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MECHANICALLY-INJURED WHEAT PLANTS RELEASE GREATER AMOUNTS OF THE SECONDARY METABOLITES LINALOOL AND LINALOOL OXIDE

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Abstract: Plants under attack of herbivores can emit increased amounts of volatile compounds from their leaves. Similarly, mechanically-injured plants can emit volatile chemicals that differ both quantitatively and qualitatively from undamaged plants. In this experiment, mechanical injury increased the release of the secondary metabolites linalool (3,7-dimethyl-1,6-octadien-3-ol) and linalool oxide (5-ethenyltetrahydro-2-furanmethanol) by wheat plants. The amounts released varied significantly with injury type and the period of time after injury. The time interval for the volatile collection within the photophase also influenced the amount collected for each day. The increased emission of these compounds, as a result of injury, may be explained as a defense mechanism against wounding. The role of these plant volatiles can be further investigated in the context of plant response to mechanical injury, within the broader context of all types of injury.

Key words: wheat, *Triticum aestivum*, volatiles, semiochemicals, odours

INTRODUCTION

Plants are not merely passive victims of attacking herbivores; they have evolved an arsenal of physical and chemical defenses to protect themselves (Rasmann et al. 2005). All plant species are vulnerable to injury by a number of organisms during their life and are also subjected to mechanical damages. In response to these injuries, they have evolved defense mechanisms to fend off parasitic organisms (De Moraes et al. 2001; Cardoza et al. 2002, 2003) or herbivores (Karban and Baldwin 1997; Agrawal et al. 1999). Inducible defenses based on production and release of volatile secondary metabolites that attract natural enemies of the

herbivores were studied. Manipulating these signals may help increase the effectiveness of these natural enemies as control agents (Dicke and Sabelis 1988; Turlings et al. 1990; De Moraes et al. 1998; Thaler 1999; Kessler and Baldwin 2001; Reddy and Guerrero 2004). Other volatile compounds could also have an inhibitory or repellent effect on pest herbivores (De Moraes et al. 2001; Cardoza et al. 2003). Volatile emissions from injured plants have been the subject of research for many years.

The knowledge of the blend of volatiles that wheat produces may be useful in understanding the attraction of insect pests to wheat and other cereal crops (Buttery et al. 1985). Volatile compounds produced by wheat, *Triticum aestivum* L., were collected and identified using several techniques (Hamilton-Kemp and Anderson 1984, 1986, Buttery et al. 1985; Hatanaka 1993; Batten et al. 1995). The volatile compounds from wheat are similar to the major contributors to a characteristic odour of green leaves for other cereals (Buttery et al. 1985). The principal volatile compounds found in wheat and oat seedlings were characterized for attractiveness to insect herbivores (Quiroz and Niemeyer 1998a), but wheat infested by insects also produced differing volatile signals as a result of infestation (Quiroz and Niemeyer 1998b). Similarly, laboratory studies showed that *Sitobion avenae* F., when feeding together with *Rhopalosiphum padi* L., probed tissue less, had a longer ingestion time, and had increased fecundity on wheat seedlings, relative to pure colonies as a function of the specific odours involved (Johansson et al. 1997). These studies show that induced compounds can play an important role in modulating the level of damage associated with injury.

The purpose of the current research was to collect basal information on the effect of several types of mechanical injuries used to simulate various forms of insect herbivory. The amount of linalool and linalool oxide produced by each type of wounded and the control wheat plants were quantified. The effect of post-injury duration on the amount of linalool and linalool oxide was also quantified for each type of wound.

