Variation in susceptibility of rapeseed cultivars to the peach potato aphid

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Abstract
Considering the need for reduction in insecticide use, we studied the potential for antibiosis and the potential for antixenosis in seven highly yielding winter Brassica napus L. cultivars against Myzus persicae (Sulz.). We found evidence for antixenosis, i.e., disruption in probing in non-phloem tissues and a failure in reaching sieve elements in cultivar ‘Alister’. We found evidence for antibiosis, i.e., reduced ability of the plant to serve as a host, in cultivar ‘Florida’. On ‘Alister’ and ‘Florida’, net reproduction and reproductive period duration of M. persicae were the lowest of all studied cultivars. ‘Adriana’, ‘Andromeda’, ‘Gladius’, and ‘Kolumb’ are intermediately susceptible to M. persicae infestation with medium values of net reproduction and reproduction period duration, and slight disturbances in aphid probing and feeding. ‘Artoga’ is highly susceptible. On ‘Artoga’, reproduction period was the longest, daily fecundity and net reproduction of M. persicae were highest, and probing and feeding behaviors were unaltered. Glucoallysin, glucobrassicanapin, gluconapin, gluconapoliferin, progoitrin, glucobrassicin, and 4-OH-glucobrassicin occurred in the leaves of all rapeseed cultivars in similar quantities and proportions and did not affect aphid performance and phloem sap ingestion by M. persicae.

Keywords Plant resistance · Glucosinolates · Probing behavior · Electrical penetration graph

Key message

- Probing behavior and development of Myzus persicae were studied to select the least susceptible Brassica napus cultivars.
- Low susceptibility of cultivar ‘Alister’ depends on antixenosis, and low susceptibility of ‘Florida’ is caused by antibiosis.

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• Cultivars ‘Adriana’, ‘Andromeda’, ‘Gladius’, and ‘Kolumb’ are intermediately susceptible, and ‘Artoga’ is highly susceptible to *M. persicae* infestation.
• Glucosinolates in leaves of rapeseed cultivars studied do not affect *M. persicae* probing and feeding behaviors.

**Introduction**

Oilseed rape *Brassica napus* L. (Brassicaceae) is one of the most cultivated and profitable crops worldwide due to its rising significance in food and feed production, industry, energy generation, and environmental protection (Ackman 1990; Jung et al. 2011; Nosenko et al. 2014; Jankowski et al. 2015a, b; FAOSTAT 2018). Within the guild of herbivores that reduce rapeseed yield, the polyphagous and cosmopolitan peach potato aphid *Myzus persicae* (Sulz.) (Hemiptera: Aphididae) has a particular status. In addition to plant nutrient removal by feeding on phloem sap, *M. persicae* transmits more than 100 plant viruses, including the persistent *Turnip yellows virus* (TuYV) (Stevens et al. 2008; Ekborn 2010; Nooh 2012; Blackman and Eastop 2017). An increased risk of virus infection in the growing acreage of oilseed rape may be expected, since *M. persicae* annual numbers are positively correlated with the acreage of agricultural crops, especially oilseed rape (Cocu et al. 2005). The population of *M. persicae* is usually dispersed over the crop area (Blackman and Eastop 2017). The infestation by *M. persicae* may also increase the susceptibility of rapeseed to fungal pathogens (Drizou et al. 2018). The timing of *M. persicae* spring migration is determined by winter temperature (Bale et al. 1988). Warmer conditions due to climate change will encourage the survival and multiplication of *M. persicae* throughout the winter (Cocu et al. 2005), which may lead to extensive spread of TuYV in the following spring (Stevens et al. 2008). If aphid attacks become more frequent, possibly in association with climate change, virus problems in oilseed rape may become more serious (Ekborn 2010). Exceptionally high infestations by *M. persicae* and TuYV infections occurred in oilseed rape in Poland and other European countries in the autumn seasons of 2016, 2017 and 2018 (Lima-grain Central Europe 2018).

The cessation of neonicotinoid seed treatments in oilseed rape, which became effective in 2013, caused serious crop losses in 2014, 2015 and 2016 owing to insect pests, including aphids (Dewar 2017). Until present, the major goals for oilseed rape breeding were tolerance to late planting and winter hardiness, plant height and lodging resistance, resistance to blackleg disease, very low contents of erucic acid and glucosinolates, high oil content and marketable seed yield (Friedt and Snowdon 2009). Considering the trends for reduction of insecticide use, the exceptional ability of *M. persicae* to overcome the effect of insecticide application (Bass et al. 2014) and the growing risk of aphid population increase due to climate change, the attention of plant breeders should be turned toward plant resistance to this aphid species, especially antixenosis and antibiosis mechanisms. Antixenosis is based on the modification of herbivore behavior by plant mechanisms, which results in the inability of a plant to serve as a host. Antixenosis against aphids is manifested in the disturbance in aphid probing and feeding behaviors leading to low or non-acceptance of the plant. Antibiosis occurs when the resistant plant affects the biology of an herbivore trying to use that plant as a host, without changing herbivore behavior (Smith 2005; Le Roux et al. 2008; Smith and Chuang 2014; van Emden 2017). In Brassicaceae, glucosinolates are the major defensive constitutive and inducible metabolites responsible for antixenosis and/or antibiosis-based resistance to most of the insect herbivores, including *M. persicae* (Cole 1997a; Brader et al. 2006; Kim and Jander 2007; Ahuja et al. 2010). Breeding efforts gave rise to oilseed rape cultivars whose glucosinolate content was reduced 15–16-fold, which maximized the utilization of protein from the fat-free seed residues but increased susceptibility to the infestation of a number of pests (Przybylinski 2011). A limited search for oilseed rape genotypes resistant to *M. persicae* has been conducted, but the published reports are scarce and contain only fragmentary data on aphid population development and response to glucosinolates (Weber et al. 1986; Fathi et al. 2010; Sarwar and Sattar 2013). Aphids may contact glucosinolates that are stored in mesophyll cells (Gabryś and Tjallingii 2000) during short (5–10 s) probes into these cells when small samples of sap are taken for gustatory purposes (Powell, 1991; Martin et al. 1997) and during the ingestion of the phloem sap (Chen et al. 2001). The electronic recording of aphid probing behavior known as Electrical Penetration Graph (EPG) technique is an invaluable tool in revealing the tissular localization of antixenosis mechanisms in the host plant and the influence of these mechanisms on particular phases of aphid probing (Gabryś and Tjallingii 2000). There exists only one report on *M. persicae* probing behavior on rapeseed (Cole 1997b). The susceptibility of rapeseed cultivars to *M. persicae* has never been evaluated basing on such studies.

