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Increased Susceptibility to Aphids of Flowering Wheat Plants Exposed to Low Temperatures

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ABSTRACT Frost is known to directly affect flowering wheat plants (*Triticum aestivum* L.) and lead to reduced grain yield. Additionally, it may increase wheat susceptibility to economically important pests, such as aphids (Hemiptera: Aphididae). Wheat plants at flowering stage were exposed to one of the three temperature treatments: ambient (11–12°C), 0°C, and –3°C for 60 min. Preference (3-choice) and performance (no-choice) bioassays with aphids (*Rhopalosiphum padi* L.) were conducted 1, 3, 6, and 12 d after temperature treatments to assess effects of temperature-induced stress over time. As an initial feasibility study of using remote sensing technologies to detect frost-induced stress in flowering wheat plants, hyperspectral imaging data were acquired from wheat plants used in preference bioassays. Element analysis of wheat plants was included to determine the effect of temperature-induced stress on the nutritional composition of flowering wheat plants. The results from this study support the following cause–effect scenario: a 60-min exposure to low temperatures caused a significant decrease in potassium and copper content of wheat plants 6 d after temperature exposure, and it coincided with a marked increase in preference by aphids of wheat plants. The preference exhibited by aphids correlated positively with performance of aphids, so the preference–performance hypothesis was confirmed and possibly driven by potassium and copper content of wheat plants. In addition, we demonstrated that hyperspectral imaging data can be used to detect frost-induced susceptibility to aphid infestation in flowering wheat plants. These findings justify further research into airborne remote sensing of frost-induced stress and the possible secondary effects on crop susceptibility to arthropod pests.

KEY WORDS frost, hyperspectral imaging, remote sensing, plant nutrition, IPM

Changes in weather patterns and steady increases in global average surface temperatures are believed to be driven by rising atmospheric CO₂ concentration (Intergovernmental Panel on Climate Change (IPCC) 2013). The future impacts of climate change on dryland cropping systems have been widely studied in different agricultural regions (Thomas 2008, Xiao et al. 2010, Özdoğan 2011, Gohari et al. 2013, Sommer et al. 2013), including Australia (Ludwig and Asseng 2006, Anwar et al. 2007, Luo et al. 2009, Asseng et al. 2011, Barlow et al. 2013). Countries with Mediterranean-type climates, particularly semiarid regions like the grain belt of southwestern Australia, appear to be most vulnerable to climate change and the subsequent

reduction in water resources (Ali et al. 2012, Silberstein et al. 2012). Although the overall frequency of frost events is likely to decrease with rising temperature, drier atmospheric conditions may result in radiative frosts earlier in the growing season (Zheng et al. 2012). This would increase the risk of frost damage in early and medium maturity wheat (*Triticum aestivum* L.) cultivars in southwestern Australia and elsewhere. Frost during early flowering and ear emergence of wheat may lead to partial or complete sterility of florets and whole spikelets and therefore reduced grain number and yield (Marcellos and Single 1984, Al-Issawi et al. 2012, Frederiks et al. 2012). Freezing injury is largely caused by cellular dehydration and, for this reason, freezing stress, drought stress, and salt stress share many physiological and molecular plant responses (Xin and Browse 2000).

Winter cereals are the economically most important crops in Australia, with a production of about 36 million tons in the 2013–2014 growing season (ABARES 2014). In Western Australia, about 5.8 million ha is used for dryland cereal production with wheat being the dominating crop (Seymour et al. 2012). Frost may directly affect flowering wheat plants and lead to reduced grain yield. Additionally, it may increase wheat susceptibility to economically important pests, such as aphids (Hemiptera: Aphididae). In Australia, the adverse effect of

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frost events in spring on flowering wheat is estimated to cause an annual loss of AUS\$ 120 million (Barlow et al. 2013). This problem is most severe in areas like some Mediterranean and subtropical climates, where the heat and drought of summer restrict the main growing season to the late winter and spring and where daytime temperatures are often ideal for growth, but night temperatures can fall to damaging levels (Frederiks et al. 2012). In Mexico, frost damage to cereals at flowering has also been reported to cause substantial losses in some years (Macedo-Cruz et al. 2011).

