

A comparison of the host preference of monarch butterflies (*Danaus plexippus*) for milkweed (*Asclepias syriaca*) over dog-strangler vine (*Vincetoxicum rossicum*)

Heather R. Mattila & Gard W. Otis

Department of Environmental Biology, University of Guelph, Guelph, ON, Canada, N1G 2W1

Accepted: 6 March 2003

Key words: *Danaus plexippus*, *Asclepias*, *Vincetoxicum rossicum*, host plant preference, oviposition preference, Lepidoptera, Nymphalidae, invasive species, conservation

Abstract

Observations in the field indicate that monarch butterflies will oviposit on dog-strangler vine, an invasive introduced species in the same family as milkweed (*Asclepias* spp.), the principal larval host of monarchs. The potential impact of this behaviour depends on the strength of the preference of monarch adults to oviposit on these two hosts and the relative ability of larvae to survive on each. We determined the preference for milkweed vs. dog-strangler vine of ovipositing adults and first instar larvae in choice and no-choice tests. We also compared the ability of larvae to consume, develop, and survive on either host. In the presence of both hosts, adults exhibited a strong preference to oviposit on milkweed over dog-strangler vine (mean 80.7 eggs compared to 0.4 eggs over 48 h, respectively). In the absence of milkweed, adults ceased oviposition (mean 0.9 eggs in 48 h), but resumed oviposition when the dog-strangler vine was replaced with milkweed (mean 99.1 eggs in 48 h). Given a choice between hosts over 24 h, 92% of larvae moved to milkweed leaves and consumed 3.94 cm² of milkweed leaves compared to 2% of larvae that moved to dog-strangler vine and consumed negligible amounts of leaf material (0.01 cm²). Without a choice, larvae on dog-strangler vine never consumed more than mean 0.02 cm² larva⁻¹ in a 24-h period, did not develop beyond the first instar, and died within 96 h. We obtained no data in support of an effect of the presence of dog-strangler vine on monarch butterfly populations.

Introduction

The eastern Nearctic population of the monarch butterfly (*Danaus plexippus* L., Lepidoptera: Nymphalidae, Danainae) migrates seasonally from overwintering sites in Mexico across the eastern US and into southern Canada (Urquhart & Urquhart, 1977, 1978, 1979; Brower, 1996). Northward migrating monarchs breed continuously as they recolonize their temperate range (Urquhart et al., 1970; Cockrell et al., 1993), utilizing milkweeds (*Asclepias* spp., Asclepiadaceae) as their principal larval host plants, with records of oviposition on 33 of the 108 North American milkweed species (Ackery & Vane-Wright, 1984; Malcolm & Brower, 1986; Lynch & Martin, 1993).

Beyond this limited group, Ackery & Vane-Wright (1984) listed six families (including nine additional genera of Asclepiadaceae) that are exploited by monarchs as larval host plants based on references in the literature. There are numerous additional reports of monarchs ovipositing on non-*Asclepias* species (Saunders, 1873, 1932; Burns, 1983; Lynch & Martin, 1993), although little work has been done to fully document these claims (Shields et al., 1969; Borkin, 1993). One such potential host is the dog-strangler vine (*Vincetoxicum rossicum* (Kleopov) Barbarich, also known as swallowwort), which is an invasive European perennial that was introduced to eastern North America in the latter part of the nineteenth century (Moore, 1959; Sheeley & Raynal, 1996). The taxonomy of *V. rossicum* is convoluted; some authors place *V. rossicum* in the genus *Cynanchum* (Moore, 1959; White et al., 1993; Kartesz, 1994; Darbyshire et al., 2000), or with the species *V. hirundinaria* Medicus (Gleason & Cronquist, 1991). We follow the

Correspondence: Heather R. Mattila, Department of Environmental Biology, University of Guelph, Guelph, ON, Canada, N1G 2W1.
E-mail: hmattila@uoguelph.ca

work of Tutin et al. (1972), who have the support of many other authors (Pringle, 1973; McNeill, 1981; Sheeley & Raynal, 1996). Dog-strangler vine has spread into natural areas where it forms monodominant stands that suppress the growth of other herbaceous plants, including *Asclepias*, and is presently well established in localized populations throughout southern Ontario and the north-eastern USA (Moore, 1959; Kirk, 1985; Sheeley & Raynal, 1996). Dog-strangler vine is viewed as a threat to natural ecosystems because of its extensive foliage and root systems, abundant wind-borne seeds, and ability to flourish in diverse habitats (Pringle, 1973; Kirk, 1985; Riley, 1989; White et al., 1993; Sheeley & Raynal, 1996).