Considering the recurring autumn outbreaks of *M. persicae* in winter oilseed rape, the risk of TuYV infection and the lack of literature data on potential resistance mechanisms against *M. persicae* in rapeseed, the aim of the present study was to evaluate the susceptibility of several popular and highly yielding winter *B. napus* cultivars to *M. persicae* at vegetative growth stage (2–3 leaves unfolded) that represents the early autumn phase of *B. napus* winter cultivars development. The probing behavior of *M. persicae* using the EPG technique was studied to reveal the antixenosis potential in these cultivars. The qualitative and
quantitative spectrum of glucosinolates in plant leaves was also determined to investigate the possible role of these allelochemicals as resistance mechanisms that may impede *M. persicae* probing and feeding on *B. napus*. Additionally, the development and life parameters of *M. persicae* were studied to examine the antibiosis potential in *B. napus* cultivars.

### Material and methods

#### Plants

Seven cultivars of winter oilseed rape were studied:

1. ‘Adriana’—open-pollinated cultivar (Limagrain Europe S.A.; registered in Poland in 2008), seed glucosinolates 8.8–11.9 µM/g.
2. ‘SY Alister’—hybrid cultivar (Syngenta Crop Protection AG; registered in Poland in 2014), seed glucosinolates 7.8–12.2 µM/g.
3. ‘Andromeda’—hybrid cultivar (Limagrain Europe S.A.; registered in Poland in 2012), seed glucosinolates 8.3–12.0 µM/g.
4. ‘Artoga’—hybrid cultivar (Limagrain Europe S.A.; registered in Poland in 2010), seed glucosinolates 9.5–12.6 µM/g.
5. ‘SY Florida’—hybrid cultivar (Syngenta Crop Protection AG; registered in Poland in 2015), seed glucosinolates 10.2–13.6 µM/g.
6. ‘Gladius’—hybrid cultivar (Syngenta Crop Protection AG; registered in Poland in 2010), seed glucosinolates 10.4–12.5 µM/g.
7. ‘SY Kolumb’—hybrid cultivar (Syngenta Crop Protection AG; registered in Poland in 2010), seed glucosinolates 7.4–11.2 µM/g.

These cultivars were selected basing on their yielding and economic efficiency. The yielding of the studied cultivars was 10–20% higher than that of reference cultivar in crop cultivar trials conducted by The Research Centre for Cultivar Testing (COBORU) in Słupia Wielka near Poznań (Bundessortenamt 2014; Porejestrowe Doświadczalnictwo Odmianowe 2019; Wyniki Porejestrowych Doświadczeń 2015, 2018). The seeds were provided by the University of Warmia and Mazury Experimental Station Balczyn, Sp. Z o. o. Plants were grown in the chamber Sanyo MLR-351H (Sanyo Electronics Co. Ltd.). Parameters were designed to mimic typical climatic field conditions during planting season of winter oilseed rape: L14:10D photoperiod, 70% r.h., and temperature, as presented in Figure S1.

### Aphids

The peach potato aphid *Myzus persicae* (Sulz.), kept as a multiclonal colony on Chinese cabbage *Brassica rapa* subsp. *pekinensis* (Lour.) Hanelt., was reared in the laboratory at 20° C, 65% r.h., and L16:D8 photoperiod. The laboratory culture of *M. persicae* has been maintained at the Department of Botany and Ecology, University of Zielona Góra, since 2008. To maintain the colony vitality, apterous aphids were transferred to non-infested plants every other week. Transfer of aphids to new plants consisted of excising an aphid-infested leaf and placing it atop of new plants to allow independent aphid movement to fresh plant leaves.

#### Aphid performance

One adult apterous female *M. persicae* was placed on a plant at BBCH growth stages 12–13 (two to three leaves unfolded, according to the universal plant development decimal code provided by Biologische Bundesanstalt, Bundessortenamt and CHemical industry) (Meier 2018) for 24 h. After 24 h, the female and all progeny except one nymph were removed. Each plant was isolated within a plastic cylinder with a fine mesh on top. The development of the nymph until maturity and the number of the newly born nymphs were monitored daily, and all newborn nymphs were removed. The experiment was terminated with the death of the mother aphid. The following parameters were evaluated: duration of pre-reproductive period (from birth to the first nymph laid), daily fecundity (number of nymphs laid each day), total fecundity (number of nymphs laid by one female), mother aphid longevity, net reproductive rate (*R*; females/female−1 generation−1), intrinsic rate of natural increase (*r* subm = [0.74(ln*Md*)]/*D*), where 0.74 is the constant for aphids and mites, Md is the number of nymphs produced in the first *D* days of reproduction after the adult moult, and *D* is the development time of the aphid (i.e., from birth to the final moult but before the onset of reproduction), mean generation time (*T* = ln(*R*0)/*r* subm) (Wyatt and White 1977; Awmack and Leather 2002; Leather et al. 2017). The experiment was replicated 15 times for each oilseed rape cultivar.

#### Aphid probing behavior

*Myzus persicae* probing and feeding were monitored using the technique of electronic recording of aphid probing in plant tissues, known as Electrical Penetration Graph (EPG) (Tjallingii 1995). Aphid and plant are made parts of an electric circuit, which is completed when the aphid inserts its stylets into the plant. Weak voltage is supplied in the circuit, and all changing electric properties are recorded as EPG waveforms that can be correlated with aphid activities and stylet position in plant tissues (Martin et al. 1997;
Pettersson et al. 2017). In the present study, aphids were attached to a golden wire electrode with conductive silver paint and starved for 1 h prior to the experiment. Probing behavior of *M. persicae* on rapeseed cultivars was monitored for 8 h continuously with 4- and 8-channel DC EPG recording equipment (www.epgsy.systems.eu). Signals were saved on the computer and analyzed using the PROBE 3.1 software provided by W. F. Tjallingii (www.epgsy.systems.eu). The following aphid behaviors were distinguished: no penetration (waveform ‘np’—aphid stylets outside the plant), pathway phase—penetration of non-phloem tissues (waveforms ‘A, B, and C’), derailed stylet movements (waveform ‘F’), salivation into sieve elements (waveform ‘E1’), ingestion of phloem sap (waveform ‘E2’), and ingestion of xylem sap (waveform ‘G’). The parameters derived from EPGs were analyzed according to their frequency and duration in configuration related to activities in peripheral and vascular tissues (van Helden and Tjallingii 1993). The E1/E2 transition patterns were included in E2. ‘G’ and ‘F’ occurred sporadically; therefore, these events were combined with pathway activities in all calculations and defined as non-phloem activities. The waveform patterns that were not terminated before the end of the experimental period (8 h) were included in the calculations. In sequential parameters, when time to waveforms related to phloem phase (E1 or E2) was calculated, the time from the 1st probe until the end of the recording was used if no phloem phase occurred. In non-sequential parameters, when a given waveform had not been recorded for an individual, the duration of that waveform was given the value of 0.

