, Leather 2001) to 80 (Mittler, 1958b). Judenko (1930) also emphasises the lower fecundity of the winged forms. Moreover, winged aphids bred lighter larvae (0.28–0.33 mg) than the wingless forms (0.37 mg) (Collins, Leather, 2001). Both very high and very low aphid aggregation negatively affected reproduction (Hargreaves, Llewellyn, 1978). During the last week of life, wingless aphids bred very few larvae. At dissection, no more than 4 embryos were found in their bodies. In the post-reproductive period, their abdomens remained distended as they were filled with "thousands of deeply pigmented globules" (Mittler, 1958b). Aphids continued to excrete a large amount of honeydew. There is a theory that the feeding of adult aphids, even those that are already not fecund, has a positive effect on the development of larvae in a colony (Charles et al., 2014).

The abdomen of winged viviparous aphids shrank at the end of the reproductive period and was filled with wax-like concretions (Mittler, 1958b). The post-reproductive period in winged aphids was 2–3 times longer than the reproductive period, and in wingless individuals, it was the same length or shorter (Collins, Leather, 2001). The lifespan of adult aphids depended on the temperature. At 10°C, it was approximately 40 days both for winged and wingless forms. An increase by 10°C did not make a difference in the case of wingless forms, but shortened the lifespan of winged aphids to several days (Collins, Leather, 2001).

The lifespan, fecundity and larval development time influence the intrinsic rate of increase. It was found that it depended on the species of willow and was the greatest at 20–25°C (Collins, Leather, 2001; Özder et al., 2007; Özder, Sağlam, 2008).

GENETIC STUDIES

The first study on the genus *Tuberolachnus* in relation to genetics dates back to 1931 (Shinji, 1931). The author argues that an increased number of chromosomes in aphids is connected with higher evolutionary advancement. In the case of the *Tuberolachnus* genus, his conclusions concerned a male aphid; therefore, it was probably not *T. salignus*.

T. salignus has also been theoretically included in genetic analyses of aphids from India (Raychaudhuri, Das, 1987). However, its feeding on *Pinus cassia* raises doubts about the correctness of the species determination. Studies by Dhatwalia and Gautam (2009) were also conducted in India in the Himachal Pradesh province. In their work, embryos of *T. salignus* were used due to the availability of cells in metaphase. In 3 out of 4 locations, the number of chromosomes (2n) was 20, and only in one location, it varied from 18 to 20. The total complement length of 20 chromosomes ranged from 50.56 to 68.50 μm, while the length of individual chromosomes ranged from 1.98 to 3.63 μm.

Figure 2. Giant willow aphids on willow shoot.

Figure 3. Winged giant willow aphid.

Figure 4. Giant willow aphids probably infected with *Neozygites turbinatus* (R.G. Kenneth) Remaud. & S. Keller.

Figure 5. *Harmonia axyridis* (Pallas) ladybird feeding in giant willow aphid colony.

Research carried out by Aradottir et al. (2012) covered a much larger area than the previous studies. For a total of 660 individuals, the aphid samples predominantly originated from Great Britain, but also from Sweden, Spain, Canada and the USA. Seven microsatellite markers were used in the research. The samples exhibited very little genetic diversity, which according to the authors confirmed the hypothesis that *T. salignus* reproduced solely parthenogenetically. The examined aphids were classified into 16 genotypes. Two of them accounted for 65.7% of the total assay. They were considered to be the most widespread due to their easy adaptation to different willow species and locations. In one colony, two or even three genotypes were present at the same time. The low genetic diversity of *T. salignus* was also confirmed by Fang et al. (2016) using material from China.

RELATIONSHIPS OF *T. SALIGNUS* WITH OTHER ANIMALS

In the temperature climate, *T. salignus* appears on plants later than other aphids. Moreover, the colonies are the largest in the autumn (Jurekova, Drazic, 2011; Molnár, 2003). Dransfield and Brightwell speculate that it is a defence strategy against birds, which most intensively search for food in the spring and summer. The only bird reported in the studied sources, which feeds on *T. salignus*, is the Australian silvereye *Zosterops lateralis* (Latham) (Martin, 2017). The remains of *T. salignus* were found in the stomachs of bats of the *Pipistrellus pygmaeus* Leach species associated with riparian areas (Rydell et al., 2016).