The genus *Vincetoxicum* is in the family Asclepiadaceae (Gleason & Cronquist, 1991), and is a known host of Danainae butterflies, including two species of *Danaus* in Australia and Mexico (Ackery & Vane-Wright, 1984). It is possible that monarch butterflies may be using this exotic species as a new host in North America. Observations of monarchs in the field include the apparent attraction of females to dog-strangler vine and the actual oviposition or discovery of eggs on leaves (N. Cappuccino & G. Stell, pers. comm.), but the strength of this attraction is not known. In addition, if monarchs are stimulated to oviposit on dog-strangler vine, this could affect their reproductive success if the larvae have little or no ability to utilize it as a host plant. The northern reproductive range of the eastern migrating monarch population overlaps the distribution of dog-strangler vine in North America, and more importantly, the density of monarchs is relatively high in the areas surrounding the Great Lakes due to an abundant supply of larval host plants such as common milkweed (*Asclepias syriaca* L.) (Urquhart & Urquhart, 1977). This creates the potential for a large portion of the eastern population to come into contact with this aggressive invasive species. The spatial distribution and temporal abundance of the monarch has been closely tied to the presence of its *Asclepias* hosts throughout North America (Malcolm et al., 1993; Riley, 1993) and an interruption in the availability of hosts within this range has the potential to disrupt the annual migration of monarch butterflies. The consequences of the introduction of an aggressive exotic like dog-strangler vine that could potentially act as a sink in the population through an 'oviposition mistake' by laying females (either through reduced growth or survival of the larvae) are not known at this point. Such a host switch may also have ramifications for the protection conferred to monarchs from the sequestration of toxic compounds found in their typical *Asclepias* hosts (Reichstein et al., 1968). In the past, conservation efforts have focussed on the limited overwintering sites of the monarch in Mexico, but the introduction of dog-strangler vine could

compromise the ability of monarchs to thrive in its north-eastern range.

The significance of oviposition on dog-strangler vine would depend on the strength of the preference for either host, the relative ability of larvae to survive on dog-strangler vine and milkweed and the relative growth rates of larvae on the two host plants. We examined the potential utilization of dog-strangler vine by monarch butterflies by estimating adult and larval host plant preferences in choice and no-choice tests, as well as the survival and development of first instar larvae on common milkweed and dog-strangler vine.

Materials and methods

Materials

In early May, dog-strangler vine root stocks were obtained from an established growth site in the Rouge River Valley (near Toronto, ON) and potted in a 1 : 1 mixture of calcined clay and potting soil. The pots were placed outdoors and watered and fertilized every 2 days (100 p.p.m. of all-purpose 20-20-20, N-K-P) until survival and host preference tests were conducted in mid-July. Milkweed stems (*Asclepias syriaca*) were harvested from sites around Guelph, Ontario, for use in the study. The study was initiated on 19 July, when adult female monarch butterflies ($n = 12$) were net collected from a disturbed meadow in Elora, Ontario. All individuals were observed ovipositing in the field prior to collection to ensure that they were capable of doing so in the laboratory. The larvae used in survival and host preference tests were obtained from the eggs of these adults. All tests were conducted in a growth room maintained at 27 °C, 50% r.h., and L16:D8. Data were analyzed with SAS System for Windows version 8.02 (SAS Institute). All means are presented with standard errors.