MATERIALS AND METHODS

Plant Culture. Experiments were performed at the Plant Growth Center, Montana State University in 2002 and 2003. McNeal spring wheat seeds were sown daily and plants were grown in a greenhouse with supplemental light and ambient humidity. The photoperiod was 16L: 8D. Daytime temperature was 22±2°C and overnight temperature was 18±2°C. Plants were grown two per pot in equal parts of MSU PGC soil mix (equal parts of sterilized Bozeman Silt Loam soil: washed concrete sand and Canadian sphagnum peat moss) and Sunshine Mix 1 (Canadian sphagnum peat moss, perlite, vermiculite, and Dolmitic lime). The plants were watered four times weekly, and fertilized with Peters® General Purpose Fertilizer at 100 ppm in aqueous solution twice each week as part of the regular watering schedule. Fertilizing commenced when the plants reached the third leaf stage.

Wounding. Plants were wounded immediately before each replication of the experiment. The main stem from each plant was subjected to volatile collection, while the tillers were outside volatile collection chamber. All plants used were at the Zadoks 32 stage, with the emergence of an elongating stem section separating

the first two nodes. At this stage, there are three large leaves projecting upwards from the area of the elongating stem in addition to numerous more mature leaves lower on the plant and on the tillers. Five types of injuries were performed on the plants. These were:

1. Pierced Stem – the main stem was punctured by a small-bore needle (diameter 0.34 mm) to simulate the mechanical damage done by an ovipositor or piercing mouthparts. Five holes were made in each stem.
2. Scraped Stem – the main stem interior was abraded by a single rasp with a large bore needle (diameter 1.64 mm, 3.3 cm in length). This was used to simulate mechanical larval feeding damage inside the stem by a stem-boring species.
3. Top Half Leaf Cut – the distal half of the uppermost leaf on the main stem was cut off with scissors. The cut was made perpendicular to the main vein running along the midline of the leaf's length, leaving a short length of wounded tissue. This simulated defoliation of leaf tissue by an insect with chewing mouthparts.
4. Top Quarter Leaf Cut – one quarter of the distal portion of the uppermost leaf on the main stem was cut with scissors to simulate defoliation. The perpendicular cut was made only to the midline vein of the leaf and then continued alongside the vein to the tip of the leaf. This removed half of the leaf tissue that the "Top Half Leaf Cut" treatment did, while increasing the relative length of the wound on the apical portion of the leaf. This simulated less defoliation by an insect with chewing mouthparts.
5. Bottom Quarter Leaf Cut – one quarter of the proximal portion of the uppermost leaf on the main stem was cut with scissors to simulate defoliation. The perpendicular cut was made only to the midline vein of the leaf and then continued alongside the vein to the basal portion of the leaf, where it joined the main stem. Once again, this removed approximately half of the leaf tissue that the "Top Half Cut" treatment did, while increasing the relative length of the wound on the proximal portion of the stem. This also simulated less defoliation by an insect with chewing mouthparts on a different area of the leaf than for "Top Quarter Leaf Cut".

Volatile Collection System. The custom built apparatus (Analytical Research Systems, Inc. Gainesville, Florida, USA) used to collect volatiles featured a set of six glass volatile collection chambers that are open at one end to enclose the growing plant. A flexible Teflon® sleeve was tape-sealed around the base of the main stem to prevent the collection of excess soil volatiles. The chambers were 40-mm-diameter X 800-mm-long. Volatiles were collected simultaneously from all six chambers. Each volatile collection chamber was fitted with a manifold that had 8 ports. Each port was fitted with threaded air inlet caps and threaded volatile collector ports, both fitted with No. 7 ChemThread inlets (inner diameter 6.35-mm) and sealed using rubber O-rings. A volatile collector trap (6.35-mm-OD, 76-mm-long glass tube; Analytical Research Systems, Inc., Gainesville, Florida, USA) containing 30 mg of Super-Q (Alltech Associates, Inc., Deerfield, Illinois, USA) adsorbent was inserted into each port, and was sealed by the O-ring/ChemThread assembly. Purified, humidified air was delivered at a rate of 1.0 l/min over the plants, and the flow and pressure were maintained by a vac-