The late appearance of *T. salignus* is also not favourable for predatory insects. In the literature, one can mainly find reports of attacks on *T. salignus* by adult aphids and ladybird larvae (Dransfield, Brightwell; Jurekova, Drazic, 2011; Martin, 2017). Tun et al. (2020b) from New Zealand conducted laboratory studies on this relationship. They found that *Harmonia axyridis* (Pallas) ladybird could survive on a diet consisting of only first stage larvae of *T. salignus*; however, its biological parameters (survival, body weight, development length) were worse than those in the presence of more suitable food (eggs of *Ephestia kuehniella* Zeller normally used in commercial rearing). The highest mortality, reaching up to 25%, concerned the first larval stage of *H. axyridis*, which the authors attributed to the large size of the victims. The greatest number of aphids, i.e. nearly 30 within 24 hours, was eaten by female ladybirds. However, *H. axyridis* has not been identified as a predator predisposed for the biological control of *T. salignus*, for example due to different food preferences.

One article from Germany concerns observations of adult female of dragonfly *Enallagma cyathigerum* feeding on *T. salignus* aphids on a willow branch submerged in water (Weichrauch, 2002).

The close mutualistic relationships between aphids and ants are well known. There are no reports on *T. salignus* creating such relationships, although studies from Hungary found the co-occurrence of *Lasius flavus* (Fabr.) and *L. fuliginosus* (Latr.) with this aphid on a white willow in one of two observed sites (Szathmáry et al., 2005).

Honeydew produced by aphids attracts various insects, including bees, wasps and bumblebees. Their buzzing informs about the presence of *T. salignus* on willows already from a distance (Cameron et al., 2019). In Great Britain, it was observed that in the case of a prolonged period of dry, hot weather, which limits flower nectaring, short-tongued bumblebees *Bombus terrestris* (L.) used the honeydew of *T. salignus* (Cameron et al., 2019). They typically collected it from the litter under aphid colonies when the sugar concentration increased following the evaporation of water. Wasps feeding on honeydew were also observed in this location. They were significantly more abundant than bumble bees, fed for longer periods of the day and usually collected honeydew from plants in the vicinity of aphid colonies.

In the studied literature sources, there are no articles on *T. salignus* parasitoids in Europe. Several species of Braconidae are reported from Asia (Akhtar et al., 2011; Sopow et al., 2017; Takada, 1968). In 2019, the association of beekeepers in New Zealand applied to the environmental protection agency for permission to use *Pauesia nigrovaria* for control *T. salignus* (Apiculture..., 2019). In the database covers Chalcidoidea (Noyes, 2019), *T. salignus* is noted as the primary host of two species of the family Pteromalidae, i.e. *Asaphes suspensus* Nees and *Euneura lachni* (Ashamead).

RELATIONSHIPS OF *T. SALIGNUS* WITH MICROORGANISMS

Parasitic fungi

The parasite of *T. salignus* is *Neozygites turbinatus* (R.G. Kenneth) Remaud. & S. Keller (Keller, 1997), which has been reported in Europe and Israel. In willow plantations, especially in the years of outbreak of *T. salignus*, strong infestation of willow aphids by this fungus is observed. Barta and Cagáň (2006) found that it could lead to the destroy of the insect population, while Jurekova and Drazic (2011) state that in 2010, the fungus successfully stopped the spread of aphids in willow plantations. A distinctive sight was inactive aphids hanging from the plant on their proboscis. Their bodies were filled with black spores of the fungus. The spores released from liquefied aphid cadavers could be found on trees even after a year (Barta, Cagáň, 2006).

Symbionts

Poor diet consisting exclusively of phloem sap forces the aphids to coexist with microorganisms, which provide them with necessary nutrients, including essential amino acids. The obligatory symbiosis between aphids and bacterium *Buchnera aphidicola* is known. In the case of *T. salignus*, Manzano-Marin et al. (2016) also observed the presence of *Serratia symbiotica* in bacteriocytes. The authors believe that both microorganisms form a consortium and developed joined, complementary metabolic pathways, thanks to which they can synthetize, for example, biotin, essential for the host.

THE INFLUENCE OF HONEYDEW PRODUCED BY *T. SALIGNUS* ON THE SOIL ENVIRONMENT AND WILLOW

There are hypotheses indicating that the negative impact of aphid feeding on the host plant is reduced due to the production and deposition of honeydew. Milcu et al. (2015) tested this assumption in relation to *T. salignus*. They found that the addition of artificial honeydew to the soil caused significant changes in the composition and functioning of organisms. Microbial biomass carbon, soil respiration and mineralisation kinetics increased. The number of representatives of the microfauna per g of dry matter of soil increased. This was particularly evident in the case of amoebae and ciliates. The number of nematodes, collembola and soil mites significantly decreased, while the number of earthworms increased. There was no effect on the nitrogen content in the leaves and the weight of the willow shoots and roots; however, increased branching was noted. An interesting effect was the emergence of flowers in September, which the authors attributed to the stress caused by the lack of microbiologically immobilised nitrogen.