Aphids for EPG experiments were 2–3 days old (2–3 days after the final moult) viviparous apterous females selected randomly from the stock culture. According to Ten Broeke et al. (2013), the use of aphids of random ages gives a clear view of the behavior of adult aphids within a population. The plants used in the bioassays were at BBCH growth stages 12–13 (two to three leaves unfolded) (Meier 2018). Each aphid was given access to a freshly prepared plant. Each plant-aphid set was considered as a replication and was tested only once. The number of replications (= EPG recordings) for each plant cultivar was 20. Recordings that terminated due to aphid falling from the plant or where EPG signal was unclear were discarded from analysis. Only the replications that included complete 8-h recording were kept for analysis, which were: ‘Adriana’, *n* = 13; ‘Alistar’, *n* = 12; ‘Andromeda’, *n* = 12; ‘Artoga’, *n* = 12; ‘Florida’, *n* = 12; ‘Gladius’, *n* = 15; ‘Kolumb’, *n* = 10. All experiments were carried out under the same conditions of temperature, relative humidity (r.h.) and photoperiod as those used for the rearing of plants and aphids. All bioassays started at 10:00–11:00 h MEST (Middle European Summer Time). Aphids show distinct diurnal feeding activity, with peak activity during day time, independently of host plants (Joschinski et al. 2016; Beer et al. 2017; Pettersson et al. 2017).

### Statistical analysis

Firstly, the normality of the distributions of the observed traits was tested using Shapiro–Wilk’s normality test. Life table parameters and EPG parameters describing aphid probing behavior were calculated manually, and the mean and standard errors were subsequently calculated using the analysis Excel worksheet created by the authors especially for this study. Data thus obtained were analyzed by Kruskal–Wallis test and post hoc multiple comparisons of mean ranks for all groups (Dunn’s test). All statistical calculations were performed using StatSoft, Inc. (2014) STATISTICA (data analysis software system), version 12. Additionally, the relationships among all the traits were estimated on the basis of correlation coefficients. The results were also analyzed using multivariate methods. The graphic distributions of cultivars, described by means of the observed traits: life table parameters, EPG-recorded aphid probing parameters and glucosinolate content, were obtained by means of the principal components analysis (PCA). These analyses were done in GenStat 18.

### Glucosinolate analysis

The plant material was obtained from winter oilseed rape plants at BBCH growth stages 12–13, which corresponded with plant stage used for experiments on aphid development and probing behavior. Plant samples were stored under −80 °C for 24 h and lyophilized. Glucosinolates were isolated by the enzymatic desulfation procedure according to the Commission Regulation (EC) No 1864/90 (Commission of the European Communities 1990). In total, 200 mg of freeze-dried material was transferred to test tubes and heated at 75 °C in a hot water bath for 1 min. Next, glucosinolates were extracted three times with 2 ml of boiling methanol (70%), stirring occasionally with the UltraTurrax IKA T-25 homogenizer (Jankel & Kunkel, Germany). The supernatants were centrifuged, combined and filled up to 10 ml. Glucotropaeolin was used as an internal standard. Desulfo-glucosinolates were analyzed by HPLC according to the method described by Ciska et al. (2008). The separation was performed in an HPLC system with an autosampler (LC-20) and the SPD-M20A DAD detector (Shimadzu, Japan) using the LiChrospher® 100 RP-18 (5 µm, 250 × 4 mm) column (Merck, Darmstadt, Germany) with a flow rate of 1.2 mL/min. Desulfo-glucosinolates were separated in a gradient of water and 20% acetonitrile as previously described (Ciska et al. 2008).
Results

Aphid performance

Lifetime duration of *M. persicae* females varied, depending on the winter oilseed rape cultivar and ranged from 50.7 ± 6.4 days on *B. napus* ‘Artoga’ to 62.3 ± 11.3 days on ‘Alister’ (Table 1). The highest survival of aphids occurred on ‘Alister’ and the lowest on ‘Andromeda’, where 50% of aphids survived 59 and 51 days, respectively (Fig. 1). The mean duration of pre-reproductive period of *M. persicae* did not differ significantly among aphids on oilseed rape cultivars studied and was approximately 14–15 days, which was roughly 25–29% of aphid lifetime (Table 1, Figs. 1, S2). The duration of reproductive period was the longest on ‘Adriana’ (35.1 ± 4.7 days) and the shortest on ‘Florida’ (21.8 ± 4.8 days), which accounted for 9.1% and 34.2% of aphid lifetime, respectively (Table 1, Figs. 1, S2). Daily fecundity was the highest on ‘Artoga’ (3.6 ± 0.7 nymphs per day) and the lowest on ‘Alister’ (1.9 ± 0.6 nymphs) (Table 1). The dynamics of reproduction also varied among aphids on different oilseed rape cultivars. On ‘Adriana’, ‘Andromeda’, ‘Artoga’ and ‘Gladius’, *M. persicae* consistently gave birth to 3–4 nymphs per day during the whole reproductive period, while on ‘Alister’, ‘Florida’ and ‘Kolumb’, the majority of nymphs were born during the first two weeks of the reproductive phase (Fig. 1). The net reproduction was the highest on ‘Artoga’ (112.0 ± 26.8 nymphs per female) and the lowest on ‘Alister’ and ‘Florida’ (47.9 ± 16.2 and 56.7 ± 17.8, respectively). The mean time of generation development was the shortest on ‘Florida’ and the longest on ‘Adriana’ (25.2 ± 2.8 and 31.2 ± 3.8 days, respectively). The intrinsic rate of natural increase was similar in all aphids in all oilseed rape cultivars studied (0.18–0.21) (Table 1).

Aphid probing behavior

Non-probing and pathway activities predominated during the initial 1–2 h of the experiment in all aphid individuals on all plants (Fig. 2). During the following hours, the proportion of non-probing phase activity decreased, while the proportion of non-phloem and phloem probing phases in aphid activities increased on ‘Artoga’, ‘Florida’ and ‘Gladius’. At the end of the 8-h experiment, phloem phase was the main aphid activity on these cultivars, ranging from 53% on ‘Artoga’ to 78% time on ‘Florida’. The proportion of phloem phase remained relatively low on ‘Adriana’, ‘Andromeda’, and ‘Kolumb’ and scarce on ‘Alister’ during the whole experimental time (Fig. 2).

