

- ol. 213, 1159 (1962); M. J. Wayner *et al.*, *Physiol. Behav.* 7, 881 (1971).
4. A. N. Epstein and P. Teitelbaum, *Proceedings of the International Union of Physiological Scientists, XXII International Congress* (Excerpta Medica, Amsterdam, 1962), abstract 361.
 5. E. M. Stricker, M. I. Friedman, M. J. Zigmond, *Science* 189, 895 (1975); R. B. Kanarek, S. Melinda, A. Khadivi, *Am. J. Physiol.* 241, R362 (1981).
 6. H. J. Grill and R. Norgren, *Brain Res.* 143, 281 (1978).
 7. ———, *Science* 201, 267 (1978).
 8. H. J. Grill and R. R. Miselis, *Am. J. Physiol.* 240, R81 (1981).
 9. R. C. Ritter, P. G. Slusser, S. Stone, *Science* 213, 451 (1981).
 10. A 1-mm slit was made in the frontal plane of the skull, 40 percent of the distance between bregma and lambda, from lambda. The dura was cut and an L-shaped spatula inserted to the base of the brain and, in a sawing-like motion, moved medially through the brain to the midline. The cut was then retraced laterally. The wound was closed and each animal was allowed to recover for 7 days before contralateral completion of the decerebration. Rats received 15,000 U of bicillin every other day for 4 days after the first stage and completion of the decerebration (6).
 11. The liquid diet was comprised of equal parts of Borden's sweetened condensed milk and water with a vitamin supplement (Poly Vi Sol, Mead Johnson).
 12. S. Kaufman, *Am. J. Physiol.* 239, R123 (1980).
 13. A. B. Steffens, *Physiol. Behav.* 4, 823 (1969).
 14. Comparison of plasma glucose values and the behavior of rats from which blood had been withdrawn from the tail vein and vena cava revealed no systematic differences. Blood was collected into 250- μ l heparinized capillary tubes and centrifuged at 2650 rev/min for 7 minutes. Plasma glucose assays were performed on 10- μ l samples with a Beckman glucose oxidase analyzer.
 15. The stimulus was infused at a slower rate for decerebrate rats than for intact rats to allow for their slower rate of ingestion and correlated rhythmic cycle of mouth movements (5.1 cycle/sec, compared with 6.6 cycle/sec in intact rats) and of tongue protrusions (6.3 cycle/sec, compared with 8.8 cycles in intact rats).
 16. V. B. Mountcastle, in *The Mindful Brain*, G. M. Edelman and V. B. Mountcastle, Eds. (MIT Press, Cambridge, Mass., 1978), p. 7; H. J. Jackson, in *The Selected Writings of John Hughlings Jackson*, J. Taylor, Ed. (Basic Books, New York, 1958).
 17. D. G. Mook and N. J. Kenney, in *Drinking Behavior*, J. A. W. M. Weijnen and J. Mendelson, Eds. (Plenum, New York, 1977), p. 275.
 18. In the present study, insulin treatment did not promote water ingestion. Insulin treatment can elicit thirst, but to do so it must be administered in doses larger than those used here [D. A. Booth and M. E. Pitt, *Physiol. Behav.* 3, 447 (1968); D. Novin, in *Thirst in the Regulation of Body Water*, M. J. Wayner, Ed. (Pergamon, Oxford, 1964), p. 177; R. J. Waldbillig and T. J. Bartness, *Physiol. Behav.* 26, 787 (1981)]. Furthermore, the ingestion of sucrose solution by decerebrate rats in response to insulin is unlikely to reflect thirst since such rats do not increase their water intake in response to dehydration (8).
 19. Supported by grants AM 21397 and T32-MH15012. We thank K. Berridge, R. DiRocco, M. Friedman, R. Miselis, A. Epstein, and D. Ganster for reading the manuscript.