Adult host preference

On the day of collection, each butterfly was randomly assigned to a screened cage (0.5 × 0.5 × 0.3 m) containing a potted dog-strangler vine, a milkweed plant in water (harvested at the base of the stem), and a nectar station (screen-covered Petri dish) filled with Gatorade (Stokely Van Camp, Inc.). Plants of approximately equal size were placed at opposite ends of the cage and did not touch each other. Flowers were removed from all plant material to avoid increased attraction of adults to either host. The adults were allowed to oviposit over 48 h, at which time egg counts on both plant types were made. The number of eggs laid on each plant was compared with a t-test. No-choice tests commenced at this time; milkweed plants were removed from the cages and the butterflies were exposed to dog-strangler vine alone for 48 h, then milkweed alone for

a subsequent 48 h. At the end of each test, the number of eggs laid by each butterfly on the plant material was determined and the difference in oviposition was evaluated with a paired t-test. Due to mortality towards the end of the oviposition period, the number of adults in the no-choice test was reduced ($n = 9$).

Larval host preference

All tests were conducted in ventilated Petri dish arenas (15 cm in diameter) with cut leaves, the petioles of which were placed in vials filled with deionized water and wrapped in parafilm to prevent moisture loss.

In choice tests, the preference of the larvae for either host was estimated by comparing the number of larvae found on milkweed and dog-strangler leaves in the arenas and by differences in the consumption of these leaves. A dog-strangler vine leaf and milkweed leaf of approximately equal size were positioned on either side of an arena ($n = 10$) and a cohort of 10 first instar larvae (< 24 h old) was placed between the leaves of each arena with a paintbrush. The number of larvae that were observed on the dog-strangler vine or milkweed leaves was determined after 2, 6, and 24 h. The data were analyzed as a split-plot in time (Bowley, 1999) and the variance was partitioned into the following effects: treatment (leaf type), time, treatment by time, arena (block), and arena by treatment effects (subject effect). The area of leaf consumption (cm^2) for both plant types was estimated after 24 h by creating digital images of backlit leaves with a black and white video camera module (Model XC-75CE, Sony of Canada Ltd) and a 16 mm CCTV camera lens (Cosmicar-Pentax). The images were processed with image analysis software (Northern Exposure 2.93, Empix Imaging, Inc.) to determine the area of the leaf that had been removed by larval feeding. The preference for milkweed or dog-strangler vine based on leaf consumption was estimated by partitioning the variance into treatment and arena effects.

In the no-choice tests, a cohort of 10 first instar larvae (< 24 h old) was placed in an arena containing either a dog-strangler vine or milkweed leaf ($n = 10$ for each plant type). The number of larvae from each cohort that were found on the leaf provided was determined after 2, 6, and 24 h of exposure. These data were analyzed by the method used in the choice test, except that two arenas, each containing a different leaf type, were placed side by side to act as a block instead of having both treatments in the same arena.

Survival

The same arenas that had been assembled for the no-choice tests were used to compare larval survival, development, and leaf consumption. At 24 h intervals, the arenas were

examined to determine the percentage survival of the cohort and mean instar of larvae present (estimated using head capsule width). Larvae were transferred to fresh leaves every 24 h and leaf consumption for each interval was determined with the image analysis method described above. These measurements were recorded until all the larvae in a single treatment died or pupated. For all of these responses, differences due to treatment (exposure to milkweed or dog-strangler vine) were estimated by the same split-plot in time model described above. A multiple comparison of means for significant effects was conducted with a Tukey–Kramer adjustment.

Results

Adult host preference

When given a choice, adult monarchs preferred to oviposit on milkweed (mean 80.7 ± 28.08 eggs) rather than dog-strangler vine (mean 0.4 ± 0.26 eggs) (t-test: $t = 2.86$, d.f. = 22, $P = 0.009$). Of the 12 individuals in the test, only three oviposited on dog-strangler vine, whereas all individuals oviposited on milkweed. After 48 h, a total of five eggs were found on dog-strangler vine compared to 968 eggs on milkweed. Without a choice, adults laid significantly more eggs on milkweed (mean 99.1 ± 23.28 eggs) than on dog-strangler vine (mean 0.9 ± 0.89 eggs) (paired t-test: $t = 4.23$, d.f. = 8, $P = 0.003$). In total, 892 eggs were laid on milkweed and only eight eggs on dog-strangler vine in the no-choice situation.

