Bumble bee (Hymenoptera: Apidae) activity and loss in commercial tomato greenhouses

LA Morandin,^{1,2} TM Laverty

Department of Zoology, The University of Western Ontario, London, Ontario, Canada N6A 5B7

PG Kevan

Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

S Khosla

Ontario Ministry of Agriculture, Food and Rural Affairs, Greenhouse and Processing Crops Research Centre, Harrow, Ontario, Canada NOR 1G0

L Shipp

Agriculture and Agri-Food Canada, Greenhouse and Processing Crops Research Centre, Harrow, Ontario, Canada NOR 1G0

The Canadian Entomologist 133: 883 - 893 (2001)

Abstract—Activity of bumble bees, *Bombus impatiens* Cresson, was examined in commercial tomato, Lycopersicon esculentum Mill. (Solanaceae), greenhouses in relation to greenhouse covering type, solar radiation, greenhouse temperature and humidity. Bumble bee activity was measured by photodiode monitors inserted into the entrance of the colonies. Colony sizes were monitored as an indicator of bee loss through gutter ventilation systems in relation to covering. Activity monitors were found to be a good predictor of actual bumble bee entrances and exits ($r^2 = 0.85$). Bumble bee activity was 94.0% greater under the ultravioltet (UV)-transmitting covering than under ones that transmitted less UV light. No relationship was found between bee activity and the amount of solar radiation or internal greenhouse humidity. Bee activity was weakly positively correlated with internal greenhouse temperature ($r^2 = 0.18$). Bee activity was not different during three periods of the day: morning, midday, and evening. The mean ± SE colony size under the UVtransmitting covering was 86.0 ± 2 bees per colony after 10 days within the greenhouses, compared with 36.4 ± 5.8 bees per colony under the other three types of covering. Our results suggest that bee activity is greatest and bee loss through gutter ventilation systems lowest in greenhouses made with coverings that transmit high levels of UV light.

Morandin LA, Laverty TM, Kevan PG, Khosla S, Shipp L. 2001. Activité et pertes chez les bourdons (Hymenoptera : Apidae) dans les serres de culture commerciale de tomates. *The Canadian Entomologist* 133 : 883–893.

Résumé—L'activité des bourdons, *Bombus impatiens* Cresson, a été étudiée dans des serres de culture commerciale de tomates, *Lycopersicon esculentum* Mill. (Solanaceae), en fonction du type de couverture de la serre, de la radiation solaire, des conditions de température et d'humidité. L'activité des bourdons a été mesurée au moyen de sondes à photodiodes insérées à l'entrée des colonies. Les tailles des colonies servaient d'indicateurs des pertes de bourdons par le système de ventilation des gouttières en relation avec la couverture. Les sondes d'activité se sont avérées

¹Author to whom all correspondence should be addressed (E-mail: lmorandi@sfu.ca).

² Present address: Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia,

Canada V5A 1S6.

de bons outils pour prédire les entrées et sorties réelles des bourdons ($r^2 = 0.85$). L'activité des bourdons était de 94,0 % plus importante sous les couvertures qui laissent passer l'ultraviolet (UV) que sous les couvertures qui transmettent moins bien la lumière UV. Nous n'avons pas trouvé de relation entre l'activité des bourdons et la quantité de radiation solaire ou d'humidité à l'intérieur des serres. L'activité des bourdons était en faible corrélation positive avec la température à l'intérieur des serres ($r^2 = 0.18$). L'activité ne différait pas au cours des périodes de la journée : matin, midi et soir. La taille moyenne \pm écart type des colonies sous la couverture qui laisse passer l'ultraviolet a été estimée à 86,0 \pm 2 individus par colonie après 10 jours en serre, comparativement à $36,4 \pm 5,8$ individus par colonie sous les trois autres types de couverture. Nos résultats indiquent que l'activité des bourdons est maximale et la perte d'individus par le système de ventilation des gouttières, minimale dans les serres ou la couverture laisse passer l'ultraviolet.