13 December 1982; revised 8 March 1983

Leaf Color Used by Cabbage Root Flies to Distinguish Among Host Plants

Abstract. *In experiments in which spectrophotometric reflectance patterns of real leaves were mimicked with mixtures of artists' pigments, leaf color was shown to be a character used by cabbage root flies, before landing on leaves, to discriminate among the host plant cultivars radish, green cabbage, and red cabbage. It may be possible to take advantage of factors that affect leaf color, such as epicuticular bloom, pubescence, and masking of chlorophyll by other pigments, to decrease the attraction of certain pest insects to plants.*

Compared with the substantial progress that has been made in identifying specific sexual attractants of herbivorous insects, little progress has been made in identification of specific attractive chemical or visual components of plants (1, 2). Several reports suggest, but do not directly prove, that certain insect herbivores are able to discriminate among plant species or cultivars partly on the basis of one or more leaf color attributes (hue, saturation, or intensity) (3–8). Direct proof is lacking because no studies have been done of herbivore response to artificial leaves having spectral reflectance properties equivalent to those of real leaves. By analogy, direct proof of insect response to chemical stimuli from host plants may be lacking because of failure to identify and synthesize the chemical stimuli.

The host range of the cabbage root fly *Delia radicum* includes more than 40 species of wild and cultivated Cruciferae of diverse morphologies (9). Although

plant odor attracts gravid females to patches of host plants (10), visual as well as olfactory stimuli determine whether insects will land on individual plants (11). We coated leaf-shaped pieces of cardboard with mixtures of artists' pigments (12) to mimic spectrophotometrically the reflectance patterns of real leaves. Our results provide strong evidence that leaf color is a character used by cabbage root flies, before landing, to discriminate among three types of host plants—radish, green cabbage, and red cabbage. We suggest that foliage bearing epicuticular bloom (such as green and red cabbage) or red-colored foliage may be less detectable by (or less attractive to) certain insect herbivores than green foliage.

All but one of our tests were conducted in a cage (125 by 125 by 100 cm tall), constructed of white Terylene netting, in a greenhouse illuminated solely by skylight. Single real leaves or oval-shaped artificially pigmented leaves, approxi-

mately 64 cm², were placed, adaxial surface up at an angle of 45°, into black plastic pots (8 by 8 cm) filled with soil. If the real leaves were smaller than 64 cm², two or more were attached with double-sided tape to a 64-cm² clear cellulose acetate leaf to give the appearance of a single large leaf. Testing was completed within 2½ hours of removal of real leaves from plants. Colors for the artificial leaves were produced by mixing oil pigments (13). Reflectance from 350 to 650 nm (the visible spectrum of the insect) was measured against a MgO standard with a spectrophotometer (Pye-Unicam ST 1800). For testing, leaf-containing pots were placed 25 cm apart on the soil-covered floor of the cage, which contained 150 to 300 gravid laboratory-cultured females (14), 5 to 7 days old when introduced, that had been reared under diapause conditions. We counted each female that landed on a leaf and removed her immediately from further testing.

More females landed on real leaves of mature radish plants (*Raphanus sativus* cv. Cherry Belle) than on real leaves of mature green cabbage plants (*Brassica oleracea* var. *capitata* cv. Avon Coronet), which had a distinct layer of epicuticular bloom. The latter received more landings than real leaves of mature red cabbage plants (*B. oleracea* var. *capitata* cv. Mammoth Red Rock), which likewise had distinct bloom, or than clear cellulose acetate leaves (experiment 1 in Table 1). Landings on the artificial mimics of radish, green cabbage, and red cabbage leaves of mature plants were similar in proportion to those on real leaves (experiment 2 in Table 1). Spectral reflectance curves of the artificial leaves closely approximated those of their real-leaf counterparts (Fig. 1A) (15). The curves reveal a distinct peak of reflectance from radish leaves at 500 to 600 nm. In contrast, although there was a slight peak of reflectance at 500 to 600 nm from green cabbage leaves, this was coupled with more intense reflectance than that from radish at all wavelengths from 350 to 650 nm. There was no reflectance peak at 500 to 600 nm from red cabbage leaves. In two-choice tests (eight replicates per treatment), direct comparison of landings on mature real versus artificial leaves, respectively, showed the following: radish (41 versus 39), green cabbage (27 versus 26), red cabbage (18 versus 21).