In addition to direct and adverse effects of frost (and other abiotic stressors), a range of secondary or “down-stream” effects may pose additional risks to cereal cropping systems, such as increased risk of insect pest infestation. Several species of aphids (Hemiptera: Aphididae) are considered major pests on wheat and other cereals, as they cause direct feeding damage and also are vectors of important viruses (Powell et al. 2006). Adverse climatic events (abiotic stress) can alter the plants’ water status (Auclair 1963), chemical and nutritional composition (Moheb et al. 2011, Tariq et al. 2012, Walter et al. 2013), and lead to a decrease in the concentration of defense compounds (Rhoades et al. 1979, Rosenzweig et al. 2001, Fuhrer 2003); some or all of which alter the fitness and abundance of pest populations (Kennedy and Booth 1951; Dixon 1971; Tariq et al. 2012, 2013). Remote sensing technologies have been used widely to detect aphid infestations in wheat and other crops (Yang et al. 2005, 2009; Mirik et al. 2006, 2012; Elliott et al. 2009). Such studies, showing that established aphid infestations can be detected based on changes in crop reflectance, are promising and important as part of developing sensitive, reliable, and cost-effective crop surveillance systems to improve input management in large-scale agriculture. Similar to Nansen et al. (2013a), we argue that it is equally important to develop remote sensing technologies to monitor crop susceptibility, so that “hot spots” with high risk of arthropod infestation can be detected (and necessary responsive actions be implemented) before arthropod-induced crop damage occurs. In other words, it would be preferable to predict crop plant susceptibility based on detectable changes in leaf reflectance, so that crop surveillance can be used in spatio-temporal targeting of insect pest management tactics.

In this study, we experimentally exposed flowering wheat plants to ambient (11–12°C), 0°C, and –3°C for 60 min and conducted preference (3-choice) and performance (no-choice) bioassays with bird cherry-oat aphids (*Rhopalosiphum padi* L.) 1, 3, 6, and 12 d after the imposed temperature treatments. Bird cherry-oat aphids are considered one of the most agriculturally important pests worldwide (Blackman and Eastop 2007) and therefore a good candidate for a study on host susceptibility in response to an abiotic stressor. As an initial feasibility study of using remote sensing technologies to detect frost-induced stress in flowering wheat plants, hyperspectral imaging data were acquired from wheat plants used in preference bioassays. Element analysis of wheat plants was included to determine the effect of frost-induced stress on the

nutritional composition of flowering wheat plants. The results from this study are used to discuss: 1) the possible down-stream (secondary) effects of low temperatures on pest susceptibility of winter cropping systems; 2) the validity of the “preference–performance hypothesis” (Jaenike 1978), which suggests that, in a choice scenario, insects should prefer the host which gives themselves and their offspring the highest fitness; and 3) the importance of remote sensing as part of monitoring and early detection of crop susceptibility to economically important pests.