Total probing time was the longest on ‘Andromeda’ (89% of experimental time) and the shortest on ‘Alister’ (34%) (Table 2, Fig. 2). On ‘Adriana’, ‘Artoga’ and ‘Kolumb’, all aphids reached sieve elements and all showed sustained ingestion (Fig. 3). The proportion of phloem phase during probing was the highest on ‘Florida’ (60% of experimental time), ‘Artoga’ (50%) and ‘Gladius’ (50%) and the lowest on ‘Alister’ (10%) (Table 2, Fig. 2). The average probe was from 2.1 min on ‘Alister’ to 32 min long on ‘Gladius’.

| Table 1 Population parameters of *Myzus persicae* on oilseed rape *Brassica napus* cultivars studied |
|----------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
|                                    | Adriana | Alister | Andromeda | Artoga | Florida | Gladius | Kolumb | p |
| Female longevity (days)           | 56.0 ± 7.8a | 62.3 ± 11.3a | 51.7 ± 4.4ab | 50.7 ± 6.4b | 52.6 ± 10.6ab | 56.4 ± 5.8ab | 52.7 ± 9.4ab | 0.0181 |
| Pre-reproduction period            | 14.0 ± 2.9 | 15.3 ± 2.26 | 14.2 ± 1.0 | 14.6 ± 1.6 | 14.6 ± 1.8 | 14.0 ± 2.7 | 14.1 ± 2.2 | 0.6444 |
| Reproduction period (days)        | 35.1 ± 4.7a | 25.3 ± 5.9b | 32.6 ± 6.5a | 31.5 ± 5.7a | 21.8 ± 4.8b | 33.3 ± 8.3a | 29.6 ± 7.1ab | 0.0000 |
| Post-reproduction period (days)   | 6.9 ± 6.6bc | 21.1 ± 10.3a | 4.9 ± 4.0c | 4.6 ± 2.5c | 16.2 ± 9.2ab | 9.1 ± 8.9bc | 8.9 ± 7.3abc | 0.0000 |
| Daily fecundity (D)               | 2.9 ± 0.9ab | 1.9 ± 0.6c | 2.9 ± 0.5ab | 3.6 ± 0.7a | 2.7 ± 0.9bc | 2.8 ± 0.5ab | 2.4 ± 0.5bc | 0.0000 |
| Net reproduction (R0)             | 99.7 ± 24.4ab | 47.9 ± 16.2c | 92.5 ± 18.4ab | 112.0 ± 26.8a | 56.7 ± 17.8c | 91.5 ± 21.4ab | 70.3 ± 15.2bc | 0.0000 |
| Md/R0*                           | 0.43 ± 0.13e | 0.77 ± 0.15abc | 0.53 ± 0.18ede | 0.50 ± 0.09e | 0.75 ± 0.20bc | 0.55 ± 0.19ede | 0.68 ± 0.18cde | 0.0000 |
| Mean time of generation development (T) | 31.2 ± 3.8a | 26.3 ± 2.7abc | 28.7 ± 3.9abc | 29.9 ± 2.9ab | 25.2 ± 2.8c | 29.1 ± 5.6abc | 26.3 ± 5.4bc | 0.0005 |
| Intrinsic rate of natural increase (ra) | 0.20 ± 0.03 | 0.18 ± 0.03 | 0.20 ± 0.02 | 0.20 ± 0.03 | 0.20 ± 0.03 | 0.19 ± 0.03 | 0.21 ± 0.03 | 0.0673 |

Values are means (± SD), n=15. Different letters in rows show significant differences at p<0.05 (Kruskal–Wallis test and post hoc multiple comparisons of mean ranks for all groups Dunn’s test)

*Md*: number of nymphs produced in the first D days of reproduction after the adult moult
Fig. 1 Survival and fecundity of *Myzus persicae* on *Brassica napus* cultivars studied
Fig. 2  Trends in Myzus persicae probing activities on Brassica napus cultivars studied, expressed as the proportion of time spent on different stylet activities during the 8-h experiment: np, non-probing; $C+G+F$, probing in non-phloem tissues (probing in non-vascular tissues+derailed stylet activities+xylem phase), $E$, total phloem phase ($E1+E2$, watery salivation+sap ingestion)
Non-probing intervals were the shortest on ‘Andromeda’ and the longest on ‘Gladius’ (1.8–6.8 min) (Table 2).

Time to 1st phloem phase from the onset of probing was the shortest on ‘Florida’ (1.6 ± 1.7 h) and ‘Artoga’ (1.7 ± 1.2 h) and the longest on ‘Alister’ 6.4 ± 2.9 h. On ‘Florida’ and ‘Artoga’, time to reach 1st sustained (E2 > 10 min) sap ingestion period was the shortest. On ‘Artoga’ and ‘Gladius’, the total time of non-probing activities before first phloem phase was the shortest (25% and 21% of total non-probing time, respectively) and the longest on ‘Alister’ (98%). Number of probes before 1st phloem phase was the lowest in aphids on ‘Artoga’ and ‘Gladius’ (7.0 ± 4.4 and 6.7 ± 5.4, respectively) and the highest on ‘Alister’ (72.5 ± 52.3). These probes were separated by non-probing intervals, which were the shortest (1.5 ± 5.6 min) on ‘Andromeda’ and the longest on ‘Artoga’ (5.6 ± 27.4 min) (Table 2).

On ‘Adriana’, ‘Artoga’ and ‘Kolumb’, all aphids achieved phloem phase and all showed sap ingestion activity (Figs. 3, S3). On ‘Florida’, 92% of aphids showed periods of sustained sap ingestion, while on ‘Andromeda’ and ‘Gladius’, 92% and 93% of aphids showed phloem phase, but 83% and 87% of aphids on these cultivars showed sap ingestion activity, respectively. On ‘Alister’, only 25% of aphids attained phloem phase and sap ingestion phase during the 8-h experiment (Figs. 3, S3). The duration of 1st phloem phase did not differ significantly among aphids, but there was a visible trend: the first phloem phase was the shortest on ‘Alister’. 