[Traduit par la Rédaction]

Introduction

The farm value of greenhouse tomato crops in southern Ontario was estimated at \$177 million in 2000 (Ontario Ministry of Food and Rural Affairs 2001). Before 1992, pollination of greenhouse tomato crops in Ontario was done by hand vibration. Bumble bees were found to be effective pollinators of greenhouse tomatoes (*e.g.*, Banda and Paxton 1991; Kevan *et al.* 1991; Asada and Ono 1996; Dogterom *et al.* 1998; Pressman *et al.* 1998). Now, virtually all Ontario commercial growers use bumble bees as their sole means of pollination. Although the use of bumble bees as greenhouse pollinators has spread rapidly, little basic research has been conducted to answer many important questions linked to loss of bees through the ventilation systems and variation in levels of bee activity among greenhouses.

Anecdotal reports from growers and bee suppliers suggest that variation in colony size occurs among greenhouses as a result of the loss of bees through cooling vents. Because of the expense of this problem and the effect on pollination levels, it is important to determine what causes the substantial loss of bees in some greenhouses.

The level of bee activity varies among greenhouses, but there is no information about the factors that may be responsible for the variation, such as the type of polyethylene covering, internal greenhouse temperature and humidity, and internal light levels. Various types of polyethylene, which have unique transmission spectra and differ in the amount of ultraviolet (UV) light transmitted, are used in different greenhouses.

Bumble bees and honey bees have trichromatic colour vision (*e.g.*, Menzel and Backhaus 1991; Peitsch *et al.* 1992) spanning about 300 nm of natural daylight starting at about 310 nm (Kevan and Backhaus 1998). The three colour receptors are stimulated by UV, blue, and green wavelengths, with peak sensitivities at 345, 440, and 550 nm, respectively (Kevan and Backhaus 1998; similar to Peitsch *et al.* 1992). It has been shown that honey bees and other insects are four to six times more sensitive to UV light than to other parts of the spectrum, suggesting that UV is an important component of insect vision (Kevan 1970, 1979, 1983; Laughlin 1976; Menzel and Backhaus 1991); this high responsiveness to UV light may result from the insects' taking it as an indicator of an open environment (von Hess 1913; Laughlin 1976; Menzel and Greggers 1985).

In addition, UV light may be an important component of bumble bee orientation. As light passes through the atmosphere, the rays become scattered, resulting in partial polarization of the light. The result is a symmetrical ray pattern that is fixed with respect to the solar meridian (Brines and Gould 1982). The polarization pattern of the sky may be used as a celestial compass even under cloudy conditions (Brines and Gould 1982). Von Frisch (summarized 1965) showed that honey bees use polarized light as a

means of orientation and navigation. With increasing wavelengths, the polarized pattern becomes subject to atmospheric disturbance (Rozenberg 1966) and, consequently, it is believed that bees primarily use polarized light within the UV range for orientation. Von Helverson and Edrich (1974) tested the sensitivity of honey bees to different wavelengths of polarized light and found a maximum sensitivity at 345 nm; they determined that polarized light was detected exclusively by the UV receptors.

In southern Ontario, commercial tomato growers use various greenhouse polyethylene coverings that differ in intensity and spectrum of light transmission. Coverings that transmit more of the UV range may result in greater levels of activity. High levels of UV light within a greenhouse may entice more bees to leave the colony or enable the bees to better orient and navigate, resulting in shorter, more efficient foraging trips. Because bee activity increases with increasing temperature (bumble bees, Lundberg 1980; alfalfa-pollinating bees, Abrol 1990, 1998; euglossine bees, Armbruster and McCormick 1990; honey bees and bumble bees, Corbet *et al.* 1993), variation in the intensity of transmission and the wavelengths transmitted by the coverings, which can cause differences in internal temperature and humidity, may also affect bee activity.

Loss of bees through ventilation systems may also be affected by greenhouse covering. In greenhouses with coverings that transmit large amounts of UV light, there will be little visual contrast between the open vents and the rest of the roof, whereas in greenhouses with UV-blocking coverings, there will be a large visual contrast between the light coming through the open vents and the light coming through the rest of the roof.