uum pump. The volatile collection system was computerized and had software inputs, which allowed two event controllers to switch solenoid switches off and on. These switches allowed the airflow of entrained volatiles to be switched from one port to another. This capability allowed for the programming of six sequential two-hour collections from each plant during photophase. Volatiles were collected from the main stem and the three large, uppermost leaves of each plant only. The volatile collection sequence (six, consecutive two hour collections) was initiated immediately after injury, again at two days after injury, and again at four days after injury. There were seven temporal replicates of each plant and wounding type. For each collection interval, eleven plants were collected: seven random treatment replicates and four controls. Specific treatment replicates for collection were assigned randomly each day and experiments were staged daily until the completion of the experiment. Additionally, one control chamber was collected each day. This control consisted of the airspace above of a pot containing soil only.

Analytical Methods. Volatiles were eluted from the Super-Q in each volatile collection trap with 225 µl of hexane. After this 7 ng of decane was added as an internal standard. Volatiles were analyzed by coupled gas chromatography-mass spectrometry (GC-MS). The GC was an Agilent Technologies 6890 instrument fitted with a 30-m DB-1MS capillary column (0.25-mm-ID, 0.25 µm film thickness; J & W Scientific, Folsom, California). The temperature program increased chromatography oven temperature from 50°C to 280°C at 10°C/min The MS instrument was an Agilent Technologies 5973. The identification of volatiles was verified with authentic standards purchased from commercial sources that had the same GC retention times and mass spectra.

Statistical Methods. The amounts of linalool and linalool oxide for each plant at each collection interval were subjected to the analysis of variance. The independent variables included injury type (INJURY), days after injury (0, 2 or 4 DAYS), and collection interval in each day (each consecutive two hour interval – HOURS). The interactions were included in the model. Mean amounts were separated after analysis of variance using Tukey's test for significant differences at $\alpha = 0.05$.

RESULTS

Overall, greater amounts of linalool (Table 1) and linalool oxide (Table 2) were released following mechanical injury relative to the control. A significant amount of variation was explained by injury type for both linalool ($F = 20.5$, $DF = 5$) and linalool oxide ($F = 9.6$, $DF = 5$). There were significant interactions between injury types and days for both compounds, and for linalool there was also significant interaction between injury types and hours, as well as a significant three-way interaction (Table 3). Within injury types, only the two "Quarter Cut Leaf" treatments had significantly greater amounts of linalool than the control (Table 1), although all injury types had greater amounts of this compound relative to the control.

In contrast, the "Pierced Stem" and both "Quarter Cut Leaf" injury types caused the release of significantly greater amounts of linalool oxide, while all injury types released numerically greater amounts (Table 2).

Table 1. The amount of linalool collected from mechanically-injured and control wheat plants

DAYS	HOURS collection interval	Control [ng]	INJURY				
			Pierced Stem [ng]	Scraped stem [ng]	Top half leaf cut [ng]	Top quarter leaf cut [ng]	Bottom quarter leaf cut [ng]
0	0–2	0.70	2.90	4.44	0.88	4.16	4.34
	2–4	1.44	2.59	3.41	1.78	5.44	8.41
	4–6	1.63	3.09	3.27	2.28	6.28	9.01
	6–8	1.22	2.84	4.82	1.31	2.96	5.20
	8–10	0.32	0.75	0.69	0.24	1.35	0.66
	10–12	0.16	0.27	0.24	0.00	0.32	0.16
Mean		0.91	2.07	2.81	1.08	3.42	4.63
2	0–2	0.66	1.39	1.19	1.21	11.68	2.46
	2–4	1.91	1.61	1.58	1.12	15.70	3.12
	4–6	0.84	1.86	1.59	1.37	30.06	3.55
	6–8	1.84	1.23	1.18	0.68	20.97	2.78
	8–10	0.06	0.64	0.63	0.57	2.03	0.90
	10–12	0.00	0.12	0.09	0.53	0.25	0.27
Mean		0.89	1.14	1.04	0.92	13.45	2.18
4	0–2	0.19	4.28	1.14	0.64	1.43	1.25
	2–4	0.27	3.00	0.91	0.77	2.78	1.67
	4–6	0.21	4.09	0.99	0.74	3.16	1.41
	6–8	0.13	4.44	0.95	0.55	2.48	2.17
	8–10	0.07	1.76	0.68	0.24	0.98	0.95
	10–12	0.00	0.17	0.07	0.00	0.14	0.16
Mean		0.14	3.12	0.79	0.49	1.83	1.27
Mean for DAYS	0–2	0.52	2.86	2.26	0.91	5.76	2.68
	2–4	1.20	2.73	1.97	1.23	7.97	4.40
	4–6	0.89	3.01	1.95	1.46	13.17	4.66
	6–8	1.07	2.84	2.32	0.85	8.80	3.39
	8–10	0.15	1.05	0.67	0.35	1.45	0.84
	10–12	0.05	0.19	0.14	0.18	0.24	0.20
Mean for INJURY		**0.65**	**2.11**	**1.55**	**0.83**	**6.23**	**2.69**
Mean for HOURS	0–2	**2.49**					
	2–4	**3.25**					
	4–6	**1.19**					
	6–8	**3.21**					
	8–10	**0.75**					
	10–12	**0.17**					