Similar studies using natural honeydew were carried out by Tun et al. (2020a). The researchers determined an increase in the microbial biomass carbon, intensity of soil respiration, overall activity of the soil enzymes as well as the population of yeast and mesofauna, including collembola. There were no changes in the soil nitrogen content. The obtained results became the base for interesting studies on the interrelationships between different groups of organisms living in the soil; however, they did not confirm the hypothesis concerning the beneficial effect of the *T. salignus* honeydew on the willow.

PIGMENTS (AFINS) PRODUCED BY *T. SALIGNUS*

Pigments produced by aphids are subjects an entire series of studies included in the SCOPUS database. References to *T. salignus* are found in Part III (Duewell et al., 1950), V (Johnson et al., 1951) and XXXVII (Banks et al., 1969) of this review. Alexander Todd (1963) studied the structure and properties of these substances. They were classified as quinone pigments (NIIR Board..., 2005), and they occur in the hemolymph of aphids. In live insects, these are golden-yellow protoaphins, which turn red-purple in alkaline solutions. Upon injury or death of aphids, the pigments are enzymatically converted into unstable xantoaphins, which exhibit strong green fluorescence. They transform into equally unstable orange chrysoaphins and are subsequently converted into stable erythroaphins. This transformation cycle is the same in many dark coloured aphids. Nonetheless, although the structures of subsequent compounds are similar, those characteristic of *T. salignus* are unique isomers and are distinguished by the annotation sl (aphins-*sl*) (Todd, 1963; Achremowicz, 1968). Charles et al. (2014) report attempts of using *T. salignus* aphins, for example, to dye military uniforms.

In 2018, Nabil published a paper on the possibility of use ancient practices described in medieval manuals for painters and illuminators to create natural flesh tone colourants. He found that although the pigment produced by *T. salignus* exhibited a promising, intense colour, upon the addition of potassium carbonate, the colour rapidly faded when exposed to daylight. The addition of $CaCO_3$ did not stabilise the colour.

The chemical structures and transformations of pigments produced by *T. salignus* have been well studied; however, the literature lacks data on the role of these substances in the aphid organisms.

EFFECTS OF VARIOUS SUBSTANCES ON THE NERVOUS SYSTEM OF *T. SALIGNUS*

Toppozada and O'Brien (1967) studied the penetration of organic substances into the ganglia of *T. salignus*. They found that increased liposolubility enhanced the permeability, while the large size of particles reduced it due to the small cross-sectional area of the target organ. The permeability of fatty acids was significantly higher than that of quaternary ammonium compounds. The authors suggested the presence of a system that limits the influx of particularly large, polar and unmetabolisable cations.

Nguyen et al. (2012) investigated the electrical activity of the central nervous system dissected from adult wingless females of *T. salignus*. They found that preparations displayed spontaneous electrical activity, which in 90% of the samples lasted for at least 1 hour. Its parameters were significantly affected by addition of imidacloprid. The authors attributed this reaction to the effect of the preparation on the cholinergic neurons. They concluded that the employed method could be used to study the effects of the plant protection products on the nervous system of insects.

ECONOMIC IMPORTANCE OF *T. SALIGNUS*

Impact on the willow

The feeding of aphids does not cause spectacular effects similar to those observed in the case of phyllophagous insects. However, a large number of insects forming extensive colonies may give an idea of their potential negative impact on the plant. This is confirmed by a often quoted calculation by Mittler (1958a): a single *T. salignus* individual consumes 10–40 mm^3 of sap per day. The saccharose concentration is 10%; therefore, the plant is deprived of 1–4 mg of saccharose per day. If it is assumed that the plant produces 2 mg of saccharose from an area of 100 cm^2 of leaves, the aphid ingests the equivalent of carbohydrate production from the photosynthesis of leaves with an area of 50–200 cm^2 during one hour.

In New Zealand, where the willow has been widely used in many areas, *T. salignus* has been recognised as a dangerous pest (Sopow et al., 2017). In Europe, this species is considered as a potential source of problems in the short rotation willow cultivation (Collins et al., 2001b). According to the Institute of Plant Protection in Poland, *T. salignus* on plantations of willow grown for energetic purposes is a pest of minor and only local importance (Nijak et al., 2018).