### Table 2 Probing behavior of *Myzus persicae* on oilseed rape *Brassica napus* cultivars studied

| General aspects of aphid probing behavior | Adriana | Alister | Andromeda | Artoga | Florida | Gladius | Kolumb | p |
|------------------------------------------|---------|---------|-----------|--------|---------|---------|--------|---|
| n= 13                                    | n= 12   | n= 12   | n= 12     | n= 12  | n= 15   | n= 10   |        |   |
| Total non-probing time (h)               | 1.4 ± 0.5ab | 5.3 ± 2.8a | 0.9 ± 1.0b | 1.2 ± 1.2b | 1.2 ± 2.1b | 1.9 ± 1.8ab | 1.3 ± 1.1ab | 0.0000 |
| Total probing in non-phloem tissues (h)  | 4.3 ± 1.7ab | 1.9 ± 1.8a | 5.3 ± 2.4b | 3.2 ± 1.8ab | 2.6 ± 1.4ab | 3.0 ± 2.0a | 4.7 ± 1.7b | 0.0013 |
| Total phloem phase (h)                   | 2.2 ± 1.9ab | 0.8 ± 1.7b | 1.8 ± 2.5ab | 3.6 ± 2.0a | 4.2 ± 2.0a | 3.1 ± 2.5a | 2.0 ± 1.6ab | 0.0002 |
| Proportion of phloem phase in total probing | 0.3 ± 0.3ab | 0.1 ± 0.2b | 0.3 ± 0.3ab | 0.5 ± 0.3a | 0.6 ± 0.3a | 0.5 ± 0.3a | 0.3 ± 0.2ab | 0.0001 |
| Number of probes                         | 38.8 ± 24.3a | 78.5 ± 45.3a | 29.3 ± 20.4ab | 16.6 ± 17.4b | 28.7 ± 17.1ab | 11.7 ± 7.8b | 21.0 ± 9.7ab | 0.0000 |
| Duration of 1st probe (h)                | 0.1 ± 0.1ab | 0.0 ± 0.0b | 0.1 ± 0.2ab | 0.9 ± 2.3a | 0.7 ± 2.3ab | 0.9 ± 2.0ab | 0.4 ± 0.7a | 0.0027 |
| Mean duration of a probe (min)           | 10.3 ± 33.4cd | 2.1 ± 16.8a | 14.6 ± 49.3d | 24.8 ± 78.0bcd | 14.1 ± 50.7bc | 31.6 ± 77.6bcd | 19.2 ± 42.9a | 0.0000 |
| Mean duration of non-probing intervals (min) | 2.1 ± 4.7de | 4.1 ± 9.3ab | 1.8 ± 6.5f | 4.1 ± 19.7cd | 2.2 ± 8.2ef | 6.8 ± 24.9bcd | 3.7 ± 12.8cde | 0.0000 |
| A. behavior in non-phloem tissues prior to the 1st phloem phase | | | | | | | | |
| Number of probes before 1st phloem phase | 14.7 ± 12.7ab | 72.5 ± 52.3a | 12.1 ± 10.3ab | 7.0 ± 4.4b | 13.7 ± 6.8ab | 6.7 ± 5.4b | 13.2 ± 6.3ab | 0.0000 |
| Time from 1st probe to 1st phloem phase (h) | 2.1 ± 1.2ab | 6.4 ± 2.9a | 2.6 ± 2.7ab | 1.7 ± 1.2ab | 1.6 ± 1.7b | 2.2 ± 2.1ab | 3.7 ± 2.3ab | 0.0003 |
| Time from 1st probe to 1st sustained sap ingestion period (h) | 4.2 ± 2.5ab | 6.8 ± 2.8a | 5.0 ± 3.2ab | 2.3 ± 2.0b | 2.4 ± 1.7b | 3.3 ± 2.6ab | 4.4 ± 2.4ab | 0.0007 |
| Total duration of non-probing before 1st phloem phase (h) | 0.6 ± 0.4ab | 5.2 ± 3.0a | 1.0 ± 2.3b | 0.3 ± 0.3b | 0.7 ± 1.5b | 0.4 ± 0.6b | 0.7 ± 0.8ab | 0.0000 |
| Mean duration of non-probing intervals (min) | 2.2 ± 5.9de | 4.3 ± 9.6ab | 1.5 ± 5.6f | 5.6 ± 27.4cdef | 2.9 ± 11.2ef | 4.0 ± 8.7bcd | 3.0 ± 10.3ef | 0.0000 |
| A. behavior during phloem phase           | n=13 | n=3 | n=11 | n=12 | n=11 | n=14 | n=10 |   |
| Duration of 1st phloem phase (h)          | 1.0 ± 2.1 | 0.4 ± 0.6 | 0.8 ± 2.1 | 1.8 ± 2.2 | 1.1 ± 2.3 | 2.3 ± 2.8 | 1.3 ± 1.2 | 0.1487 |
| Duration of 1st ingestion phase (h)       | 0.4 ± 1.2 | 0.4 ± 0.6 | 1.3 ± 2.4 | 1.8 ± 2.2 | 1.2 ± 2.2 | 2.5 ± 2.9 | 1.3 ± 1.2 | 0.0971 |
| Proportion of salivation in phloem phase  | 0.1 ± 0.1 | 0.2 ± 0.3 | 0.3 ± 0.4 | 0.0 ± 0.0 | 0.1 ± 0.2 | 0.1 ± 0.3 | 0.1 ± 0.1 | 0.0677 |

Values are means (± SD). n = number of replications analyzed. Different letters in rows show significant differences at p < 0.05 (Kruskal–Wallis test and post hoc multiple comparisons of mean ranks for all groups Dunn’s test).
and the longest on ‘Gladius’. Similar trend occurred in the duration of the first sap ingestion phase: it was the longest on ‘Gladius’ and the shortest on ‘Adriana’ and ‘Alister’ with aphids on other cultivars showing intermediate values of this parameter (Table 2). The proportion of E1 salivation during phloem phase was relatively high in all cultivars (from 10% on ‘Artoga’ to 30% on ‘Andromeda’), but did not differ significantly among aphids (Table 2).

**Glucosinolate content**

Total amount of glucosinolates in leaves of oilseed rape cultivars studied ranged from 1.834 ± 0.049 μmol/g dry weight (d.w.) in ‘Andromeda’ to 3.229 ± 0.061 μmol/g d.w. in ‘Alister’. No qualitative differences occurred among the cultivars. Seven glucosinolates were found: aliphatic glucoallysin, glucobrassicanapin, gluconapin, gluconapoliferin and progoitrin and indole glucobrassicin and 4-OH-glucobrassicin (Table 3). In total, aliphatic glucosinolates predominated, whose amount ranged from 61% of all glucosinolates in ‘Gladius’ to 74% in ‘Alister’. In all cultivars, glucobrassicanapin and progoitrin, and 4-OH-glucobrassicin were the most abundant (Figure S4).