HSD Tukey $\alpha = 0.05$ for INJURY (I) = 1.83
HSD Tukey $\alpha = 0.05$ for DAYS (II) = 1.06
HSD Tukey $\alpha = 0.05$ for HOURS (III) = 1.83
HSD Tukey $\alpha = 0.05$ I/II = 3.17
HSD Tukey $\alpha = 0.05$ II/I = 2.61
HSD Tukey $\alpha = 0.05$ I/III = 4.48
HSD Tukey $\alpha = 0.05$ III/I = 4.48

Table 2. The amount of linalool oxide collected from mechanically-injured and control wheat plants

DAYS	HOURS collection interval	Control [ng]	INJURY				
			Pierced Stem [ng]	Scraped stem [ng]	Top half leaf cut [ng]	Top quarter leaf cut [ng]	Bottom quarter leaf cut [ng]
0	0–2	0.18	0.19	0.78	0.00	0.44	0.53
	2–4	0.14	0.31	0.55	0.00	0.36	0.76
	4–6	0.31	0.19	0.80	0.22	0.46	2.27
	6–8	0.09	0.18	1.00	0.00	0.21	0.84
	8–10	0.01	0.04	0.15	0.00	0.00	0.00
	10–12	0.02	0.00	0.00	0.00	0.07	0.00
Mean		0.13	0.15	0.55	0.04	0.26	0.73
2	0–2	0.00	0.13	0.50	0.28	1.48	0.62
	2–4	0.10	0.53	0.20	0.21	3.26	1.01
	4–6	0.16	0.68	0.51	0.00	3.63	1.12
	6–8	0.00	0.42	0.32	0.12	3.25	4.67
	8–10	0.00	0.00	0.00	0.12	0.79	0.37
	10–12	0.00	0.00	0.00	0.00	0.00	0.00
Mean		0.04	0.29	0.26	0.12	2.07	1.30
4	0–2	0.23	1.19	0.00	0.54	0.54	0.71
	2–4	0.00	1.67	0.00	0.21	1.65	0.51
	4–6	0.25	2.16	0.19	0.58	0.84	1.04
	6–8	0.21	2.12	0.00	0.08	0.73	1.17
	8–10	0.14	1.01	0.00	0.30	0.75	0.78
	10–12	0.00	0.29	0.00	0.00	0.00	0.00
Mean		0.14	1.41	0.03	0.28	0.75	0.70
Mean for DAYS	0–2	0.14	0.50	0.43	0.27	0.82	0.62
	2–4	0.08	0.83	0.25	0.14	1.76	0.76
	4–6	0.24	1.01	0.50	0.27	1.64	1.48
	6–8	0.10	0.91	0.44	0.07	1.40	2.23
	8–10	0.05	0.35	0.05	0.14	0.51	0.38
	10–12	0.01	0.10	0.00	0.00	0.02	0.00
Mean for INJURY		**0.10**	**0.62**	**0.28**	**0.15**	**1.03**	**0.91**
Mean for HOURS	0–2	**0.46**					
	2–4	**0.64**					
	4–6	**0.86**					
	6–8	**0.86**					
	8–10	**0.25**					
	10–12	**0.02**					