Larval host preference

In the 24 h choice tests, significantly more larvae moved to milkweed leaves compared to dog-strangler leaves when given the choice between the two hosts (treatment effect: $F = 1924.44$, d.f. = 2, 36, $P < 0.0001$). This trend did not change over time (time effect: $F = 1.58$, d.f. = 2, 36, $P = 0.22$; time by treatment effect: $F = 2.02$, d.f. = 2, 36, $P = 0.15$). Pooled over time, the mean number of larvae found on milkweed was 9.2 ± 0.15 and 0.2 ± 0.15 on dog-strangler vine. After 24 h with a choice of two hosts, mean consumption of milkweed leaves was significantly greater than dog-strangler vine leaves ($3.94 \pm 0.122 \text{ cm}^2$ and $0.01 \pm 0.122 \text{ cm}^2$, respectively; treatment effect: $F = 521.86$, d.f. = 1, 9, $P < 0.0001$).

When the larvae were not given a choice between host types, significantly fewer larvae moved to dog-strangler vine compared to milkweed (treatment effect: $F = 192.26$, d.f. = 1, 9, $P < 0.0001$) for all observation times (time effect: $F = 0.44$, d.f. = 2, 36, $P = 0.65$; time by treatment effect: $F = 0.33$, d.f. = 2, 36, $P = 0.72$). The mean number of larvae on milkweed was 9.9 ± 0.36 and on dog-strangler vine was 4.1 ± 0.36 when pooled over time.

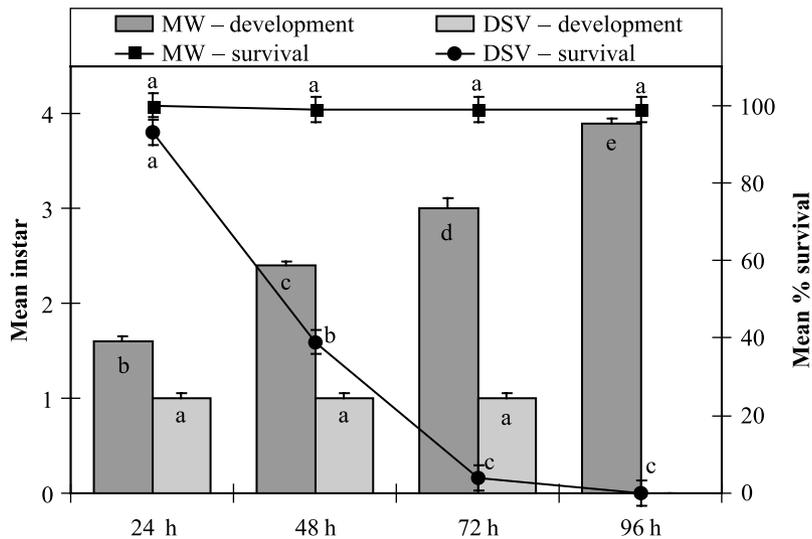


Figure 1 The mean instar \pm SE (bars) and the mean percentage survival of larvae \pm SE (lines) for cohorts of monarch larvae exposed to leaves of milkweed (MW) or dog-strangler vine (DSV) over 96 h. Treatment by time means for each response were separated by a Tukey–Kramer adjustment and significant differences are indicated by different letters ($P < 0.05$).

Survival

Analysis of the percentage survival of larvae indicated a significant treatment by time interaction ($F = 106.96$, $d.f. = 3, 54$, $P < 0.0001$), which corresponded to differences in larval survival over time, depending on the leaf to which the larvae were exposed (treatment effect: $F = 640.06$, $d.f. = 1, 9$, $P < 0.0001$; time effect: $F = 106.96$, $d.f. = 3, 54$, $P < 0.0001$). The means revealed a general trend for each treatment (Figure 1); survival of larvae on milkweed over time was very high, but rapidly declined for larvae on dog-strangler vine, where all the larvae were dead after 96 h. The effect on larval development was as dramatic. Mean instar steadily increased for larvae on milkweed, whereas larvae on dog-strangler vine never developed beyond the first instar (Figure 1), which resulted in a highly significant treatment by time interaction ($F = 81.67$, $d.f. = 2, 36$, $P < 0.0001$), as well as a treatment effect ($F = 400.55$, $d.f. = 1, 9$, $P < 0.0001$) and time effect ($F = 388.55$, $d.f. = 3, 36$, $P < 0.0001$).