The purpose of our experiments was to assess if the type of greenhouse covering affects loss of bees and if covering type and other internal and external climatic conditions affect the activity of bees. Factors that were investigated in relation to average daily activity per bee include external light levels, greenhouse temperature and humidity, and greenhouse covering. Because bees see within the UV range, we tested the prediction that coverings that transmitted high amounts of UV light would be associated with high levels of bee activity. It was also expected that daily ambient sunlight levels and internal greenhouse temperature would be positively correlated with bee activity. Because UV light has been shown to act as a positive phototaxis for bees (von Hess 1913; Laughlin 1976; Menzel and Greggers 1985), it was expected that there would be greater loss of bees under coverings that transmitted less UV light. Daily activity patterns within greenhouses were also assessed.

Materials and methods

Study area

All greenhouses were in the Learnington $(42^{\circ}N, 82^{\circ}W)$, Ontario, area and were devoted to growing tomatoes. Environmental conditions, such as temperature and humidity, were kept within standards optimal for tomato growth; greenhouses were vented using "gutter venting." Gutter vents are hinged openings that extend the length of the roof of the greenhouse and are computer controlled, being triggered when the internal greenhouse humidity or temperature reaches a specific preset value. None of the greenhouse were screened and, as a result, bees were able to exit the greenhouse when the vents were open. Greenhouses were constructed of various polyethylene coverings and ranged in size from 6.4 to 32.1 ha. Beefsteak tomatoes [*Lycopersicon esculentum* Mill. (Solanaceae)] were grown in all greenhouses, with the cultivars Trust and Grace being the most common. *Bombus impatiens* Cresson (Hymenoptera: Apidae) was used

exclusively in all greenhouses and, in all cases, colonies were located along the center walkway.

Colonies

Colonies of *B. impatiens* were obtained from two suppliers: Koppert Biological Systems Canada, and Biobest Canada Ltd. Colonies from both suppliers were housed in plastic containers approximately $20 \times 28 \times 18$ cm, surrounded by an outer cardboard casing. Because tomato flowers do not produce nectar, colonies were equipped with a bag containing a nectar substitute. Commercial colonies provided for greenhouse pollination normally contain cotton but, for the purpose of estimating bee numbers, experimental colonies with no cotton were used. Upon delivery, each colony contained approximately 60–90 workers and one queen. Colonies were used for no more than 2 months, after which they began to produce males and new queens. Foragers moved in and out of the colony through a 1.5-cm hole, which was fitted with an electric-powered photodiode tunnel and monitor (herein referred to as a "bee counter") designed to count entries and exits from the colony.

Commercial-greenhouse experiments

Within the commercial greenhouses, three response variables were examined: average daily activity (mean number of trips per bee), daily activity patterns (mean number of trips per bee per period), and bee loss. Average daily activity was assessed in relation to four predictor variables: type of plastic, ambient sunlight, internal temperature, and internal humidity. Daily activity patterns were assessed in relation to the time of the day, and bee loss was measured in relation to type of plastic.

General experimental setup

Types of greenhouse covering were grouped into four categories: (1) Patilux (Pati Corporation, Armin Films, City of Industry, California); (2) AT Bee Plastic (AT Plastics, Brampton, Ontario) and De Klerk (Klerk's Group, Richburg, South Carolina); (3) AT Duratherm 3 (AT Plastics); and (4) CT (Huntsman Films, Salt Lake City, Utah). AT Bee Plastic and De Klerk were grouped together based on similar light-transmission spectra. Four of the covering types were chosen because they are among the most commonly used in the Learnington area. CT plastic was chosen because of its high degree of UV transmittance and because of verbal reports from growers of high levels of bee activity under this type of covering. Spectral distributions were measured in commercial greenhouses using an LI-1800 portable spectroradiometer (Fig. 1). All readings were recorded on the same day within a 1-h period. Five bumble bee colonies were monitored at a time in each of four greenhouses, one from each group of coverings. All greenhouses were oriented in a north-south direction and were greater than 6.4 ha in area. With the exception of one greenhouse, all used only one type of covering. In the first set of four greenhouses, AT Bee plastic and AT Duratherm 3 were used in the same greenhouses, but the colonies monitored for the two types of covering were separated by at least 200 m. As CT plastic was used in only one greenhouse in the study area, all CT activity readings are from the same site; however, colonies were placed in different sections of the CT greenhouse for each of the three sets of experiments.