Comprehensive studies on the harmfulness of *T. salignus* were conducted by Collins et al. (2001b). They found that aphid feeding exhibited a strong negative effect on the willow. Depending on the date of the plant infestation by the pest and the condition of the plant, aphid feeding caused a reduction of the aboveground mass by up to a half, dehydration of shoots, delayed plant regrowth and decrease in the mass of the created wood tissue. The adverse effects were also noted in the following year, despite the absence of aphids. The intensity of net photosynthesis considerably increased (nearly two-fold). In addition, the nitrogen content in the leaves increased by 20% (Collins et al., 2001b), which might contribute to the attraction of phyllophagous insects. Information from producers in New Zealand cited by Sopow et al. (2017) concern the weakening of the root system, deterioration of seedling survival in nurseries, dying of plants in collections and an increase in the susceptibility of the willow to secondary pathogens. Styszko and Pałosz (2008) estimated that high infestation (7 colonies per plant, 52% of plants occupied) caused a decrease in the length of willow shoots by 8%.

From a practical point of view, the information on the susceptibility of willow species/varieties to *T. salignus* attack is important. In laboratory and field studies, a large diversity of these properties was found. They were evident by the changes in the developmental parameters of aphids and the degree of plant colonisation. In field studies conducted by Collins et al. (2001a), which covered four willow clones, the infestation of plants was very high. In many cases, it was up to 100%, and the aphids remained on the plants for 5 to 20 weeks. The interaction of the year and variety was found to impact the population of the pest. In the years favourable for aphids, the infestation of Dasyclados variety was significantly lower and lasted shorter than in the case of other varieties. In the studies conducted by Tun et al. (2020c), it was found that *S. viminalis* and *S. candida* were most heavily infested by aphids, while *S. eriocephala*, *S. matsudana* and *S. lasiolepsis x viminalis* were the least affected. The differences were even ten-fold. Özder et al. (2007) determined worse development potential of aphids feeding on *S. matsudana* than of those feeding on *S. babylonica*. Mittler (1957) believed that *T. salignus* developed best on *Salix acutifolia* (=*S. daphnoides*). In the experiment carried out by Styszko and Pałosz (2008), there were no aphids on the plants of one of 9 clones (1033 *S. viminalis*), although 40%–60% of other shrubs were colonised by these insects. Moreover, Nijak (2009) found differentiation in the aphid population on willow varieties. The largest concerned the Inger variety distinguished by its fine bark. In laboratory tests, alatae pre-reproductive aphids did not show varietal preferences (Collins et al., 2001a). Based on an experiment using an olfactometer, it was possible to determine the willow varieties that were more readily chosen by the aphids, which was confirmed in field studies (Aradottir et al., 2009).

Resistance to pest attacks can be determined, among others, by the composition of volatile organic compounds (VOCs) secreted by the plant. For this purpose, Tun et al. (2020c) tested 15 willow species/hybrids. There was no clear relationship between the VOC emission and *T. salignus* attack. Significant changes included only a decrease in the total emission and emission of individual groups of these compounds in several locations. The authors attribute this to the weaker response of the plant to an attack by sucking insects than that observed in the case of phyllophagous insects.

Willow production is generally considered as a low-input cultivation. The use of insecticides is economically and environmentally unjustified, and during the period of *T. salignus* occurrence, it is technically impracticable (Nijak et al., 2018; Sopow et al., 2017). Hence, research on the protection of plants against this aphid species focuses on using both environmental resistance and natural willow resistance to pest attacks.

The influence of honeydew produced by *T. salignus* on beekeeping, sheep farming and fruit growing

Willow is remarkably useful to bees and is valued in honey production. The honeydew produced by *T. salignus* in the largest quantities is available to worker bees in late summer and autumn. It contains large amounts of melezitose, which crystallises easily. The use of willow honeydew by bees results in production of so-called cement honey, which forms a compact mass at the bottom of honeycomb cells. It cannot be centrifuged from de-capped honey frames and clogs filters. This leads to a reduction of the yield of late-summer honey by several dozen percent (Sopow et al., 2017). Melezitose is not utilised by bees and its crystals must be removed by the insects from the hive. Some reports indicate that honey produced from the *T. salignus* honeydew causes diseases in bees and increases their mortality (Imdorf et al., 1985 a,b). Beekeepers in Poland have similar problems with larch honeydew (Szczęsna et al., 2003). Additionally, the availability of honeydew strengthens the population of wasps, which rob honey, disturb and kill bees (Sopow et al., 2017).

In New Zealand, honeydew dripping from willows is a problem in pastures because it sticks sheep's wool together and causes other debris to stick to it. Honeydew in orchards stains fruit and leads to the development of black sooty mould on them, which reduces their commercial value (Sopow et al., 2017).

