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FOURLINED PLANT BUG (HEMIPTERA: MIRIDAE), A REAPPRAISAL: LIFE HISTORY, HOST PLANTS, AND PLANT RESPONSE TO FEEDING

A. G. Wheeler, Jr. and Gary L. Miller¹

ABSTRACT

Phenology of the fourlined plant bug, *Poecilocapsus lineatus*, is presented for southcentral Pennsylvania; life history and habits are re-examined. Although breeding was previously thought to occur only on woody plants, we found that nymphs develop on numerous herbs. An extensive list of hosts, more than 250 species in 57 families, is compiled from the literature and the authors' observations; preferences are noted for plants in the Labiatae, Solanaceae, and Compositae. Damage consists of lesions on foliage, the size and shape of the spots varying with leaf texture, pubescence, and venation. Plant response to feeding is immediately visible, the lesions seeming to appear simultaneously with insertion of the bug's stylets. Histolysis of plant tissues, the most rapid response to mirid feeding yet reported, is attributed to a potent lipid enzyme whose active constituents are under investigation.

The fourlined plant bug, *Poecilocapsus lineatus* (Fabricius), is not only one of the most easily recognized members of the taxonomically difficult family Miridae, but one of the first mirids observed to damage plants. *Lygus lineolaris* (Palisot de Beauvois), the familiar tarnished plant bug, was the first North American mirid to attract attention of economic workers (Harris 1841); the second species appears to have been *P. lineatus*. In a little-known note, Harris (1851) identified this mirid (as *Capsus quadrivittatus*) for a correspondent who feared that the unfamiliar insect injuring foliage of burdock might well become a crop pest. Indeed, within a few years there were reports of severe injury to currants (Walsh and Riley 1869, Le Baron 1871) and to dahlias and weigela (Fitch 1870). In 1892 *P. lineatus* was found in "alarming numbers" on currants and gooseberries at Ithaca, New York, bushes in the horticultural gardens at Cornell University appearing "as though a fire had swept quickly through and killed the terminal leaves." This severe damage prompted M. V. Slingerland to investigate the life history. In what was to become a model study in the emerging field of economic entomology, Slingerland (1893) dispelled some of the "unfortunate guesses of earlier entomologists," namely that two annual generations are produced with the adults hibernating in protected areas (Fitch 1870, Le Baron 1871). Slingerland showed that the fourlined plant bug overwinters as eggs inserted in woody tissue of currant and gooseberry and suggested that this univoltine pest can be alleviated by pruning and burning tips of infested plants during the dormant season.

Slingerland's bulletin, typical of his nearly monographic treatments of insect life histories (Comstock 1909), remains the principal biological study of *lineatus*. Subsequent workers merely have added to the list of host plants and refined techniques of chemical control. In this paper we re-evaluate the habits of fourlined plant bug and correct several misconceptions perpetuated in the literature. We report on the life history of *lineatus* in southcentral

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Pennsylvania, noting that nymphs develop not only on woody plants but on numerous herbs; compile from the literature and our observations a list of plants injured by *lineatus* and analyze the host spectrum; and describe for the first time the unique and immediate damage inflicted to host foliage, speculating that some lipid enzyme is responsible for the remarkably rapid breakdown of plant tissues.

METHODS

Our phenological data are based on collections made at 7- to 10-day intervals at Harrisburg, southcentral Pennsylvania, during April and May 1973–1974 and irregular sampling in other areas of the state during 1973–1976. We also collected weekly at Harrisburg during June and July 1980. We accumulated host records in a number of Pennsylvania garden centers and nurseries and in herb gardens at the Morris Arboretum, Philadelphia, and Cornell University, Ithaca, New York. We also reviewed the literature for published host records and obtained several unpublished hosts from Slingerland's experiment file, Department of Entomology, Cornell University.

SEASONAL HISTORY

Overwintered eggs began to hatch in mid- to late April. Instars II–III were found in early May, stages III–IV by mid-May, and the first adults by late May (24 May is the earliest record). Fifth instars, however, may be found until about 10 June. Mating and oviposition take place during June, and by early July most of the males have died. Our latest records of this univoltine species in the Harrisburg area are two females taken 19 and 21 July.