HSD Tukey $\alpha = 0.05$ for INJURY (I) = 0.52
HSD Tukey $\alpha = 0.05$ for DAYS (II) = 0.30
HSD Tukey $\alpha = 0.05$ for HOURS (III) = 0.52
HSD Tukey $\alpha = 0.05$ I/II = 0.89
HSD Tukey $\alpha = 0.05$ II/I = 0.73

The variation in the amounts of linalool (F = 9.8, DF = 2) and linalool oxide (F = 4.3, DF = 2) were also significantly explained by the post-injury interval (0, 2 or 4 days). The overall amount of linalool produced across all injury types was significantly greater immediately after injury (day 0) and at two days after injury than for four days after injury (Table 1). In contrast, the amount of linalool oxide was significantly lower only immediately after injury (day 0) when compared to two days after injury (Table 2).

A significant portion of the variation in the amount of linalool (F = 11.9, DF = 5) and linalool oxide (F = 6.9, DF = 5) was explained by the collection interval. The last collections each day (8–10 hours and 10–12 hours) obtained significantly less linalool than the greatest intermediate collection intervals (2–4 hours and 6–8 hours) (Table 1). A similar trend was seen for linalool oxide with significantly less collected later (8–10 hours and 10–12 hours) compared to the amounts for the intermediate collection intervals (4–6 hours and 6–8 hours) (Table 2). The variance contributions for both linalool and linalool oxide showed significant interactions across some explanatory variables, indicating that the effects of collection day and collection interval for each day varied by injury type (Table 3).

Table 3. The contribution of each of classification variables to the variation in the amount of linalool and linalool oxide produced by mechanically-injured wheat plants

Linalool	SS	DF	MS	F	p
Intercept	4152.71	1	4152.715	160.1175	0.000000
INJURY	2658.50	5	531.700	**20.5009**	0.000000
DAYS	509.45	2	254.724	**9.8215**	0.000063
HOURS	1547.71	5	309.541	**11.9351**	0.000000
INJURY x DAYS	3286.08	10	328.608	**12.6702**	0.000000
INJURY x HOURS	1546.47	25	61.859	**2.3851**	0.000193
DAYS x HOURS	373.65	10	37.365	1.4407	0.158169
INJURY x DAYS x HOURS	2240.53	50	44.811	**1.7278**	0.001830
Error	16806.15	648	25.935		

Linalool oxide	SS	DF	MS	F	p
Intercept	199.667	1	199.6674	96.59707	0.000000
INJURY	99.628	5	19.9256	**9.63980**	0.000000
DAYS	17.939	2	8.9694	**4.33930**	0.013427
HOURS	71.384	5	14.2769	**6.90700**	0.000003
INJURY x DAYS	112.167	10	11.2167	**5.42653**	0.000000
INJURY x HOURS	67.293	25	2.6917	1.30223	0.148857
DAYS x HOURS	21.054	10	2.1054	1.01857	0.425817
INJURY x DAYS x HOURS	97.256	50	1.9451	0.94103	0.591135
Error	1339.425	648	2.0670		

Some other general comparisons for linalool production were apparent from these experiments. Linalool release by "Pierced Stem" plants was clearly highest across the collection intervals on the fourth day after injury, peaking at a mean of 4.4 ng over the

6–8 hour collection interval (Table 1). In contrast, the amounts of linalool for the "Scraped Stem" were highest immediately after injury, peaking at a mean of

4.8 ng over the 6–8 hour collection interval, and were much lower for subsequent days (Table 1). For the "Top Quarter Cut Leaf", the greatest amount of linalool was collected at two days after injury, peaking at a mean of 30.1 ng over the 4–6 hour collection interval, which was the greatest mean amount for any two hour interval (Table 2). In contrast, the amount of linalool collected for the "Bottom Quarter Cut Leaf" was greatest for the same interval (4–6 hours), but during the day the injury occurred (Table 1).