The bee counters recorded all movements over the photodiode cells, including the activity of "guard bees" at the nest entrance. Thus, it was necessary to calibrate the bee counters for the actual number of foraging trips. A regression line was generated relating bee-counter values to actual observed bee entrances and exits by observing 23 colonies, on different days and at various times, for 10-min intervals, in commercial tomato



FIGURE 1. Spectral distributions of daylight and light transmitted through five types of commercial greenhouse covering in the Learnington, Ontario, area recorded using a LI-1800 portable spectroradiometer.

greenhouses and regressing the actual number of bee entrances and exits on the beecounter number. The bee-counter values for each day were transformed using the regression equation, to estimate the actual number of entrances and exits per colony. This value was divided by two to estimate the daily number of trips per colony. The hourly number of trips per colony was divided by the number of bees per colony, resulting in activity in mean daily trips per bee.

Activity

Type of plastic

Three sets of four greenhouses, each of the four covered with plastic from one of the four groups, were monitored for 4 d each. Three replicates resulted in a balanced design, with a total of 36 d of activity readings for each group of coverings.

To begin monitoring, five unopened colonies were placed within each of the four greenhouses. The number of bumble bees per colony was recorded before opening, and all 20 colonies were fitted with a bee counter and opened on the same day. After opening, the colonies were left for an acclimation period of 3–10 d. After sunset the evening before the monitoring day, the number of bees per colony was visually estimated and bee-counter tunnels were cleaned and set to zero. After sunset the following evening, bee-counter numbers were recorded.

New colonies were introduced into the greenhouses after the second round of data collection, following the same procedure used for the initial colonies. Repeated-measures ANOVA was used to determine if activity was different among the four groups of plastic coverings, followed by Tukey's pairwise comparison test. Interactions between day, plastic, and experimental round were assessed. In all experiments, significant differences among means were detected using $\alpha < 0.05$.

Other predictor variables

Bee activity was also assessed in relation to factors other than type of plastic. The average daily number of trips per bee in the above experiment was regressed on total daily external radiation (mJ/m^2) recorded at the Greenhouse and Processing Crops Research Centre weather station (Harrow, Ontario). Because all greenhouses were within the Learnington area, one daily radiation value was used for all greenhouses.

The temperature and humidity within the CT greenhouse and one Patilux greenhouse were recorded at 5-min intervals, using Priva Control Systems[®]; also, the mean daily temperature and humidity were calculated from sunrise to sunset over a 2-month period for these two greenhouses. Multiple regression and ordinary least squares regression was used to assess the relationship between bee activity and both temperature and humidity.

Daily activity

This experiment was designed to assess activity patterns throughout the day. The average number of trips per bee per period of the day was calculated for morning (about 06:00-10:30), midday (about 10:30-15:00), and evening (about 15:00-19:30). The experimental design was the same as that used when average daily trips per bee was estimated but, in this case, mean trips per bee per period of the day was calculated. Time periods were always of the same length and were adjusted slightly over the 5 weeks of the experiment (24 March – 1 May), to compensate for increasing day length. Average number of trips per bee per period was log-transformed, and ANOVA was used to test for significant differences among periods of the day.

Loss of bees

Bee loss was quantified in relation to type of greenhouse covering. The actual number of bees lost through the ventilation systems could not be directly assessed, hence, colony size was used as an indicator of the number of bees lost. Bee loss is only a problem during the winter months when temperatures are too cold for the bees that escape out the vents to survive. In the summer, bees escaping through the vents are able to return to the colonies. Data were collected from 7 March to 31 March 1998. Counts were made in greenhouses over two 10-day periods during the first two sets of the activity experiment, after which, temperatures were warm enough for bees to survive outside and the experiment was terminated. Mean proportion of bees remaining in the five colonies was arcsine square root transformed and repeated-measures ANOVA was used to test for differences among the types of plastic covering, followed by Tukey's pairwise comparison test.

Results

Activity

The bee-counter value and the actual number of bee entrances and exits were highly correlated ($r^2 = 0.85$, $F_{1,24} = 129.75$, P < 0.0001). The regression equation used to transform the bee-counter numbers into actual entrances and exits was Y = 2.704 + 0.2896x (Fig. 2).