Due to the high mortality of the larvae on dog-strangler vine, leaf consumption was only measured up to 72 h. Consumption had a significant treatment by time interaction ($F = 26.17$, $d.f. = 2, 24$, $P < 0.0001$), treatment effect ($F = 129.01$, $d.f. = 1, 9$, $P < 0.0001$), and time effect ($F = 25.32$, $d.f. = 2, 24$, $P < 0.0001$), where mean consumption per larva was consistently low for larvae on dog-strangler vine, but steadily increased over time on milkweed. The most that larvae on dog-strangler vine consumed during a 24 h period was a mean of $0.02 \pm 0.008 \text{ cm}^2 \text{ larva}^{-1}$, while larvae on milkweed consumed a mean of $0.42 \pm 0.018 \text{ cm}^2 \text{ larva}^{-1}$ in the first 24 h and 0.58 ± 0.072 and $1.78 \pm 0.196 \text{ cm}^2 \text{ larva}^{-1}$ in the subsequent intervals.

Discussion

Monarch host preference is a function of the acceptability of a specific plant for adult oviposition and larval feeding, and the suitability of the plant for larval development (Singer, 1986; Borkin, 1993). Monarchs demonstrated a lack of preference for dog-strangler vine as a host in all of these respects. Despite anecdotal reports to the contrary, in our study, females refused to oviposit on dog-strangler vine, but immediately resumed oviposition when provided with milkweed. Given a choice between leaves of each host, larvae were found almost exclusively on milkweed, and consumed much more milkweed than dog-strangler vine. All individuals that were exposed to dog-strangler vine alone consumed very little leaf material, never developed beyond the first instar and died within 96 h, whereas larvae on milkweed leaves flourished and 99% survived over the same period. In no-choice tests where milkweed was provided, larvae were almost always found on the leaves. When offered dog-strangler vine leaves alone, 60% of larvae were off the leaves and searching the arena.

The monarch has been the focus of conservation efforts in North America because their spectacular annual migration is considered an ‘endangered phenomenon’ due to the sensitivity of their limited overwintering sites in Mexico (Wells et al., 1983; Brower & Malcolm, 1991). The introduction of dog-strangler vine has the potential to threaten monarch habitat within its northern range because it is an aggressive exotic, one that has been observed in the field to overgrow stands of milkweed, and at the present time its spread is unchecked and difficult to prevent (Pringle, 1973; Kirk, 1985). Over time, the increasing range and density of dog-strangler vine in the North-east could have disrupted

the production of the migrating monarch population if females had utilized it for oviposition to an appreciable extent, but larvae were unable to develop on it. In such a case, larvae emerging on dog-strangler vine would be unlikely to find a suitable food source and would die. Such a situation was found for two *Pieris* spp. that oviposit on most plants that contain glucosinolates, but could not survive to pupation on an introduced crucifer species that was found within their range (Chew, 1975). For *Pieris*, there would be heavy selection pressure favouring preferences for oviposition on crucifers supporting complete larval development. In light of our results, this scenario is not probable because monarchs generally refused to oviposit on dog-strangler vine.

Our results could have been influenced by the field collection of adults that were ovipositing on milkweed for use in the study. This prior experience could have caused a preference for milkweed in our tests because experience as a young adult can induce preferences for hosts in later encounters for other insect species (Jaenike, 1982; Mark, 1982; Hanson, 1983; Rausher, 1983). Fortunately, we have support for a lack of preference for dog-strangler vine for monarchs without prior oviposition experience. We conducted a preliminary trial in which newly emerged lab-reared adults were moved to a cage and allowed to mate and oviposit in the presence of both milkweed and dog-strangler vine. With 20 adults caged over a 12-day period, 11 eggs were laid on dog-strangler vine compared to > 1000 eggs on milkweed. Even without prior egg-laying experience, a strong preference to oviposit on milkweed was evident.