**Correlation analysis**

The correlation analysis revealed significant relationships among the aphid probing behavior parameters studied. Positive correlations occurred (1) between the total duration of non-probing and the total number of probes, number of probes before 1st phloem phase, time from 1st probe to 1st phloem phase, and total duration of non-probing before 1st phloem phase, (2) between the total duration of phloem phase and the proportion of phloem phase in total probing and the duration of 1st probe, (3) between the proportion of phloem phase in total probing and the duration of 1st probe (Figure 3).

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**Table 3** Glucosinolate profiles of oilseed rape *Brassica napus* cultivars studied

|          | Adriana | Alister | Andromeda | Artoga | Florida | Gladius | Kolumb |
|----------|---------|---------|-----------|--------|---------|---------|--------|
| **Aliphatic** |         |         |           |        |         |         |        |
| Glucoallysin   | 0.106 ± 0.001 | 0.243 ± 0.001 | 0.066 ± 0.004 | 0.117 ± 0.006 | 0.250 ± 0.004 | 0.049 ± 0.001 | 0.064 ± 0.000 |
| Glucobrassicanapin | 0.486 ± 0.006 | 0.619 ± 0.019 | 0.371 ± 0.018 | 0.441 ± 0.001 | 0.419 ± 0.021 | 0.573 ± 0.021 | 0.523 ± 0.023 |
| Gluconapin    | 0.184 ± 0.006 | 0.154 ± 0.007 | 0.109 ± 0.005 | 0.357 ± 0.010 | 0.108 ± 0.008 | 0.180 ± 0.011 | 0.120 ± 0.010 |
| Gluconapoliferin | 0.098 ± 0.004 | 0.251 ± 0.011 | 0.059 ± 0.004 | 0.099 ± 0.001 | 0.130 ± 0.006 | 0.047 ± 0.000 | 0.068 ± 0.004 |
| Progoitrin    | 0.556 ± 0.024 | 1.051 ± 0.031 | 0.659 ± 0.003 | 0.759 ± 0.016 | 1.083 ± 0.013 | 0.570 ± 0.009 | 0.650 ± 0.004 |
| **Indole**    |         |         |           |        |         |         |        |
| Glucobrassicin | 0.079 ± 0.011 | 0.106 ± 0.003 | 0.095 ± 0.001 | 0.094 ± 0.007 | 0.059 ± 0.004 | 0.046 ± 0.006 | 0.079 ± 0.005 |
| 4-OH-glucobrassicin | 0.860 ± 0.005 | 0.806 ± 0.011 | 0.477 ± 0.023 | 0.858 ± 0.038 | 0.862 ± 0.025 | 0.887 ± 0.038 | 0.814 ± 0.005 |
| **Total**     | 2.368 ± 0.017 | 3.229 ± 0.061 | 1.834 ± 0.049 | 2.723 ± 0.065 | 2.910 ± 0.046 | 2.351 ± 0.075 | 2.317 ± 0.015 |

Values are means (± SD), μM/g dry weight
probe, (4) between the number of probes and the number of probes before 1st phloem phase, time from 1st probe to 1st phloem phase, time from 1st probe to 1st sustained sap ingestion period and total duration of non-probing before 1st phloem phase, (5) between the number of probes before 1st phloem phase and time from 1st probe to 1st phloem phase, time from 1st probe to 1st sustained sap ingestion period and total duration of non-probing before 1st phloem phase, (6) between time from 1st probe to 1st phloem phase and time from 1st probe to 1st sustained sap ingestion period and (7) between time from 1st probe to 1st sustained sap ingestion period and total duration of non-probing before 1st phloem phase. Negative correlations occurred (1) between the total duration of phloem phase and time from 1st probe to 1st phloem phase and time from 1st probe to 1st sustained sap ingestion period, (2) between the proportion of phloem phase in total probing and time from 1st probe to 1st phloem phase and time from 1st probe to 1st sustained sap ingestion period and (3) between the duration of 1st probe and time from 1st probe to 1st sustained sap ingestion period (Table S1).

The correlation analysis revealed also significant positive relationships between traits of *M. persicae* probing behavior and glucosinolate content in leaves of *B. napus* cultivars studied. Most notably, the values of aphid total non-probing, total non-probing before the first phloem phase, number of probes and number of probes before the first phloem phase were positively related to the concentration of gluconapiferin. Total duration of non-probing was also positively correlated with glucobrassicanapin concentration. None of aphid probing behavior traits was correlated with the total amount of glucosinolates in plant leaves (Table S1).

Distribution of winter oilseed rape cultivars in terms of the first two principal components of seven aphid life table observed traits is presented in Figure S5. The first two principal components accounted for 98.34% of total multivariate variability between winter oilseed rape cultivars. The greatest, significant linear relationship with the first principal component was found for reproduction period, net reproduction R0, daily fecundity (positive dependencies) and post-reproduction period and Md/R0 (negative). The second principal component was significantly positively correlated with aphid longevity (Figure S5).

Distribution of winter oilseed rape cultivars in terms of the first two principal components of nine aphid probing observed traits is presented in Figure S6. The first two principal components accounted for 97.59% of total multivariate variability between winter oilseed rape cultivars. The first principal component was significantly positively correlated with total non-probing, number of probes, number of probes before 1st phloem phase, time from 1st probe to 1st phloem phase, time from 1st probe to 1st sustained sap ingestion period and total duration of non-probing before 1st phloem phase; PC1 was significantly negatively correlated with total phloem phase and proportion of phloem phase in total probing (Figure S6).

Distribution of winter oilseed rape cultivars in terms of the first two principal components of eight glucosinolate content observed traits is presented in Figure S7. The first two principal components accounted for 95.17% of total multivariate variability between winter oilseed rape cultivars. The first principal component was significantly positively correlated with progoitrin, glucoallysin, gluconapiferin and total glucosinolates (Figure S7).

**Discussion**

The present assessment of the rapeseed cultivars susceptibility to *M. persicae* infestation was based on two lines of inquiry. First, aphid probing and feeding were evaluated in relation to qualitative and quantitative content of glucosinolates. Plant secondary chemistry is among the most important mechanisms that determine host plant suitability to aphids (Douglas 2003; van Emden 2017). This line of study was designed to reveal antixenosis mechanisms in young plants that are particularly vulnerable to aphid infestation during the autumn period of winter rapeseed development. Second, we monitored *M. persicae* development in concurrence with rapeseed growth to expose antibiosis mechanisms in these plants.