Materials and Methods

Plant Material and Growth Conditions. A long maturity, high yielding noodle wheat (*Triticum aestivum* L. ‘Fortune’), which is grown in Western Australia (Shackley et al. 2013), was used in this study. Wheat plants were grown at The University of Western Australia Crawley campus (31° 59′03.80″ S; 115° 49′08.57″ E) in a deep sandy soil. The area was outdoors in a netted enclosure exposed to natural sunlight conditions (day: 17.6°C ± 2.75 [SE] temperature and 71.6% ± 14.4 relative humidity [RH], night: 15.3°C ± 2.1 temperature and 79.4% ± 9.8 RH, and midday photon flux density 899.3 ± 433.4 $\mu\text{mol m}^{-2}\text{s}^{-1}$). Plants were fertilized with Osmoform NXT slow release fertilizer (Everris Australia Pty Ltd, Bella Vista NSW 2153, Australia) (N 22, P 2.2, K 9.1, Mg 1.2 plus trace elements) as required and irrigated. Once the plants reached stem elongation (approximately Z45–49 [Zadoks et al. 1974]), 96 plants were transplanted to individual 3-liter pots containing pasteurized potting mix (heated at 63°C for 30 min) and transferred to a glasshouse with evaporative cooling. The pots were irrigated every 2 d. Two mobile commercial convective freezers of 10.3 m³ (2.4 m in length by 1.8 m in width by 2.4 m in height) were carefully calibrated to 0°C and –3°C. When the wheat plants had reached the flowering stage (between Z60–65 [Zadoks et al. 1974]), on 25 October 2013, one-third of the plants were placed into each freezer for 60 min, between 4:30 to 5:30 a.m., and the remaining one-third of wheat plants were kept under ambient conditions between 11.8 and 12.3°C. This time of the morning was chosen, as it is when frost is most likely to occur under field conditions. Data loggers were placed inside freezers to confirm that the correct temperatures were maintained during each treatment. After temperature treatments, all wheat plants were transferred to the glasshouse for aphid performance and preference bioassays. Based on aphid responses in preference and performance bioassays, we collected and oven dried (at 60°C) leaf material from wheat plants 5 d after the temperature treatments, and this plant material was submitted to a commercial laboratory for element analysis (CSBP Soil and Plant Analysis Laboratory, WA, Australia). The following 14 wheat plant elements were quantified in five replicated samples from each temperature treatment: nitrogen (LECO dry combustion), potassium, phosphorus, sulfur, copper, zinc, manganese, calcium, magnesium, sodium, iron, boron (ICP atomic

emission spectrometry), and nitrate (520 nm) and chloride (480 nm; Lachat flow injection analyser).

Aphid Bioassays. The experimental design for performance and preference bioassays comprised three temperature treatments, including a control (wheat plants maintained at ambient glasshouse temperature) and wheat plants exposed to 0°C or -3°C for 60 min, and four time points of aphid infestation after the imposed temperature treatments (1, 3, 6, and 12 d). All treatment combinations were replicated four times. Adult wingless bird cherry-oat aphids were obtained from an established colony reared on wheat plants at Shenton Park Field Station. "Performance" bioassays were conducted separately on individual plants, giving the aphids no choice of host, to determine the effect of temperature treatment on population growth of aphids. In addition, we conducted "preference" bioassays, with aphids given a choice of three plants, with one from each temperature treatment. Thus, the combination of these bioassays enabled us to potentially validate the "preference-performance hypothesis" (Jaenike 1978).

In performance bioassays, five adult wingless aphids were placed inside a cone-shaped paper cup (made from half a piece of 9-cm-diameter filter paper), which was attached with a paper clip to the center of the wheat flag leaf on individually caged wheat plants. Total numbers of aphids per plant (nymphs and adults combined) were counted 6–8 (count 1) and 12–15 (count 2) d after each time point of infestation. In preference bioassays, the tip of each of the three flag leaves was secured with a paper clip so that all tips were inside the cone-shaped paper cup. Subsequently, 15 adult wingless aphids were introduced into the cup. Total numbers of aphids on each of the three wheat plants were counted 3 d after each time point of infestation. All bioassays were conducted inside custom-made meshed cages. Immediately before each preference bioassay, we assessed the following plant characteristics: 1) plant height from the soil to the base of the ear (cm), 2) width of widest leaf (mm), 3) total number of tillers per wheat plant, and 4) number of tillers in ear were recorded. The same plant characteristics were also assessed before and after aphid infestations in performance bioassays.