Looking at the trends for linalool oxide production, the patterns were similar for the amounts of linalool released by "Pierced Stem" and "Scraped Stem" injury. The greatest amount collected was at 4–6 hours of the fourth day after injury for the Pierced Stem (mean of 2.2 ng), while the greatest amount for the "Scraped Stem" was a mean of 1.0 ng collected at 6–8 hours on the day of injury (Table 2). However for the "Quarter Cut Leaf" injuries the results appear different for linalool oxide compared to linalool with the greatest production for the "Top" (mean of 3.6 ng for the 4–6 hour collections) and the "Bottom" (mean of 4.7 ng for the 6–8 hour collections) occurring at two days after injury (Table 2).

DISCUSSION

Plants can produce secondary metabolites, which act as signals modifying the development or behaviour of other organisms without having direct physiological activity (Chamberlain et al. 2000), although these compounds may also play a role in defense against pathogens (Wang et al. 2003). This integration can be apparent from the effects induced by host plants on insect physiology and behaviour, including reproduction, and by the plant defense responses to herbivorous insects (Reddy and Guerrero 2004). However, volatiles emitted from plants in response to insect damage can vary with insect feeding habitats (Rodriguez-Saona et al. 2003). Hoballah and Turlings (2005) reported that any type of surface damage commonly causes plant leaves to release green leaf volatiles.

In this experiment, we noted that different types of mechanical injuries induced the release of greater amount of potential secondary metabolites in elongating wheat plants. The increases in linalool and linalool oxide were quite distinct depending on injury type. Systemically released compounds like linalool are known to be induced by caterpillar feeding damage, slightly increased by mechanical injury, and are not released in significant amounts by undamaged cotton plants (Rőse et al. 1996, 1998). Engelberth et al. (2004) demonstrated a specific function of green leafy volatiles (GLV) in priming the defenses of corn plants against herbivorous insects. GLV commonly emitted by plants in response to mechanical damage induced intact undamaged corn seedlings to rapidly produce jasmonic acid (JA) and emit sesquiterpenes. Moreover, tomato plants (*Lycopersicon esculentum*), in response to insect feeding, released both locally and systemically elevated levels of volatile organic compounds (Farag and Paré 2002). Koschier et al. (2000) demonstrated that western flower thrips (*Frankliniella occidentalis*) were attracted by linalool. Banchio et al. (2005) reported that *Minthostachys mollis* plants responded to mechanical damage by dramatically increasing the concentration of the two most abundant monoterpenes (menthone and pulegone) in their essential oil.

Rodriguez-Saona et al. (2001) demonstrated that cotton plants treated with exogenous methyl jasmonate emitted elevated levels of linalool compared to those for similar plants damaged by herbivores, showing that this compound is an inducer of secondary metabolism. In the case of the current experiment, with only different forms of mechanical injury to immature wheat plants, the results are quite unexpected, particularly in the context of earlier findings comparing only one type of mechanical injury to either herbivory or an undamaged control. The dramatic treatment effects observed encourage further investigation of the ecological role of these active substances in response to varying levels of damage to different target tissues, and to fully establish their context in plant defenses in general (Ninkovic et al. 2003). In particular, it might be expected that excising 25% of a leaf would produce more volatiles than excising 50% of an identical leaf would, because our methods produce larger wounds this way. However, the differential delays in maximal production of these compounds across injury types, over time and across collection intervals merit further investigation.