Development of populations in northern Pennsylvania occurred 1–3 weeks later, oviposition having been observed as late as 23 July. Slingerland (1893), who did not record egg hatch until late May at Ithaca, New York, apparently did not appreciate how variation in latitude can affect development of insect populations. Puzzled by Webster's (1887) collection of adults at Lafayette, Indiana, on 22 May, he challenged the validity of that record. Webster was quick to inform Slingerland that Ithaca was "fully two degrees of latitude north of Lafayette" and that the earlier appearance of adults in Indiana had "not in the least transgressed the laws of nature."² Webster's letter prompted Slingerland (1894) to acknowledge that it was possible for Indiana populations of *lineatus* to develop 2–3 weeks earlier than those in New York. In fairness to Slingerland, we should point out that the "bioclimatic law" relating to biological events at different latitudes, longitudes, and altitudes, although generally recognized, had not yet been fully developed (Hopkins 1919).

HOST PLANTS

Our field studies, coupled with numerous notes scattered throughout entomological literature, allow compilation of an impressive list of hosts, or at least plants injured by *P. lineatus* (Table 1). This almost bewilderingly complex list might suggest that the fourlined plant bug is an indiscriminate feeder; certainly the list of some 250 species in 57 families rivals one that could be compiled for the ubiquitous tarnished plant bug, *L. lineolaris*. This is not to say that *P. lineatus* shows no preference for certain plant families or feeds, even as adults, on all common weeds. Monocots are rarely attacked, and among dicots such common plants as crownvetch (*Coronilla varia* L.), dock³ (*Rumex* spp.), goldenrod (*Solidago* spp.), ragweed

²Letter dated 20 Nov. 1893 from F. M. Webster to M. V. Slingerland.

³Although Harris (1851) recorded "yellow dock" (*R. crispus*) as an important host and Knight (1928) noted injury to "*Rumex*," we wonder whether the plant may have been burdock (*Arctium minus*) which, at least during our observations, was a much more common host.

(*Ambrosia* spp.), violet (*Viola* sp.), and wood sorrel (*Oxalis* spp.) are usually avoided, even when growing in colonies of plants harboring large numbers of the bug. *P. lineatus* does, however, feed on certain plants that are regarded as relatively free of insect injury, e.g., tree of heaven (*Ailanthus altissima*).

Certain patterns emerge if the host list is analyzed and *P. lineatus* populations are observed for more than one season in a number of localities. Consistently attacked are plants of the Labiatae and Solanaceae, and certain composites. Preferred hosts among so-called weed species, both native and naturalized, are bitterweet (*Solanum dulcamara*), bouncingbet (*Saponaria officinalis*), burdock (*Arctium minus*), Canada thistle (*Cirsium arvense*), catnip (*Nepeta cataria*), chicory (*Cichorium intybus*), common dandelion (*Taraxacum officinale*), common mugwort (*Artemisia vulgaris*), common mullein (*Verbascum thapsus*), dame's rocket (*Hesperis matronalis*), evening primrose (*Oenothera biennis*), ground ivy (*Glechoma hederacea*), Japanese honeysuckle (*Lonicera japonica*), and teasel (*Dipsacus sylvestris*). Since populations occur consistently in damp, shaded areas, e.g., on weeds bordering hedgerows and along streams, *P. lineatus* is sometimes regarded as typical of such habitats (Watson 1928). This mirid, though, is almost as likely to be found in old fields and gardens exposed to full sunlight; in fact, Britton (1930) referred to this pest as "always present in gardens."

The fourlined plant bug severely injures a number of flower and herb garden plants, especially members of the Compositae and Labiatae. Consistently damaged mints include hyssop (*Hyssopus officinalis*), lavender (*Lavandula* spp.), marjoram (*Origanum* spp.), peppermint and spearmint (*Mentha piperita*, *M. spicata*), and sage (*Salvia officinalis*). Among the many composites serving as preferred hosts are ageratum (*Ageratum* sp.); coreopsis (*Coreopsis* spp.); dahlia (*Dahlia* spp.); florists chrysanthemum, feverfew, and Shasta daisy (*Chrysanthemum* spp.); gaillardia (*Gaillardia* spp.); globe thistle (*Echinops ritro*); tansy (*Tanacetum vulgare*); and wormwood (*Artemisia* spp.). In the vegetable garden parsnips have been seriously damaged (Le Baron 1871); cucumbers, lettuce, peas, potatoes, radishes, squash and other vegetables are also attacked (Table 1).