Hyperspectral Imaging. Prior to performance bioassays with aphids, we acquired hyperspectral imaging data from the flag leaves of 15 wheat plants, which had the temperature treatments but were not used for bioassays. Using this approach enables us to examine the direct effect of temperature regimes on wheat leaf reflectance. The main specifications of the hyperspectral camera were—interface, Firewire (IEEE 1394b); output, digital (12 bit); 240 spectral bands from 392–889 nm (spectral resolution = 2.1 nm) (spectral) by 640 pixels (spatial); angular field of view of 7 degrees. The objective lens had a 35 mm focal length (maximum aperture of F1.4), optimized for the near-infrared and visible near-infrared spectra. Hyperspectral images were collected with artificial lighting from 15 W, two 12 V LED light bulbs mounted on either side of the lens in a room with 19–22°C temperature and 30–40% RH. Reflectance data were acquired with the spatial resolution of 5

by 5 pixels per mm². A piece of white Teflon (K-Mac Plastics, MI) was used for white calibration, and "relative reflectance" refers to proportional reflectance compared with reflectance obtained from Teflon (white = 1) and complete darkness (dark = 0). In order to ensure consistent data acquisition over time, reflectance data were acquired from a green plastic card and average reflectance profiles from each day of hyperspectral imaging data acquisition were compared. These average reflectance profiles showed that hyperspectral imaging conditions varied <3% across days. Thus, we were confident that significant changes in reflectance profiles were almost exclusively due to plant ontogeny and effects of imposed temperature treatments. Each hyperspectral image consisted of 64,000 pixels, and these were spatially averaged (binned) in a 10 by 10 grid to 640 pixels, as this has been showed to increase classification accuracy (Nansen et al. 2013b). In addition, we conducted 2 by 2 spectral binning (increased the spectral resolution from 2.1 to 4.2 nm) and omitted the first and last 10 spectral bands (these spectral bands are typically associated with proportionally higher levels of stochasticity or noise), which resulted in 111 spectral bands from 411–871 nm being included in the analysis. The spectral and spatial binning was conducted to increase classification accuracy (Nansen et al. 2013b, Zhang et al. 2015) and to reduce the risk of model overfitting (Kemsley 1996, Defernez and Kemsley 1997, Faber and Rajko 2007).

Statistical Analysis. All data processing and analysis were conducted in PC-SAS 9.3 (SAS Institute, NC). Regarding wheat plants used in preference bioassays, we used analysis of variance (proc anova option = tukey) to compare average plant characteristics (plant height [cm], width of widest leaf [mm], total number of tillers per plant, and number of tillers in ear) in response to: 1) temperature treatments, and 2) days after temperature treatment. The purpose of this analysis was to determine the level of physical differences in wheat plants over time and across temperature treatments. In the preference bioassays, total aphid counts (nymphs and adults combined) per plant were ranked, and the effect of temperature treatment was tested using a non-parametric Wilcoxon signed-rank test (proc nparway option = wilcoxon). Regarding analysis of aphid data from performance bioassays, separate pairwise comparisons (proc anova option = tukey) were conducted for counts 6–8 (count 1) and 12–15 (count 2) days after infestation. Aphid counts from both the preference and performance bioassays (both counts 1 and 2) were log₁₀₊₁ transformed and a linear regression (proc reg) analysis was used to examine the relationship between results from the two bioassays. Analysis of variance (proc anova option = tukey) was also used to compare average composition of the 14 elements in wheat plants collected 6 d after exposure to temperature treatments.

A linear discriminant analysis (Fisher 1936) was used to examine reflectance profiles from plants exposed to -3°C and acquired 6 d after temperature treatments and those from all remaining wheat plants. The logic behind this classification approach was that the bio-response (results from preference and performance

bioassays) and element analysis of wheat plants from wheat plants exposed to -3°C and acquired 6 d after temperature treatments appeared to have the highest level aphid susceptibility. Thus, we intended to determine whether reflectance profiles could be used to accurately distinguish average reflectance profiles from these plants from all other plants used in preference studies. Initially, average reflectance profiles acquired 6 d after temperature treatments ($n=45$) were used to develop a classification model based on a dichotomous dummy variable with 1 = exposure to -3°C 6 d after temperature treatments (high susceptibility, $n=15$) and 0 = all other wheat plants (low susceptibility, $n=30$). As part of developing the classification model, forward stepwise discriminant analysis (proc stepwise) was used to select the spectral bands with significant contribution to the classification. As part of validating the linear discriminant classification model, we used the remaining 135 average reflectance profiles as independent validation data. Successful validation would imply that these 135 reflectance profiles would be classified as indicative of low susceptibility to aphids.