Confirmation that females discriminated among leaves of mature host plants on the basis of color was obtained in a test conducted in a large field cage (6 by 6 by 2 m tall) in which sticky (coated with

Tangletrap), artificially pigmented, four-leaved plants of identical size and shape were positioned 140 cm apart on soil. Released wild females showed the same preference for landing on artificial radish plants as opposed to artificial green cabbage plants, and for the latter as opposed to artificial red cabbage plants, as was shown in tests of real leaves in the greenhouse cage (experiment 3 in Table 1).

Because of difficulties in producing an artificial mimic of each leaf type we wished to test, and because we could not detect any effect of host plant odor on female choice (before landing) among leaves spaced 25 cm apart in the test cage, we used only real leaves in all other tests. Landings on radish, green cabbage, and red cabbage leaves taken from plants of intermediate age showed a distribution similar to that of landings on leaves taken from mature plants (experiment 4 in Table 1). Spectral reflectance curves from leaves of corresponding cultivars of intermediate and mature plants were also similar (Fig. 1B). In contrast, leaves from young (transplant stage) plants of these three cultivars had little apparent bloom and showed a distinct reflectance peak at 500 to 600 nm, with reflectance at peak intensity (~550 nm) being greatest for radish and least for red cabbage (Fig. 1B). With young leaves, females showed much less preference for radish over green and red cabbage than they showed for leaves from intermediate or mature plants (experiment 5 in Table 1). The preference for the radish among leaves from young plants is best explained by the higher intensity of the reflectance from radish at 550 nm (2, 12).

The number of flies landing on leaves of mature green cabbage gently rubbed with a cloth to remove or reorient wax particles (16) was similar to the number of flies landing on rubbed leaves of mature radish; fewer flies landed on rubbed leaves of mature red cabbage (experiment 6 in Table 1). Reflectance curves (not shown) of the rubbed radish and green cabbage leaves were almost identical to those of unrubbed leaves of mature radish plants, whereas the curve for rubbed red cabbage paralleled that of comparable unrubbed red cabbage leaves but at a much lower intensity. Females preferred leaves of mature radish plants to unrubbed leaves of mature *Euphorbia wolffensii* and onion (*Allium cepa* cv. Prospero) plants (experiment 7a in Table 1). When the epicuticular bloom on the latter two species was rubbed, there was an increase in comparative attractiveness (experiment 7b in Table 1) (17). Finally, females preferred leaves of

mature radish plants to mature leaves of *Rhus cotinus* (purple form) and copper beech (*Fagus sylvatica atropurpurea*) and to the youngest leaves of *Rosa* sp. (hybrid tea rose) (experiment 8 in Table 1). The leaves of these three plants were

red and did not exhibit a reflectance peak at 500 to 600 nm (Fig. 1C).

Together, our findings demonstrate that, before landing, *D. radicum* females are capable of discriminating visually among radish, green cabbage, and red

Table 1. Landing of cabbage root flies on real or artificial leaves of different colors. Landing on leaves is expressed as the ratio of flies landing on the designated type of leaf to those landing on the type receiving the most visits, which is assigned the value 100 percent. The least significant difference (L.S.D.) was obtained from the means of the actual numbers of landings. Significantly different values ($P < .05$; L.S.D. test) are designated by different superscript letters. For the greenhouse cage tests, values are the means of eight replicates per treatment (four in each of two 2-hour test periods).