CONCLUSIONS

1. Different types of mechanical injury permitted the collection of greater amounts of the secondary metabolites linalool and linalool oxide compared to control wheat plants.
2. For most wounding types, the greatest collection of linalool and linalool oxide occurred at 2 days after injury. Within each post-injury interval – zero days, two days, or four days – the greatest amount collected was obtained at the intermediate part of the photophase, typically collection intervals from 4–6 or 6–8 hours. Collection intervals from 8–10 and 10–12 hours always had lower amounts of both compounds.
3. Mechanical injury in which the top quarter of the leaf is cut induced the plants to produce the highest amounts of linalool and linalool oxide.

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REFERENCES

Agrawal A.A., Tuzun S., Bent E. (eds.).1999. Induced Plant Defenses against Pathogens and Herbivores. APS Press, St Paul, Minnesota.

Banchio E., Zygadlo J., Valladares G.R. 2005. Effects of mechanical wounding on essential oil composition and emission of volatiles from *Minthostachys mollis*. J. Chem. Ecol. 31: 719–727.

Batten J.H., Stutte G.W., Wheeler R.M. 1995. Effect of crop development on biogenetic emissions from plant populations grown in closed plant growth chambers. Phytochemistry 39: 1351–1357.

Buttery R.G., Xu Cheng-Ji, Ling L.C. 1985. Volatile components of wheat leaves (and stems): possible insect attractants. J. Agric. Food Chem. 33: 115–117.

Cardoza Y.J., Albron H.T., Tumlinson J.H. 2002. In vivo volatile emissions from peanut plants induced by simultaneous fungal infection and insect damage. J. Chem. Ecol. 28: 161–174.

Cardoza Y.J., Teal P.E.A., Tumlinson J.H. 2003. Effect of peanut plant fungal infection on oviposition preference by *Spodoptera exigua* and on host-searching behavior by *Cotesia marginiventris*. Environ. Entomol. 32: 970–976.

Chamberlain K., Pickett J.A., Woodcock C.M. 2000. Plant signaling and induced defence in insect attack. Mol. Plant Pathol. 1: 67–72.

De Moraes C.M., Lewis W.J., Paré P.W., Alborn H.T., Tumlinson J.H. 1998. Herbivore-infested plants selectively attract parasitoids. Nature 393: 570–573.

De Moraes C.M., Mescher M.C., Tumlinson J.H. 2001. Caterpillar-induced nocturnal plant volatiles repel nonspecific females. Nature 410: 577–580.

Dicke M., Sabelis M.W. 1988. How plants obtain predatory mites as bodyguards. Neth. J. Zool. 38: 148–165.

Engelberth J., Alborn H.T., Schmelz E.A., Tumlinson J.H. 2004. Airborne signals prime plants against insect herbivore attack. Plant Biol. 101: 1781–1785.

Farag M.A., Paré P.W. 2002. C_6 – green leaf volatiles trigger local and systemic VOC emission in tomato. Phytochemistry 61: 545–554.

Hamilton-Kemp T.R., Andersen R.A. 1984. Volatile compounds from *Triticum aestivum*. Phytochemistry 23: 1176–1177.

Hamilton-Kemp T.R., Andersen R.A. 1986. Volatiles from winter wheat: identification of additional compounds and effects of tissue source. Phytochemistry 25: 241–243.

Hatanaka A. 1993. The biogeneration of green odour by green leaves. Phytochemistry 34: 1201–1281.

Hoballah M.E., Turlings T.C.J. 2005. The role of fresh *versus* old leaf damage in the attraction of parasitic wasps to herbivore-induced maize volatiles. J. Chem. Ecol. 31: 2003–2018.

Johansson C., Pettersson J., Niemeyer H.M. 1997. Interspecific recognition through odours by aphids (*Sternorrhyncha: Aphididaea*) feeding on wheat plants. Eur. J. Entomol. 94: 557–559.

Karban R., Baldwin I.T. 1997. Induced Responses to Herbivory. Univ. Chicago Press, Chicago.

Kessler A., Baldwin I.T. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. Science 291: 2141–2144.