The differences in aphid probing behavior observed in the present study indicate the existence of antixenosis mechanisms in certain oilseed rape cultivars. Aphids can distinguish a host from a non-host as soon as at the level of epidermis and/or parenchyma (Martin et al. 1997; Gabryś and Pawluk 2000; Gabryś and Tjallingii 2002). A high proportion of probing in non-phloem tissues in relation to total penetration time, long time to first phloem phase and a failure to find sieve elements are interpreted as effects of mechanisms that restrain probing in the non-phloem tissues and reflect antixenosis potential in these tissues (Pettersson et al. 2017; van Emden 2017; Kordan et al. 2018, 2019). There was a clear effect of antixenosis mechanisms in non-phloem tissues in ‘Alister’, on which the aphids had evident difficulties in reaching phloem vessels. The average time to reach sieve elements and start ingestion by *M. persicae* on Chinese cabbage, the plant the stock colony was kept, is approximately 2.4 h (Wróblewska-Kurdyk et al. 2019). In the present study, a similar or shorter time before the commencement of the phloem phase occurred in all aphids on all cultivars, except ‘Alister’, where aphids took almost three-fold more time to reach sieve elements. Correlation analysis showed that the time from 1st probe to 1st phloem phase is strongly affected by total duration of non-probing and the number of probes before 1st phloem phase, which means
that \textit{M. persicae} on ‘Alister’ was reluctant to probe and when it did probe, the probes were numerous and of short duration. In contrast, on ‘Adriana’, ‘Artoga’ and ‘Kolumb’, all aphids achieved phloem phase and all showed sap ingestion activity in a relatively short time, which demonstrates the absence of antixenosis mechanisms in non-phloem leaf tissues of these cultivars. The presence of antixenosis mechanisms in non-phloem leaf tissues of ‘Andromeda’, ‘Florida’ and ‘Gladius’ can also be excluded. Although some aphids failed to locate phloem on these cultivars during the 8-h experiment, the overall success rates in finding sieve elements and in the duration of feeding were relatively high and did not differ significantly from those on ‘Adriana’, ‘Artoga’ and ‘Kolumb’.

The glucosinolate spectrum in all oilseed rape cultivars studied was typical of this species (Ishida et al. 2014). The total content of glucosinolates in the leaves of all cultivars of winter oilseed rape studied was relatively low, and the total content of glucosinolates in the leaves of all cultivars and ‘Kolumb’ did not differ significantly from those on ‘Adriana’, ‘Artoga’ and ‘Gladius’. In the present study, the duration of non-probing was generally positively correlated with the concentration of glucosinoliferin. Glucosinoliferin occurred in all rapeseed cultivars studied but in low amounts and its share in the total spectrum ranged from 2.0% in ‘Gladius’ to 7.8% in ‘Alister’. The glucosinolate system in brassicaceous plants is dynamic. The quantitative as well as qualitative content of glucosinolates varies depending on species, variety and cultivar (Kjaer 1976). Moreover, the concentration of individual compounds of the species/cultivar-specific glucosinolate combination is different in different tissues and organs of the plant and depends on the developmental stage (McGregor 1988, Bodnaryk 1991; Merritt 1996; Gabryś et al. 1997; Halkier and Gershenzon 2006; Hong and Kim 2014). Glucosinolates are present in all plant compartments: on leaf surface, in apoplast, in epidermis and mesophyll cells, and in sieve elements (Matile 1984; Renwick et al. 1992; Brudenell et al. 1999; Chen et al. 2001). In sieve elements, the concentration of glucosinolates is similar to that reported for leaf extracts (Merritt 1996). Toxic to unspecialized insects (Feeny 1977), the glucosinolates stimulate the feeding of the cabbage aphid \textit{Brevicoryne brassicae} (L.) (Hemiptera: Aphididae), which depends exclusively on brassicas (Gabryś and Tjallingii 2002). However, the probability of \textit{B. brassicae} infestation decreases with the increasing concentrations of progoitrin in plants (Goody et al. 2015). At low concentrations, glucosinolates can be tolerated by some polyphagous insects, such as peach potato aphid, and under certain conditions they even increase plant suitability to \textit{M. persicae} (Nault and Styer 1972). The ubiquity of glucosinolates in the plant organism makes them easily detectable to aphids at every probing phase, in non-phloem as well as in phloem tissues (Gabryś and Tjallingii 2002). Generally, glucosinolates do not affect the consumption of phloem sap by \textit{M. persicae} (Cole 1997b). In yellow mustard \textit{Sinapis alba} L., \textit{M. persicae} ingested sap from as many sieve elements in stems as in the old leaves, and there was no difference in the time spent on the phloem sap ingestion, although in stems, the total amount of glucosinolates was nearly five times higher than in old leaves (Gabryś et al. 1997; Gabryś and Tjallingii 2000). When selecting the feeding site, \textit{M. persicae} appears to be dependent mainly on the nutritional quality of the sap (van Emden and Bashford 1969; Klingauf 1987). \textit{M. persicae} can survive the consumption of considerable amount of glucosinolates and excretes these allelochemicals unaltered in honeydew (Weber et al. 1986). Although glucosinolates are present in peripheral plant tissues and in the phloem sap (Douglas 2003), the deterrent effect of these compounds on \textit{M. persicae} probing on rapeseed cultivars may be excluded. It is likely that glucosinolates were not responsible for the varied level of susceptibility of oilseed rape cultivars to \textit{M. persicae} in the present study. The rate of phloem sap uptake is constant, so the duration of feeding periods reflects the amount of sap consumed (Tjallingii 1995; Pettersson et al. 2017). The disruption of aphid feeding, visualized as short total and mean durations of sap ingestion and high proportion of \textit{E1} salivaulation during phloem phase, points at the activity of antixenosis mechanisms in sieve elements (van Helden and Tjallingii 1993; Mayoral et al. 1996; Wilkinson and Douglas 1998; Pettersson et al. 2017; van Emden 2017; Kordan et al. 2018, 2019). The durations of ingestion in aphids on ‘Andromeda’, ‘Florida’, ‘Gladius’, ‘Adriana’, ‘Artoga’ and ‘Kolumb’ were relatively high, which suggests the absence of antixenosis mechanisms in the phloem sap in these cultivars. It may be conferred from the duration of ingestion that the quantities of the consumed sap by aphids on ‘Andromeda’, ‘Florida’, ‘Gladius’, ‘Adriana’, ‘Artoga’ and ‘Kolumb’ were generally similar. The inability to reach phloem vessels in at least 8 h, which was the duration of the EPG experiment, might have caused undernourishment in aphids on ‘Alister’. Nevertheless, the antixenosis mechanisms in ‘Alister’ remain unknown until a further study on plant chemistry is carried out.