FIGURE 2. The number of bee entrances and exits from *Bombus impatiens* colonies in commercial tomato greenhouses regressed on the value recorded by a bee counter used to monitor activity.

Type of covering

Repeated-measures ANOVA showed that the mean daily number of trips per bee differed among the four types of covering ($F_{3,20} = 5.28$, P = 0.008) and among experiments (greenhouse groups) ($F_{2,20} = 5.86$, P = 0.01). Pairwise comparisons between types of covering showed that bees under CT plastic took, on average, twice as many daily trips as bees under the other three types of plastic (an average of 4.8 daily trips per bee under CT plastic *versus* an average of 2.4 under the other three types of covering) (Fig. 3). There was no difference in activity among the other three types of covering.

Other predictor variables

There was no correlation between average daily trips per bee and total daily radiation ($r^2 = 0.002$, P = 0.59, n = 107). Multiple regression showed that activity was positively correlated with both temperature and humidity in the two greenhouses (CT and Patilux) ($F_{2,27} = 5.16$, P = 0.013). There was no relationship between bee activity and humidity ($r^2 = 0.02$, $F_{1,28} = 0.51$, P = 0.481). Bee activity was positively correlated with average daily internal greenhouse temperature in the two greenhouses ($r^2 = 0.18$, $F_{1,28} =$ 5.98, P = 0.021). Within the temperature ranges observed for these analyses ($20-28^{\circ}$ C), the relationship best fit a linear model, with no apparent decrease in activity at the upper temperature ranges. For the days used in the analysis, 28 April – 26 May, the average daily temperature in the CT greenhouse was 22.3°C, 6.3% higher than in the Patilux greenhouse ($F_{1,28} = 6.79$, P = 0.015). Activity was 4.4 daily trips per bee in the CT greenhouse during this time period, 130% higher than the 1.9 daily trips per bee in the Patilux greenhouse ($F_{1,28} = 14.92$, P = 0.001).

Daily activity

No difference in bee activity was found between the three periods of the day



FIGURE 3. Mean + SE *Bombus impatiens* activity measured at the hive entrance of five colonies under four types of commercial greenhouse polyethylene covering.

 $(F_{3,156} = 0.10, P = 0.977)$ and there was no interaction between time period and type of covering $(F_{6,156} = 0.544, P = 0.774)$.

Loss of bees

There was a difference in bee loss among the four groups of covering ($F_{3,4} = 16.29$, P = 0.010). The CT plastic experienced lower bee loss compared with the other three groups (P = 0.004, 0.004, and 0.010 for CT compared with covering types 1, 2, and 3, respectively). For CT, the mean number of bees remaining after 10 d was 86.0 ± 2 bees per colony, 136% greater than the 36.4 ± 5.8 bees per colony remaining for the other three groups of covering.

Discussion

Our results are consistent with the hypothesis that bees are most active when exposed to an extended range of UV light, although the higher internal temperatures in the CT greenhouse may have been partially responsible for the greater activity observed. It is unlikely that the 6% higher temperature in the CT greenhouse could have been solely responsible for the 4-fold increase in activity in the CT greenhouse over the Patilux greenhouse. The higher temperature, along with greater amounts of UV light, may both have been factors resulting in the greater activity observed in this greenhouse.

The greater number of bees in colonies under CT plastic suggests that bee loss was lowest under this covering, possibly because the relatively small contrast between light transmitted through the covering and light entering through the vents makes it difficult for the bees to visually detect open vents. As a result, fewer bees may have flown out of the greenhouse, suggesting that UV-transmitting coverings may help prevent bee loss during winter months. Our experiments did not support the findings of previous research that showed bee activity to be positively correlated with light intensity (bumble bees, Lundberg 1980; alfalfa-pollinating bees, Abrol 1990, 1998; euglossine bees, Armbruster and McCormick 1990). It may be that, during the daytime hours of this study, light intensity within the greenhouse was adequate for flight, regardless of the external conditions. Because the other studies were conducted outside, the positive relationship between activity and light levels may have been caused, in part, by a positive correlation between light levels and temperature.