Koschier E.H., De Kogel W.J., Visser J.H. 2000. Assessing the attractiveness of volatile plant compounds to western flower thrips *Frankliniella occidentalis*. J. Chem. Ecol. 26: 2643–2655.

Ninkovic V., Ahmed E., Glinwood R., Pettersson J. 2003. Effects of two types of semiochemical on population development of the bird cherry oat aphid *Rhopalosiphum padi* in a barley crop. Agr. Forest Entomol. 5: 27–33.

Quiroz A., Niemeyer H.M. 1998. Olfactometer-assessed responses of aphid *Rhopalosiphum padi* to wheat and oat volatiles. J. Chem. Ecol. 24: 113–124.

Quiroz A., Niemeyer H.M. 1998. Activity of enantiomers of sulcantol on apterae of *Rhopalosiphum padi*. J. Chem. Ecol. 24: 361–370.

Rasmann S., Köllner T.G., Degenhardt J., Hiltpold I., Toepfer S., Kuhlmann U., Gershenzon J., Turlings T.C.J. 2005. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. Nature 434: 732–737.

Reddy G.V.P., Guerrero A. 2004. Interactions of insect pheromones and plant semiochemicals. Trends Plant Sci. 9: 253–261.

Rodriguez-Saona C., Crafts-Brandner S.J., Paré P.W., Henneberry T.J. 2001. Exogenous methyl jasmonate induces volatile emission in cotton plants. J. Chem. Ecol. 27: 679–695.

Rodriguez-Saona C., Crafts-Brandner S.J., Cañas L.A. 2003. Volatile emissions triggered by multiple herbivore damage: beet armyworm and whitefly feeding on cotton plants. J. Chem. Ecol. 29: 2539–2550.

Röse U.S.R., Manukian A., Heath R.R., Tumlinson J.H. 1996. Volatile semiochemicals released from undamaged cotton leaves: A systemic response of living plants to caterpillar damage. Plant Physiol. 111: 487–495.

Röse U.S.R., Lewis J.W., Tumlinson J.H. 1998. Specificity of systemically released cotton volatiles as attractants for specialist and generalist parasitic wasps. J. Chem. Ecol. 24: 303–319.

Thaler J.S. 1999. Jasmonate-inducible plant defences cause increased parasitism of herbivores. Nature 399: 686–688.

Turlings T.C.J., Tumlinson J.H., Lewis W.J. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250: 1251–1253.

Wang Q.H., Dorn S. 2003. Selection on olfactory response to semiochemicals from a plant-host complex in a parasitic wasp. Heredity 91: 430–435.

POLISH SUMMARY

WPŁYW MECHANICZNEGO USZKADZANIA PSZENICY NA ZWIĘKSZONĄ PRODUKCJĘ WTÓRNYCH METABOLITÓW LINALOLU I TLENKU LINALOLU

Rośliny pod wpływem ataku roślinożerców mogą emitować większe ilości lotnych związków ze swoich liści. Podobnie, mechanicznie uszkadzane rośliny emitują lotne związki różniące się ilościowo i jakościowo od roślin nie uszkadzanych. W tym eksperymencie mechaniczne uszkadzanie pszenicy spowodowało wzrost wydzielania wtórnych metabolitów, takich jak linalol (3,7-dimethyl-1,6--octadien-3-ol) i tlenek linalolu (5-ethenyltetrahydro-2 furanmethanol). Uwolnione związki różniły się istotnie w odniesieniu do typów uszkodzeń i czasu jaki upłynął po uszkodzeniu roślin. Także czas pomiędzy kolejnymi kolekcjonowaniami istotnie wpływał na ilości uwalnianych lotnych związków. Wzrost emisji tych związków, jako rezultat uszkodzeń, może być tłumaczony jako mechanizm obronny przeciwko uszkadzaniu. Rola tychże związków powinna być dalej badana w kontekście reakcji roślin na rożne typy uszkodzeń.