Results

Direct Influence of Temperature Treatments on Wheat Plants. Direct effect of temperature treatments on wheat was assessed by comparing the various canopy characteristics of wheat plants (number of tillers per plant, number of tillers in ear, wheat plant height, and width of widest leaf), before they were subjected to preference bioassays (Table 1). We found no significant effect of temperature treatment on any of the plant characteristics for any of the four time points ($P>0.050$). As expected, all plant characteristics increased significantly over time (total number of tillers per plant [$P<0.001$], number of tillers in ear [$P<0.001$], wheat plant height [$P=0.005$], and width of widest leaf [$P=0.047$]). Pairwise comparisons of time points of infestation revealed that the significant effect of time was mainly caused by an increase in the plant canopy characteristics between 1 and 3 d after temperature treatments (Table 1). The nonsignificant temperature treatment effect is important because it highlights that the abiotic stress level was quite subtle and nondetectable based on visual inspection of wheat plants.

Preference Bioassay. Numbers of aphids per bioassay ranged from 18 to 231 aphids, which indicated

that nymphs were produced in all preference bioassays (as 15 adult aphids had been introduced into each cage with three wheat plants). There were no significant differences in total aphids per bioassay across time points ($\text{df}=3,15$, $F\text{-value}=1.72$, $P=0.215$), but there was a gradual increase over time (Fig. 1A). As indicated by standard error bars, there was considerable variability among replicates, but low temperature regimes (0°C and -3°C) were generally preferred, especially 6–12 d after temperature treatments. Ranking of aphid counts within each time point of infestation showed that there was a highly significant difference between temperature treatments ($P=0.001$), with the control plants having significantly lower numbers of aphids than the other two temperature treatments (Fig. 1B).

Performance Bioassay. Overall, there was a 468% increase in the number of aphids from 6,296 to 29,492 on the wheat plants over about a week from count 1 (Fig. 2A) to count 2 (Fig. 2B) in the performance bioassays. The average number of aphids per bioassay was very low on day 1 after temperature treatments across all temperature treatments. In fact, the number of aphids per plant at both counts was generally lower than the initial five aphids used to infest each wheat plant. This result suggested that all wheat plants infested 1 d after temperature treatments, irrespective of temperature treatment, were unsuitable as hosts for aphids. Other cohorts of wheat plants were infested 2 and 5 d later, and aphids developed successfully on these wheat plants, especially those exposed to -3°C (Fig. 2A). For both counts 1 and 2, the highest average numbers of aphids were observed when infestation occurred 6 d after temperature treatments.

As a possible explanation of the marked change in suitability of wheat plants 6 d after temperature treatments, we conducted analysis of variance of each of the 14 plant elements, and we found that there were significant reductions in plant concentrations of potassium (Fig. 3) in wheat plants exposed to -3°C . None of the other 12 elements varied significantly across temperature treatments ($P>0.050$). As part of assessing the preference–performance hypothesis (Jaenike 1978), we analyzed the correlation of data presented in Figure 2A and B. The average number of aphids in the preference bioassays at each of the four time points after temperature treatment was found to be positively correlated with the average number of aphids at the first count in the performance bioassays (adjusted $R^2=0.447$, $P=0.011$; Fig. 4).

Table 1. Average (SE, $n=4$) wheat plant canopy characteristics across temperature treatments and over time