The analysis of aphid bionomics showed interesting similarities and differences in aphid development and reproduction on rapeseed cultivars studied. The duration of pre-reproductive period did not differ among aphids on all rapeseed cultivars and lasted approximately two weeks. The pre-reproductive development of \textit{M. persicae} depends on many mechanisms, including temperature, host plant species, developmental stage of the plant and may vary from 6–7 days on \textit{Capsicum annuum} (Birgucu and Bayindir-Erol 2018), 10–11 days on \textit{Solanum tuberosum} (Alla et al. 2003), up to 12 days on \textit{Brassica caber} (Fernandez-Quintanilla et al. 2002). Additionally, maternal environment has an important influence on the performance of aphid offspring (McLean et al. 2009). The nymphs in the present study were
born by females that spent their life in stock cultures maintained on the suitable host plant. It is very likely that the transfer from a different plant and the necessity to adjust to the new plant by all aphids on all rapeseed cultivars studied caused an elongation of the pre-reproductive period, which, as a result, appeared similar in all aphids. The intrinsic rate of increase ($r_m$) was also similar in all cultivars, which might have indicated their equal suitability to *M. persicae* infestation. The explanation is in the way of calculating the $r_m$. The value of $r_m$ depends basically on two aspects, the duration of the pre-reproductive period ($D$) and the assumption that a reproducing female gives birth to 95% of her progeny in the first $D$ days of reproduction (Leather et al. 2017). This assumption has an important bearing on the value of $r_m$ and not always reflects plant suitability (Leather et al. 2017), which was the case in the present study. The duration of $D$ was similar in all *M. persicae* on all oilseed rape cultivars studied, but the 95% reproduction in the $D$ period was never reached on any oilseed rape cultivar studied. The closest to this value was the reproduction in aphids on ‘Alister’, ‘Florida’ and to a lesser degree on ‘Kolumb’ (77%, 75%, and 68%, respectively), while on other cultivars, the reproduction was more ‘regular’ and occurred essentially in all aphids throughout the whole adult life. Considering these drawbacks, we decided to focus on the reproductive activity of aphids in the assessment of rapeseed cultivars, namely the duration of the reproductive period, net reproduction and the number of nymphs born in the first $D$ days of reproduction.

*M. persicae* had longest lifetime duration and survival on ‘Alister’ but the lowest fecundity and the shortest reproductive period as compared to aphids on the remaining cultivars studied, which means that *M. persicae* is able to develop a population but only to a limited degree. Considering the possible changes in plant characteristic during the experiment, the effect of other than glucosinolate-based, unknown mechanisms, on *M. persicae* development on ‘Alister’ cannot be excluded. As commented earlier, the duration of feeding periods reflects the amount of sap consumed. The similar relatively high performance of *M. persicae* could have been attributed to unaltered rate of consumption of sap on ‘Andromeda’, ‘Glaadius’, ‘Adriana’, ‘Artoga’ and ‘Kolumb’, but not on ‘Florida’. On ‘Florida’, the performance of *M. persicae* was surprisingly poor despite high amounts of the consumed sap, as inhibition of sap consumption did not occur in aphids on ‘Florida’. We are still investigating what mechanisms are behind the low performance of *M. persicae* on ‘Florida’, but it is very likely that the low nutritional value of the phloem sap was responsible for the reduced aphid fecundity on this cultivar. Further studies on phloem sap composition in the rapeseed cultivars will be required to confirm this hypothesis.

The statistical analysis (PCA), performed independently for aphid probing, development and plant chemistry, showed no similarities in the groupings of rapeseed cultivars studied. Therefore, no unequivocal classification of cultivars that would have included all analyzed traits was possible. Nevertheless, taking into account aphid performance, probing behavior and plant secondary chemistry, the winter oilseed rape cultivars studied can be categorized according to *M. persicae* preferences and the assumed backgrounds of these preferences. Group I—least susceptible—‘Alister’ and ‘Florida’. In ‘Alister’, antixenosis mechanisms exist in non-phloem tissues, which prevent *M. persicae* from locating phloem vessels. In ‘Florida’, probably antibiosis mechanisms exist in the phloem or the phloem sap is of low nutritional value, either or both of which may cause a reduction in reproductive activity of *M. persicae*. Group II—intermediately susceptible—‘Adriana’, ‘Andromeda’, ‘Glaadius’, ‘Kolumb’—on which net reproduction of *M. persicae* was higher than on ‘Alister’ and ‘Florida’ and lower than on ‘Artoga’. No clear antixenosis and antibiosis mechanisms were detected in these cultivars although a minor disruption in sap uptake was observed. Group III—highly susceptible—‘Artoga’—longest reproduction, highest daily fecundity and net reproduction. Neither antixenosis nor antibiosis was detected in this cultivar. Glucosinolates found in the leaves of the rapeseed cultivars studied did not affect the peach potato aphid probing and feeding. From the practical point of view, *B. napus* cv. ‘Alister’ appears the most promising in respect of *M. persicae* control. The antixenosis mechanisms against *M. persicae* predicted in this cultivar are worth further studies, especially considering the prevention of plant virus transmission. Aphids acquire and inoculate semi-persistent and non-persistent viruses during brief probes in non-phloem tissues along the styles’ route to the phloem (Martin et al. 1997), while persistent viruses are transmitted during the access to sieve elements (Prado and Tjallingii 1994). The deterrence of aphid probing at the level of epidermis and/ or outer layers of mesophyll may reduce yield losses due to aphid feeding and limit the spread of plant virus diseases.

In conclusion, two mechanisms of defense against *M. persicae* (antixenosis and antibiosis) were identified among the cultivars of *B. napus*. Depending on a cultivar, these mechanisms affected different phases of aphid probing and feeding behaviors and reproduction. Antixenosis in *B. napus* caused the disruption in probing in non-phloem tissues and a failure in reaching sieve elements, while antibiosis impeded the reproductive activity of *M. persicae*. Glucosinolates identified in the leaves of *B. napus* did not affect *M. persicae* performance, sieve element finding and sap ingestion activity. There was no knowledge on the background of susceptibility or resistance of rapeseed cultivars to *M. persicae* infestation in Poland and in Europe, prior to our study. The results of our survey provide the first detailed data that can be used for reference studies in the future.
Author contributions BK performed experiments on aphid development; AW-K, KS, BG contributed to EPG experiments; KJ helped in glucosinolate analysis; JB statistically analyzed the study; and BG wrote the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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