| Experi- ment | Leaves | No. of flies | Landing on leaves | | | | L.S.D. |
|-----------------|-------------------------|--------------------|-----------------------------------|-------------------------------------|----------------------------------|---------------------------------|--------|
| | | | Radish | Green cabbage | Red cabbage | Clear | |
| 1 | Real, mature | 142 | 100 ^a | 28 ^b | 12 ^c | 14 ^c | 1.70 |
| 2 | Artificial | 182 | 100 ^a | 29 ^b | 20 ^b | 16 ^b | 1.02 |
| 3* | Artificial | 134 | 100 ^a | 27 ^b | 6 ^c | 18 ^{b,c} | 1.81 |
| 4 | Real, inter- mediate | 129 | 100 ^a | 27 ^b | 6 ^c | 17 ^{b,c} | 1.40 |
| 5 | Real, young | 103 | 100 ^a | 80 ^a | 54 ^b | 17 ^c | 1.07 |
| 6 | Real, mature, rubbed | 102 | 100 ^a | 104 ^a | 7 ^b | 16 ^b | 1.76 |
| | | | | | | | |
| 7a | Real, mature | 132 | <i>Radish</i> 100 ^a | <i>Euphorbia</i> 32 ^b | <i>Allium</i> 31 ^b | | 2.05 |
| 7b | Real, mature, rubbed | 127 | 100 ^a | 77 ^b | 67 ^b | | 1.33 |
| | | | | | | | |
| 8 | Real | 112 | <i>Radish</i> 100 ^a | <i>Rhus</i> 21 ^b | <i>Rosa</i> 20 ^b | <i>Fagus</i> 17 ^b | 1.85 |

*Field cage test with wild females (six replicates per treatment over the 3-day test period).

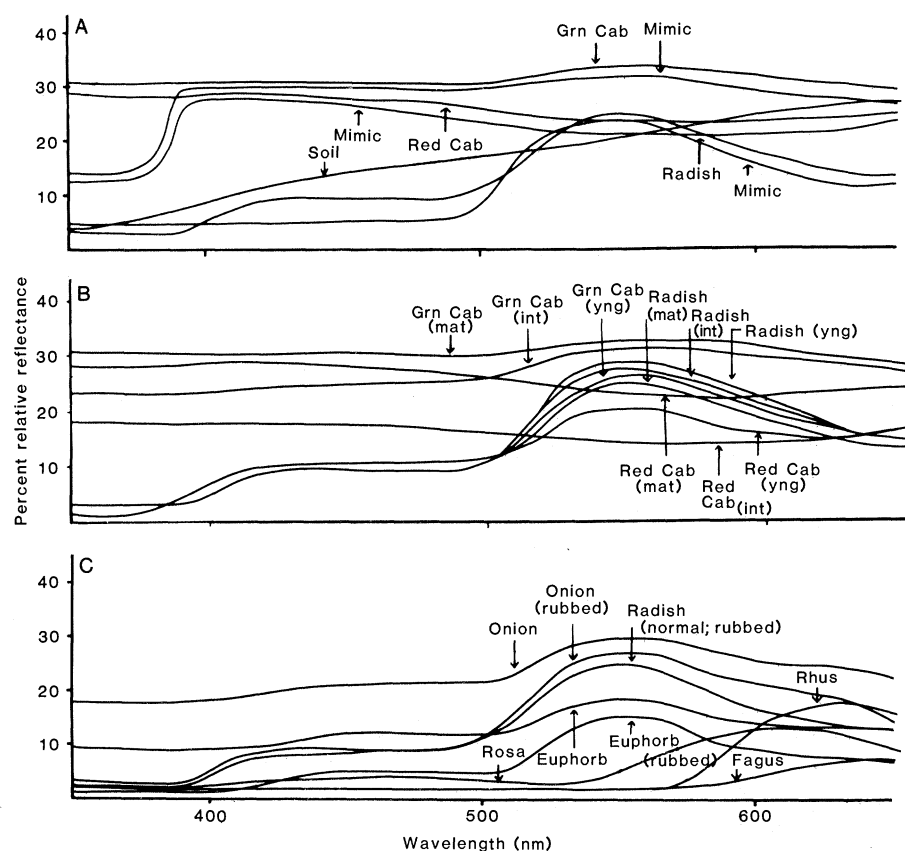


Fig. 1. (A to C) Spectral reflectance curves of real leaves or (A only) artificial mimics of real leaves. Abbreviations: Grn, green; Cab, cabbage; Euphorb, *Euphorbia*; mat, int, and yng, leaves from mature, intermediate, and young plants, respectively; rubbed, leaf rubbed to remove or reorient epicuticular wax particles.

cabbage host plants on the basis of leaf color. The ability of the flies to distinguish colors was improved in intermediate-aged and mature plants as compared with young plants. The degree to which leaf color differences, in concert with host olfactory stimuli, might influence female landings in large homogeneous agricultural patches of these three cultivars remains to be determined.