DAI	Total number of tillers			Number of tillers in ear			Plant height (cm)			Leaf width (mm)		
	Control	0°C	-3°C	Control	0°C	-3°C	Control	0°C	-3°C	Control	0°C	-3°C
1	3.0(0.4)	3.3(0.5)	3.5(0.3)	2.3(0.3)	2.3(0.5)	2.5(0.3)	40.5(2.9)	48.8(1.6)	40.9(2.7)	16.8(0.5)	15.5(0.6)	16.3(0.8)
3	4.5(0.9)	5.0(0.6)	3.8(0.5)	3.5(0.9)	4.0(0.6)	2.8(0.5)	47.8(1.7)	50.5(1.4)	47.8(1.3)	14.3(1.3)	15.8(0.3)	15.8(1.3)
6	4.0(0.7)	5.5(1.2)	4.0(0.4)	3.0(0.7)	5.0(0.7)	3.0(0.4)	47.5(2.3)	47.3(0.8)	45.5(0.5)	17.5(1.0)	16.8(0.9)	17.5(1.2)
12	5.8(0.5)	6.5(0.3)	5.8(0.5)	4.8(0.5)	5.5(0.3)	4.5(0.6)	47.0(1.1)	47.5(0.6)	46.8(0.7)	17.8(1.1)	17(0.4)	15.8(0.6)

“DAI” denotes days after wheat plants were subjected to temperature treatments.

Fig. 1. Average (SE) numbers of aphids (nymphs and adults combined) on individual wheat plants in preference (3-choice) bioassays (A) over time from 1, 3, 6, and 12 d after temperature treatments and (B) across temperature treatments. Different letters denote significant differences between times of infestation at $P \leq 0.05$.

Fig. 2. Average (SE) numbers of aphids (nymphs and adults combined) on individual wheat plants in performance bioassays, where aphids were introduced at different time points 1, 3, 6, and 12 d after temperature treatment, with counts (A) 6–8 d (count 1) and (B) 12–15 d (count 2) after each time point. Different letters denote significant differences between times of infestation at $P \leq 0.05$.

Fig. 3. Average wheat plant content of copper and potassium across temperature treatments. Different letters denote significant differences between times of infestation at $P \leq 0.05$.

Reflectance Profiling of Temperature Treatments. Based on preference and performance responses by aphids in bioassays conducted 6 d after temperature treatments, we focused the study of reflectance profiles on this subset of the data. Average reflectance profiles from wheat plants subjected to the low temperature treatments were divided with those from control wheat plants, and it is seen that exposure to low temperatures caused a decrease in relative leaf reflectance, especially in regions near 500 and 670 nm (Fig. 5). Wheat plants exposed to -3°C showed the strongest preference and performance responses, and they also had significantly lower levels of copper and potassium. Thus, we created a dichotomous dummy variable to separate wheat plants exposed to -3°C (var = 1) from those subjected to the other two temperature treatments (var = 0), and a forward linear discriminant analysis was used to select three spectral bands with the highest classification contribution

Fig. 4. Correlation between average aphid preference and performance across temperature regimes.

Fig. 5. Average flag leaf reflectance profiles from wheat plants subjected to 0°C or -3°C relative to reflectance profiles acquired from control wheat plants 6 d after temperature treatments. Black circles denote the wavelengths of three spectral bands included in the linear discriminant analysis classification of wheat plant susceptibility to aphids.

(dots in Fig. 5). Subsequently, the reflectance-based classification model based on these three spectral bands was deployed to the remaining 135 average reflectance profiles. In other words, average reflectance profiles acquired on days 1, 3, and 9 after temperature treatments were used as independent validation data, and successful validation would imply that these data would be classified as less attractive and suitable to aphids. Out of the 135 independent validation reflectance profiles, 128 (94.81%) were correctly classified as indicative of wheat plants with low susceptibility to aphids.

Discussion

We hypothesized that exposure of flowering wheat plants to low temperatures would change the nutritional composition of host plants and increase their attractiveness (increased preference) and suitability (increased performance) as hosts for aphids. Hyperspectral imaging data were acquired from wheat plants

before exposure to aphids as part of predicting wheat plant susceptibility to aphid infestation based on leaf reflectance. That is, if exposure to low temperatures alters the nutritional composition of flowering wheat plants (and therefore make the wheat plants more suitable as host plants for aphids), then it seems reasonable to assume that exposure to low temperatures also causes significant changes in reflectance profiles from leaves of flowering wheat plants. And if the low temperature-induced change in suitability of flowering wheat plants to aphids is time-delayed (if it takes several days before wheat plants become more susceptible), then it may be possible to develop remote sensing-based crop surveillance and detect “hot spots” with high risk of aphid infestation.