Reports of monarchs ovipositing on dog-strangler vine in nature do exist, and a number of reasons make this a possibility. Monarchs utilize *Cynanchum laeve* in the USA in late summer (Lynch & Martin, 1993), the genus where *Vincetoxicum* is often placed (Gleason & Cronquist, 1991). Flavonol glycosides have been isolated in both *Asclepias* spp. and *Vincetoxicum* spp., and have been identified as oviposition stimulants responsible for host plant recognition in monarchs (Haribal & Renwick, 1996, 1998b). *Vincetoxicum nigrum* (L.) Moench contains flavanol glycosides at a much lower concentration than *A. syriaca*, but data for *V. rossicum* do not exist. Similar to our results, monarchs oviposited on *V. nigrum* in choice tests, but only in small numbers, which may be a reflection of different flavonoid profiles (Haribal & Renwick, 1998b). In their study, the larvae that emerged from eggs laid on *V. nigrum* did not survive. The problem of which chemicals act as an oviposition stimuli is far from resolved (Oyeye & Zalucki, 1990; Zalucki et al., 1990 and references therein), and it is likely that there is a complex interplay of stimulants that are perceived by a number of receptors (Baur

et al., 1998; Haribal & Renwick, 1998a). It is possible that reliable reports of oviposition in the field are due to a large variation in the levels of oviposition stimulants found within and between localized stands or individual dog-strangler vine plants, or between plants of different ages, making some plants more attractive to ovipositing females than others. Extensive variation in cardenolide content has also been found between plants for many species of *Asclepias* (Nelson et al., 1981; Brower et al., 1982, 1984; Lynch & Martin, 1987, 1993; Martin & Lynch, 1988; Van Hook & Zalucki, 1991). If attraction to dog-strangler vine does vary in the field, field studies that followed the success of larvae emerging from eggs found in nature would be required.

Erroneous or unsupported reports of Lepidopteran host plants often appear in the literature and emphasis should be placed on establishing that larvae can develop on a plant where eggs have been observed, before reporting them as hosts (Shields et al., 1969). With regard to the monarch, very little work has been done to document this outside of the genus *Asclepias*. The nearest example is that of Borkin (1993), who refuted accounts that monarchs utilized *Apocynum* spp. by demonstrating that larvae could not survive in no-choice tests, but she did not examine the frequency with which adults would oviposit on these species in conjunction with larval feeding trials. There are reliable observations of monarchs ovipositing on dog-strangler vine in the field, but it is probably a rare occurrence. More importantly, even if this were observed, dog-strangler vine cannot be reported as a potential host plant for monarchs until it has been demonstrated that larvae are capable of surviving to adulthood on it.

Acknowledgements

We would like to thank N. Cappuccino and G. Stell for sharing their observations from the field, T. Mason (Curator of Invertebrates, Metro Toronto Zoo) for providing dog-strangler vine rootstock, and S. Goodfellow for technical assistance. O.R. Taylor Jr., J. Turgeon, and three anonymous reviewers provided valuable advice that improved the manuscript.

References

- Ackery PR & Vane-Wright RI (1984) Milkweed Butterflies. Their Cladistics and Biology. British Museum, London.
- Baur R, Haribal M, Renwick JAA & Städler E (1998) Contact chemoreception related to host selection and oviposition behaviour in the monarch butterfly, *Danaus plexippus*. *Physiological Entomology* 23: 7–19.
- Borkin SS (1993) Rejection of *Apocynum androsaemifolium* and *A. sibiricum* (Apocynaceae) as food plants by larvae of