THE USE OF *T. SALIGNUS* IN THE STUDY OF PLANT PHYSIOLOGY

In the studies carried out at the beginning of the 20th century on the transport of substances in plants, *T. salignus* was used as a tool of accessing the contents of sieves. The stylets of feeding aphids were cut off right next to the insects' heads. The food canal and salivary canal formed from maxillary stylets remained intact, while the mandibular part was curling away. Through this capillare, pressure pushed the phloem sap out. A special device was even constructed, which enabled the collection of phloem sap from stylets prepared in this way (Mittler, 1958a). Honeydew excreted by live feeding aphids was used for a similar purpose. Combined with the use of labelled elements, this technique allowed the study of the movement of various substances in and out of the phloem.

Concurrently, these experiments also provided important information about the biology of aphids and their food. Mittler (1958a) confirmed the assumption that the sap from the stylets was identical to that ingested by aphids and corresponded to the content of phloem sieve tubes of uninfested plants, which was important for the validation of the method. Rogers and Peel (1975) indicated factors, which must be considered during this type of research. These included increased evaporation in conditions of higher temperature and wind, dependence of the length of the stylets on the thickness of the shoot and differentiation of the radius of the stylet food canal at individual developmental stages of the insect. It was found that the sap from severed stylets usually continued to exude for 5–8 hours, but sometimes even for 2–3 days. The exudation rarely stopped after a few minutes (Mittler, 1957, 1958a). Its amount depended on the developmental stage of the insect and ranged from 0.64 to 1.89 mm^3 per hour (Mittler, 1957, 1958a).

The only sugar in the sap obtained from the stylets was saccharose, the total concentration of which ranged from 5% to 10% (Mittler, 1958a). The nitrogen compounds in the stylet sap included aspartic acid, glutamic acid, serine, threonine, alanine, valine, leucine and/or isoleucine, asparagine, glutamine and possibly gamma-aminobutyric acid. Depending on the development phase of the shoot, the total nitrogen concentration varied from 0.03% (leaf maturity) to 0.2% (beginning of bud swelling) (Mittler, 1958a). The composition of the sap from 1 stylet, both in terms of the content of carbohydrates and nitrogen-containing substances, changed very little over the course of 24 hours (Mittler 1958a).

The technique utilising severed proboscis of *T. salignus* has been used in numerous experiments. The composition of the phloem sap and the factors influencing the transport of assimilates (Ford, Peel, 1967; Gardner, Peel, 1972; Grange, Peel, 1978; Ho, Peel, 1969a,b; Hoad, Peel, 1965; Lepp, Peel, 1970; Peel, 1963, 1964, 1987) as well as the movement of other substances, such as phenolic compounds, hormones, synthetic growth regulators and herbicides, have been studied in this way (Bowen, Wareign, 1969; Hoad, Bowen, 1968; Hoad, Ellis, 1972; Hoad, 1967; Hoad et al., 1971; Macleod, Pridham, 1966; Lepp, Peel, 1970, 1971; Peel, 1972). Methods utilising severed stylets are still being developed and are also used to study other plant species and aphids (Palmer et al., 2013).

SUMMARY

The majority of 20th century scientific articles related to *T. salignus* in the SCOPUS and Web of Science databases include works, in which the aphid was not an object, but a research tool. Recent studies have aimed at obtaining results enabling the control of the aphid, which is treated as a threat to willow cultivation. The number of studies and scope of research will most likely still depend on the use of this plant, unless the aphid itself becomes the object of interest, for example, in the pharmaceutical or cosmetic industry.

The studies carried out so far have resulted in a collection of basic information on the biology of *T. salignus*; however, many aspects require further investigation. For instance, the seasonality of the aphid appearance, functions and biochemical properties of substances produced by the insects, interactions with host plants and dependence on environmental factors must be evaluated. Modern research methods can verify previous findings and allow the obtaining of new results. It is key to include in the future research on *T. salignus* links with the environment and other organisms, as well as different indirect relations. This is of particular importance in changing climatic conditions and in areas where the giant willow aphid is an invasive species. In addition to experimental work, field observations can also provide important information.

Articles collected in the SCOPUS and Web of Science databases do not cover a whole range of the literature related to *T. salignus*; however, the sources cited in reviews significantly expand its scope. A good practice, which is available thanks to the progress in collecting and transferring data, is to include photographs showing selected aspects of the methodology and research conditions in the articles or as their appendices. In the case of *T. salignus*, professional online portals collecting current observations on the biology of this insect and its relationship with the environment are considered as significant supplements to the existing scientific literature.

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