We demonstrated that wheat plants exposed to low temperatures (-3°C and 0°C) are more susceptible to aphids as both attractiveness (preference bioassay) and suitability (performance bioassay) of wheat plants increased. The strongest effect of low temperatures on wheat plant susceptibility to aphids was observed 6 d after the temperature treatment. These results imply that, in the days after flowering wheat exposure to a frost event, farmers could increase crop monitoring and possibly improve detection of developing aphid populations. Also, there was a positive linear correlation between preference and performance for aphids on frosted wheat, which supported the preference–performance hypothesis (Jaenike 1978). The current study was conducted with experimental conditions which may not simulate those in the field. For example, La Spina et al. (2013) found increased preference, but not performance, of insects on frosted beech trees by experimentally inflicting the frost damage. They concluded that the reduced performance was because the experimental conditions differed from that in natural conditions where the performance of the insects is greater. Also, Frederiks et al. (2012) asserted that convective freezing chambers fail to consistently reproduce plant damage or screening results for frost tolerance as observed in the field under natural radiant frost conditions. It is therefore important to test the findings of the current study under field conditions.

There is widespread evidence of aphid preference being influenced by the nutritional quality of the host plant (Kennedy and Booth 1951, Dixon 1971, Powell et al. 2006, Nowak and Komor 2010). We showed that aphids preferred wheat plants, which had been exposed to low temperatures for 60 min, and this correlated with significant reductions in levels of copper and potassium. It is possible that these changes in nutrient concentration were coincidental to the aphid preference, as there are other factors, including soluble carbohydrates and amino acids, which have also been linked to aphid performance (Hu et al. 2014). Although the direct link between these elements and aphid preference and performance were not established in this work, numerous studies have demonstrated the importance of potassium regarding pest infestations of crops (West and Nansen 2014). Based on choice experiments with excised leaf pieces (bio-response) and element analyses, Nansen et al. (2013a) conducted multivariate

analysis and showed that, among the main nutritional elements, leaf potassium content showed the strongest negative correlation with spider mite (Acari: Tetranychidae) bio-response. This result is corroborated by a review of >2,000 studies regarding effects of potassium on pest and disease incidence in plants, in which **Perre-noud (1990)** found that in 63% of these studies, application of potassium led to a decrease in pest pressure. The role of potassium in host plant resistance was described in detail by **Amtmann et al. (2008)**. There are also several studies demonstrating that host plant susceptibility to aphid infestations is negatively associated with plant concentration of potassium (**Brennan and Grimm 1992**, **Myers and Gratton 2006**). This study showed that the reflectance of the leaves could be used to characterize wheat plant susceptibility to aphids. Relative reflectance values in three spectral bands were identified as providing strong indication of wheat plant susceptibility to aphids, and they were located at 481, 556, and 810 nm (**Fig. 5**). Interestingly, these spectral bands have been selected in reflectance-based studies of plant responses to growing conditions and stressors. For instance, **Zhu et al. (2008)** analysed the correlation between reflectance in spectral bands between 447 and 1,752 nm and leaf N accumulation in rice and wheat, and leaf N accumulation was strongly correlated with reflectance at 660, 810, and 870 nm. In addition, the spectral region from 481 to 523 nm was identified as providing strong correlation between leaf reflectance and leaf nitrogen isotope content (**Wang et al. 2009**). Finally, reflectance at 556 nm was identified as one of 15 spectral bands for accurate prediction of nitrogen content in rice leaves (**Yang 2001**). Total nitrogen did not respond significantly to temperature treatments, but there are various and complex interactions between element uptake and content in plants (**Maathuis and Diatloff 2013**), so this is not entirely unexpected. Thus, our experimental data provide important support for further research into use of remote sensing technologies as part of monitoring of both frost-induced stress and relative susceptibility of flowering wheat plants to aphids as well as other insects and diseases.

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