- Danaus plexippus*: refutations of early accounts. *Biology and Conservation of the Monarch Butterfly* (ed. by S B Malcolm & M P Zalucki), pp. 125–128. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Bowley SR (1999) *A Hitchhiker's Guide to Statistics in Plant Biology*. Any Old Subjects Books, Guelph, Ontario, Canada.
- Brower LP (1996) Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology* 199: 93–103.
- Brower LP & Malcolm SB (1991) Animal migrations: endangered phenomena. *American Zoologist* 31: 265–276.
- Brower LP, Seiber JN, Nelson CJ, Lynch SP, Hoggard MP & Cohen JA (1984) Plant-determined variation in cardenolide content and thin-layer chromatography profiles of monarch butterflies, *Danaus plexippus*, reared on milkweed plants in California (USA); 3. *Asclepias californica*. *Journal of Chemical Ecology* 10: 1823–1858.
- Brower LP, Seiber JN, Nelson CJ, Lynch SP & Tuskes PM (1982) Plant-determined variation in the cardenolide content, thin-layer chromatography profiles, and emetic potency of monarch butterflies, *Danaus plexippus*, reared on the milkweed, *Asclepias eriocarpa*, in California. *Journal of Chemical Ecology* 8: 579–634.
- Burns JM (1983) Queen of the Carolinas (Lepidoptera: Nymphalidae: Danainae: *Danaus gilippus*). *Proceedings of the Entomological Society of Washington* 85: 388–396.
- Chew FS (1975) Coevolution of Pierid butterflies and their cruciferous foodplants. I. The relative quality of available resources. *Oecologia* 20: 117–127.
- Cockrell BJ, Malcolm, SB & Brower, LP (1993). Time, temperature, and latitudinal constraints on the annual recolonization of eastern North America by the monarch butterfly. *Biology and Conservation of the Monarch Butterfly* (ed. by S B Malcolm & M P Zalucki), pp. 233–251. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Darbyshire SJ, Favreau M & Murray M (2000) *Common and Scientific Names of Weeds in Canada*. Publication 1397/B, Agriculture and Agri-Food Canada, Ottawa.
- Gleason HA & Cronquist A (1991) *Manual of Vascular Plants in Northeastern United States and Adjacent Canada*. New York Botanical Garden, New York.
- Hanson FE (1983) The behavioural and neurophysical basis of food plant selection by Lepidopterous larvae. *Herbivorous Insects Host-Seeking Behavior and Mechanisms* (ed. by S Ahmad), pp. 3–23. Academic Press, New York.
- Haribal M & Renwick JAA (1996) Oviposition stimulants for the monarch butterfly: flavonol glycosides from *Asclepias curassavica*. *Phytochemistry* 41: 139–144.
- Haribal M & Renwick JAA (1998a) Differential postalightment oviposition behavior of monarch butterflies on *Asclepias* species. *Journal of Insect Behavior* 11: 507–538.
- Haribal M & Renwick JAA (1998b) Identification and distribution of oviposition stimulants for monarch butterflies in hosts and nonhosts. *Journal of Chemical Ecology* 24: 891–904.
- Jaenike J (1982) Environmental modification of oviposition behavior in *Drosophila*. *American Naturalist* 119: 784–802.
- Kartesz JT (1994) *A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland*. Timber Press, Portland, OR.
- Kirk M (1985) *Vincetoxicum* spp. (dog-strangling vines): alien invaders of natural ecosystems in southern Ontario. *Plant Press* 3, 130–131.
- Lynch SP & Martin RA (1987) Cardenolide content and thin-layer chromatography profiles of monarch butterflies, *Danaus plexippus* L. and their larval host-plant milkweed, *Asclepias viridis* Walt., in Northwestern Louisiana (USA). *Journal of Chemical Ecology* 13: 47–70.
- Lynch SP & Martin RA (1993) Milkweed host plant utilization and cardenolide sequestration by monarch butterflies in Louisiana and Texas. *Biology and Conservation of the Monarch Butterfly* (ed. by S B Malcolm & M P Zalucki), pp. 107–123. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Malcolm SB, Cockrell BJ & Brower LP (1993) Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? *Biology and Conservation of the Monarch Butterfly* (ed. by S B Malcolm & M P Zalucki), pp. 253–268. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Malcolm SB & Brower LP (1986) Selective oviposition by monarch butterflies (*Danaus plexippus* L.) in a mixed stand of *Asclepias curassavica* L. and *A. incarnata* L. in South Florida. *Journal of the Lepidopterists' Society* 40: 255–263.
- Mark GA (1982) Induced oviposition preference, periodic environments, and demographic cycles in the bruchid beetle *Callosobruchus maculatus*. *Entomologia Experimentalis et Applicata* 32: 155–160.
- Martin RA & Lynch SP (1988) Cardenolide content and thin-layer chromatography profiles of monarch butterflies, *Danaus plexippus* L. & their larval host-plant milkweed, *Asclepias asperula* subsp. *capricornu* (Woods) Woods, in North Central Texas. *Journal of Chemical Ecology* 14: 295–318.
- McNeill J (1981) Taxonomic, nomenclatural and distributional notes on Canadian weeds and aliens. *Le Naturaliste Canadien* 108: 237–244.
- Moore RJ (1959) The dog-strangling vine *Cynanchum medium*, its chromosome number and its occurrence in Canada. *Canadian Field-Naturalist* 73: 144–147.
- Nelson CJ, Seiber JN & Brower LP (1981) Seasonal and intraplant variation of cardenolide content in the California milkweed, *Asclepias eriocarpa*, and implications for plant defense. *Journal of Chemical Ecology* 7: 981–1010.
- Oyeyele SO & Zalucki MP (1990) Cardiac glycosides and oviposition by *Danaus plexippus* on *Asclepias fruticosa* in south-east Queensland (Australia), with notes on the effect of plant nitrogen content. *Ecological Entomology* 15: 177–185.
- Pringle JS (1973) The spread of *Vincetoxicum* species (Asclepiadaceae) in Ontario. *Canadian Field-Naturalist* 87: 27–33.
- Rausher MD (1983) Conditioning and genetic variation as causes of individual variation in the oviposition behaviour of the tortoise beetle, *Deloyala guttata*. *Animal Behaviour* 31: 743–747.
- Reichstein T, von Euw J, Parsons JA & Rothschild M (1968) Heart poisons in the monarch butterfly. *Science* 161: 861–866.