In the study greenhouses, temperatures were kept consistently above 19°C, well above the 5°C required for bumble bee flight (Heinrich 1979). Within the greenhouses, light levels were adequate for bumble bee flight soon after sunrise (LA Morandin, personal observation). Throughout the day, pollen was assumed to be in excess, because of the large numbers of open tomato flowers that remained unpollinated. The combined effect of consistently high temperatures, adequate light levels throughout the day, and excess pollen may have resulted in the consistent levels of bumble bee activity among the three periods of the day.

Extensive studies by Williams (1940, 1961) and Williams and Osman (1960) on insect activity, using trap catches, show that activity gradually increases with temperature, reaching a maximum at 29°C; further temperature increases to 34° C result in a negative correlation with activity. Many studies have found that bees become more active with increasing temperatures (bumble bees, Lundberg 1980; alfalfa-pollinating bees, Abrol 1990, 1998; euglossine bees, Armbruster and McCormick 1990; honey bees and bumble bees, Corbet *et al.* 1993). As temperatures increase from 5 to 25° C, a positive correlation between temperature and activity may be a result of decreased thermoregulation costs (Heinrich 1979). Chen and Hsieh (1996) examined bumble bee activity in tomato greenhouses and found that pollination activity was reduced in the summer as a result of extreme temperatures (up to 40° C) but, in our study, the highest average daytime greenhouse temperature was 28° C. Because there was no decreased activity up to this point, the observed greenhouse temperatures were likely within an acceptable range for foraging.

Although greenhouses with coverings that transmit more light within the UV range result in greater bee activity and less bee loss, growers must balance various factors when considering which covering to install. Increased grey mold (*Botrytis*) spore germination has been associated with plastics that transmit greater levels of UV light (Jarvis 1992), making the use of coverings that transmit high levels of UV light less desirable. In addition, greater transmission across the spectrum may result in summer temperatures that are above the optimum for tomato growth.

Maximizing bee activity and minimizing bee loss has important economic consequences for bumble bee pollination in greenhouses. Greenhouses that experience high bee loss and (or) low bee activity may require more colonies for adequate pollination and fruit quality (Morandin *et al.* 2001*a*, 2001*b*), making crop pollination more expensive. This study indicates that UV-transmitting coverings and high average daily temperatures promote colony activity, and UV-transmitting coverings result in a minimal loss of bees through ventilation systems.

Acknowledgements

We thank the growers from Flagship Farms, Mastron, Cervini, TG&G, Angelo Mastronardi, Luca Mastronardi, JEM Farms, and Double Diamond Farms. We are grateful to Koppert Biological Systems Canada and Biobest Canada Ltd for supplying the bumble bee colonies, and Gerardo Reyes for assistance with data collection. Bee counters were developed and constructed by E Praetzel. This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada to TML, and PGK, and from the Ontario Research Enhancement Program (Agriculture and Agri-Food Canada) to PGK, SK, LS, and TML.

References

Abrol DP. 1990. Pollination activity of alfalfa-pollinating subtropical bees Megachile nana and Megachile flavipes (Hymenoptera: Megachilidae). Tropical Ecology 31: 106–15

— 1998. Foraging ecology and behaviour of the alfalfa pollinating bee species Megachile nana (Hymenoptera: Megachilidae). Entomologia Generalis 22: 233–7

Armbruster WS, McCormick KD. 1990. Diel foraging patterns of male euglossine bees: ecological causes and evolutionary response by plants. *Biotropica* 22: 160–71

Asada S, Ono M. 1996. Crop pollination by Japanese bumblebees, *Bombus* spp. (Hymenoptera: Apidae): tomato foraging behavior and pollination efficiency. *Applied Entomology and Zoology* **31**: 581-6

Banda HJ, Paxton RJ. 1991. Pollination of greenhouse tomatoes by bees. Acta Horticulturae (Wageningen) 288: 194-8

Brines ML, Gould JL. 1982. Skylight polarization patterns and animal orientation. Journal of Experimental Biology 96: 69–91

- Chen CT, Hsieh FK. 1996. Evaluation of pollination efficiency of the bumblebee (Bombus terrestris L.) on greenhouse tomatoes. Zhonghua Kunchong 16: 167-75
- Corbet SA, Fussell RA, Fraser A, Gunson C, Savage A, Smith K. 1993. Temperature and the pollinating activity of social bees. *Ecological Entomology* 18: 17–30
- Dogterom MH, Matteoni JA, Plowright RC. 1998. Pollination of greenhouse tomatoes by the North American Bombus vosnesenskii (Hymentoptera: Apidae). Journal of Economic Entomology 91: 71-5