Our findings together with those of other workers (5–8) lead us to suggest that with some exceptions (3, 7) leaves of cultivated or naturally growing plants that appear whitish to the human eye, owing to buildup of epicuticular bloom (16, 18) or pubescence (19), or that are reddish, owing to masking or replacement of chlorophyll by other pigments, may be less detectable by (or less attractive to) certain insect herbivores than are green leaves. Although the presence of bloom produces an increase in overall intensity of leaf reflectance, it acts to desaturate chlorophyll reflectance and thereby to decrease the distinctiveness of peak green leaf reflectance at 500 to 600 nm and to decrease the magnitude of the difference between total insect-detectable energy reflected above 500 nm and that reflected below 500 nm (2, 5). In red-colored leaves, the masking or replacement of chlorophyll results in the absence of a reflectance peak at 500 to 600 nm.

In certain cases, buildup of epicuticular bloom could have evolved in response to strong selection pressure from a damaging insect herbivore. It is much more likely, however, that in most cases such buildup evolved in response to abiotic environmental factors or microorganisms (16, 18), with insects then obliged to "track" this character (20). Alternatively, insect herbivory may have contributed to the evolution of nonsenescent red-colored leaves in various plant species in which flushes of new growth are sometimes red.

Several crop cultivars with bloomed or red leaves are less preferred for landing or oviposition by certain insect species than are their green-leaved counterparts (5–8, 18, 21). We believe that, provided plant yield and quality can be maintained, leaf color characteristics merit further investigation by entomologists involved in plant breeding to determine whether it is possible to reduce the attraction of certain insect pests to plants.

RONALD J. PROKOPY*

ROSEMARY H. COLLIER

STANLEY FINCH

National Vegetable Research Station,
Wellesbourne, CV35 9EF, England

References and Notes

1. S. Finch, in *Applied Biology*, T. H. Coaker, Ed. (Academic Press, London, 1980), p. 67; J. R. Miller and K. L. Strickler, in *Chemical Ecology of Insects*, W. J. Bell and R. T. Cardé, Eds. (Chapman and Hall, London, in press).
2. R. J. Prokopy and E. D. Owens, *Annu. Rev. Entomol.* **28**, 337 (1983).
3. V. Moericke, *Z. Angew. Entomol.* **37**, 29 (1955); *Entomol. Exp. Appl.* **12**, 524 (1969).
4. L. Somme and T. Rygg, *Nor. Entomol. Tidsskr.* **19**, 19 (1972); J. R. Meyer, *Ann. Entomol. Soc. Am.* **68**, 1 (1975); S. M. Vaishampayan *et al.*, *Entomol. Exp. Appl.* **18**, 412 (1975).
5. J. S. Kennedy, C. O. Booth, W. J. S. Kershaw, *Ann. Appl. Biol.* **49**, 1 (1961).
6. H. J. Müller, *Entomol. Exp. Appl.* **7**, 85 (1964).
7. M. J. Way and G. Murdie, *Proc. Assoc. Appl. Biol.* **56**, 326 (1965).
8. F. G. Maxwell, *Bull. Entomol. Soc. Am.* **23**, 199 (1977).
9. S. Finch and C. M. Ackley, *Ann. Appl. Biol.* **85**, 13 (1977).
10. S. Finch, *Entomol. Exp. Appl.* **24**, 150 (1978); C. Hawkes, S. Patton, T. H. Coaker, *ibid.*, p. 219.
11. R. J. Prokopy, R. H. Collier, S. Finch, *ibid.*, in press.
12. E. D. Owens, thesis, University of Massachusetts, Amherst (1982).
13. Oil pigments (Winsor and Newton, London) were mixed in the following proportions by weight: radish (83 percent cadmium yellow 222, 12 percent Winsor green 170, and 5 percent mars black 248); green cabbage (same as radish, but when dry a thin overlay of 95 percent flake white 238 plus 5 percent cobalt blue 203 was added to mimic epicuticular bloom); red cabbage (40 per-