- Riley JL (1989) More invasive aliens. *Seasons* 29: 23.
- Riley TJ (1993) Spring migration and oviposition of the monarch butterfly in Louisiana. *Biology and Conservation of the Monarch Butterfly* (ed. by S B Malcolm & M P Zalucki), pp. 269–274. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Saunders W (1873) On some of our common insects. *Canadian Entomologist* 5: 4–8.
- Saunders W (1932) *The Butterflies of Allegany State Park*. New York State Museum Handbook 13. University of the State of New York, Albany, NY.
- Sheeley SE & Raynal DJ (1996) The distribution and status of species of *Vincetoxicum* in eastern North America. *Bulletin of the Torrey Botanical Club* 123: 148–156.
- Shields O, Emmel JF & Breedlove DE (1969) Butterfly larval foodplant records and a procedure for reporting foodplants. *Journal of Research on the Lepidoptera* 8: 21–36.
- Singer MC (1986) The definition and measurement of oviposition preference in plant-feeding insects. *Insect-Plant Interactions* (ed. by J R Miller & T A Miller), pp. 65–94. Springer-Verlag, New York.
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM & Webb DA (1972) *Flora Europaea*. University Press, Cambridge, UK.
- Urquhart FA & Urquhart NR (1977) Overwintering areas and migratory routes of the monarch butterfly (*Danaus, p. plexippus*, Lepidoptera: Danaidae) in North America, with special reference to the western population. *Canadian Entomologist* 109: 1583–1589.
- Urquhart FA & Urquhart NR (1978) Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus, p. plexippus* L., Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. *Canadian Journal of Zoology* 56: 1759–1764.
- Urquhart FA & Urquhart NR (1979) Breeding areas and over-night roosting locations in the northern range of the monarch butterfly (*Danaus plexippus plexippus*) with a summary of associated migratory routes. *Canadian Field-Naturalist* 93: 41–47.
- Urquhart FA, Urquhart NR & Munger F (1970) A study of a continuously breeding population of *Danaus plexippus* in southern California compared to a migratory population and its significance in the study of insect movement. *Journal of Research on the Lepidoptera* 7: 169–181.
- Van Hook T & Zalucki MP (1991) Oviposition by *Danaus plexippus* (Nymphalidae: Danainae) on *Asclepias viridis* in northern Florida. *Journal of the Lepidopterists' Society* 45: 215–221.
- Wells SM, Pyle RM & Collins NM (1983) *The IUCN Invertebrate Red Data Book*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- White DJ, Haber E & Keddy C (1993) *Invasive Plants of Natural Habitats in Canada*. Canadian Wildlife Service, Environment Canada, Ottawa.
- Zalucki MP, Brower LP & Malcolm SB (1990) Oviposition by *Danaus plexippus* in relation to cardenolide content of three *Asclepias* species in the southeastern USA. *Ecological Entomology* 15: 231–240.