Heinrich B. 1979. Bumblebee economics. 2nd edition. Cambridge, Massachusetts, and London, England: Harvard University Press

Jarvis WR. 1992. Managing diseases in greenhouse crops. St. Paul, Minnesota: American Phytopathological Society Press

- Kevan PG. 1970. High arctic insect flower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, N.W.T., Canada. PhD dissertation, University of Alberta, Edmonton, Alberta, Canada
- 1979. Vegetation and floral colors revealed by ultraviolet light: interpretational difficulties for functional significance. *American Journal of Botany* **66**: 749–51
- 1983. Floral colours through the insect eye: what they are and what they mean. pp 3–25 in CE Jones and RJ Little (Eds), Handbook of experimental pollination biology. New York: Scientific and Academic Editions, Van Nostrand and Co
- Kevan PG, Backhaus WGK. 1998. Color vision: ecology and evolution in making the best of the photic environment. pp 163-83 in WGK Backhaus, R Kliegl, JS Werner (Eds), Color vision: perspectives from different disciplines. New York: Walter de Gruyter

Kevan PG, Straver WA, Offer M, Laverty TM. 1991. Pollination of greenhouse tomatoes by bumble bees in Ontario. Proceedings of the Entomological Society of Ontario 122: 15–9

Laughlin SB. 1976. The sensitivities of dragonfly photoreceptors and the voltage gain of transduction. Journal of Comparative Physiology 111: 221-47

Lundberg H. 1980. Effects of weather on foraging-flights of bumblebees (Hymenoptera, Apidae) in a subalpine/alpine area. *Holarctic Ecology* **3**: 104-10

Menzel R, Backhaus W. 1991. Colour vision in insects. pp 268-88 in P Gouras (Ed), Vision and visual dysfunction. The perception of colour. London: Macmillan Press

Menzel R, Greggers U. 1985. Natural phototaxis and its relationship to colour vision in honey bees. Journal of Comparative Physiology 141: 389–93

Morandin LA, Laverty TM, Kevan PG. 2001a. Effect of bumble bee (Hymenoptera: Apidae) pollination intensity on the quality of greenhouse tomatoes. *Journal of Economic Entomology* 94: 172–9

2001b. Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. Journal of Economic Entomology 94: 462–7

- Ontario Ministry of Food and Rural Affairs. 2001. *Horticulture statistics*. Toronto, Ontario: Queen's Printer for Ontario [Available at www.gov.on.ca/OMAFRA/english/stats/hort/index.html (accessed on 28 September 2001)]
- Peitsch D, Fietz A, Hertel H, De Souza J, Ventura DF, Menzel R. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A* 170: 23-40

Pressman E, Shaked R, Rosenfeld K, Hefetz A. 1998. A comparative study of the efficiency of bumble bees and an electric bee in pollinating unheated greenhouse tomatoes. *Journal of Horticultural Science & Biotechnology* **74**: 101–4

Rozenberg GV. 1966. Twighlight. A study in atmospheric optics. New York: Plenum Press

- von Frisch K. 1965. Tanzsprache und Orientierung der Bienen. Berlin, Heidelberg, and New York, New York: Springer
- von Helverson O, Edrich W. 1974. The spectral sensitivity of polarized light orientation in the honeybee. Journal of Comparative Physiology 94: 33-47
- von Hess V. 1913. Experimentelle Untersuchungen uber den angeblichen Farbensinn der Bienen. Zoologisches Jahrbuch (Physiologie) 34: 81-106
- Williams CB. 1940. The analysis of four years captures of insects in a light trap. Part 2. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. Transactions of the Royal Entomological Society of London 90: 227–306

—— 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. Philosophical Transactions of the Royal Society of London B Biological Sciences 244: 331–78

Williams CB, Osman MFH. 1960. A new approach to the problem of the optimum temperature for insect activity. Journal of Animal Ecology 29: 187-90

(Received: 20 April 2001; accepted: 5 October 2001)