- cent French ultramarine 149, 40 percent flake white 238, 20 percent crimson lake 146, plus a thin overlay of the preceding type).
14. S. Finch and T. H. Coaker, *Bull. Entomol. Res.* **58**, 619 (1969).
15. The only appreciable deviation from close approximation occurred at about 350 to 390 nm, where the overlay of artists' pigments on green and red cabbage leaf mimics failed to reflect as much energy as the real leaf counterparts. This made no detectable difference, however, to the flies' landing rate.
16. J. T. Martin and B. E. Juniper, *The Cuticle of Plants* (Clark, Edinburgh, 1970).
17. Onion odor may have been somewhat repellent at close range, as some females approaching to within 2 cm of onion leaves veered away abruptly without alighting. Such abrupt veering behavior was not observed in female approaches to any other type of leaf tested.
18. T. W. Mulroy, *Oecologia* **38**, 349 (1979).
19. J. Ehleringer, O. Björkman, H. A. Mooney, *Science* **192**, 376 (1976).
20. T. Jermy, *Symp. Biol. Hung.* **16**, 109 (1976).
21. E. B. Radcliff and R. K. Chapman, *J. Econ. Entomol.* **59**, 116 (1966).
22. We thank J. B. Adams and the Campden Food Preservation Research Association of Chipping Campden (Glos) for use of the spectrophotometer, J. S. Kennedy for helpful criticisms, and E. D. Owens and G. F. Hubbell for assistance on pigment mixture preparation. Supported in part by a John Simon Guggenheim Memorial Foundation fellowship to R.J.P.

* Present address: Department of Entomology, University of Massachusetts, Amherst 01003.

30 December 1982; revised 11 April 1983

Antipyretic Potency of Centrally Administered α -Melanocyte Stimulating Hormone

Abstract. Centrally administered α -melanocyte stimulating hormone is much more potent in reducing fever than the widely used antipyretic acetaminophen. This finding supports the hypothesis that the endogenous neuropeptide has a role in the limitation of fever and suggests that it may be clinically useful as an antipyretic.

There is evidence that the neuropeptides adrenocorticotrophic hormone (ACTH)(1-24) and α -melanocyte stimulating hormone (α -MSH)(1-13), which share a 13-amino-acid sequence, can influence centrally mediated processes (1, 2), including central control of body temperature (3–5). Both peptides lower core temperature of afebrile rabbits when given peripherally or centrally in sufficient doses (6–8), and much smaller doses reduce fever without altering normal temperature (6, 7, 9). α -MSH is found in brain regions that govern temperature regulation, including the anterior hypothalamus and the septum (2). The concentration of α -MSH in the septum rises during fever (10), and the concentration in the arcuate nucleus tends to decline at the same time, presumably reflecting axoplasmic transport of α -MSH from its source in cell bodies of the arcuate nucleus to fibers in the septum. Microinjections of α -MSH into the septal region reduce fever (11)—possibly mimicking the result of the natural transport. To evaluate the physiological significance of fever reduction by endogenous α -MSH, it is important to compare the antipyretic

effect of this peptide with that of a well-known antipyretic drug, such as acetaminophen. Since acetaminophen and α -MSH appear to reduce fever through actions in the central nervous system, and since changes in potency can result from peripheral administration, both substances were given centrally in the experiments described here.

Adult New Zealand White rabbits were implanted with cannulas in a lateral cerebral ventricle (6) and restrained in conventional stocks in an environmental chamber at 23°C. A thermistor probe (Yellow Springs No. 701) was inserted 10 cm into the rectum and taped in place. Temperature measurements were made automatically at 10-minute intervals with a MINC 11 computer connected to a Datalogger digital temperature recorder (United Systems). Leukocytic pyrogen (6) was injected intravenously after a 1-hour baseline temperature had been determined. Tests of the antipyretic effect of α -MSH and acetaminophen were performed in two separate experiments on the same animals, with the control response to leukocytic pyrogen being determined for each animal before each