P. lineatus usually is of less importance on ornamental shrubs than on herbs and flowers, or on shade trees where feeding often is restricted to sucker shoots or water sprouts. Only on one occasion (*Catalpa bignonioides*) did we observe nymphs on foliage of larger branches of a mature tree. Damage to shrubs that might warrant control measures is most likely to be found on azalea, deutzia, dogwood, forsythia, viburnum, and weigela (Table 1). Feeding often is confined to leaves of lower branches and water sprouts.

One of Slingerland's (1893) points of emphasis was that nymphs develop only on woody plants. This interpretation of the host range is too restrictive. While it probably is true that not all the species listed in Table 1 serve as breeding hosts of *P. lineatus*, we feel that nymphs will at some time develop on nearly all these plants, including herbs. Not only have we observed nymphs on a number of herb and flower garden plants (chrysanthemums, lavender, peppermint, spearmint, sage) but on many common weeds: bouncingbet, burdock, Canada thistle, catnip, dame's rocket, dandelion, evening primrose, motherwort (*Leonuris cardiaca*), and sweet clover. We also have found eggs inserted in stems of beggar's-lice (*Hackelia virginiana*), cinquefoil (*Potentilla recta*), loosestrife (*Lythrum salicaria*) (Fig. 1), and white campion (*Lychnis alba*).

Finally we note that currants and gooseberries, the plants which stimulated the initial interest in *Poecilopsus* life history and habits, may no longer be preferred hosts. We observed only slight feeding in an experimental planting of *Ribes* being used to screen cultivars for resistance to white pine blister rust. We also did not find *P. lineatus* on native species of *Ribes*. Although the idea that *Ribes* species are no longer preferred hosts is only conjectural, it can be shown that cultivated currants and gooseberries no longer are as available to the mirid as they were in Slingerland's time. The acreage of these small fruits has declined sharply since 1900 (according to statistics of the U.S. Census of Agriculture). *Ribes* spp. serve as alternate hosts of the fungus which causes white pine blister rust, first discovered in North America at Geneva, New York, in 1906. Since that time, large numbers of plants, especially black currants, have been eradicated by the federal government (Anderson 1956).

Table 1. Plants serving as hosts of or damaged by *Poecilocapsus lineatus*.

Host, ^a Locality, and Reference ^b	
	SALICACEAE
<i>Salix nigra</i> Marsh. ^c	NY
	MORACEAE
<i>Cannabis sativa</i> L.	PA
	URTICACEAE
<i>Pilea pumila</i> (L.) Gray.	PA
	<i>Urtica dioica</i> L. PA
	POLYGONACEAE
<i>Rheum rhaponticum</i> L.	NH(USNM), ^d PA(57) PA
	<i>Rumex crispus</i> L. MA (28), NY (34)
	NYCTAGINACEAE
<i>Mirabilis nyctaginea</i> (Michx.) Macmill.	PA
	CARYOPHYLLACEAE
<i>Cerastium viscosum</i> L.	PA
	<i>Lychnis alba</i> Mill. PA
<i>Dianthus caryophyllus</i> L.	MI (39)
	<i>L. sp.</i> NY (26)
<i>D. sp.</i>	CT (7), NY (38)
	<i>Saponaria officinalis</i> L. NY (17), PA, WV
	<i>Silene caroliniana</i> Walt. PA
	CHENOPODIACEAE
<i>Beta vulgaris</i> L.	NY
	<i>Chenopodium album</i> L. PA
	AMARANTHACEAE
<i>Amaranthus sp.</i>	NY (38)
	RANUNCULACEAE
<i>Aconitum sp.</i>	(74)
	<i>Delphinium sp.</i> MA (USNM)
<i>Anemone sp.</i>	NY (26)
	<i>Paeonia sp.</i> CT (6), NY (26), PA
<i>Cimicifuga racemosa</i> (L.) Nutt.	PA
	<i>Ranunculus acris</i> L. MA (40), NY
	GUTTIFERAE
<i>Hypericum perforatum</i> L.	MA (40), NY, PA
	PAPAVERACEAE
<i>Dicentra spectabilis</i> L.	PA
	<i>Papaver sp.</i> NY (26)
	CRUCIFERAE
<i>Alliaria officinalis</i> Andrz.	WV
	<i>Hesperis matronalis</i> L. NY, PA
<i>Armoracia lapathifolia</i> Gilib.	NJ (67), WI (USNM)
	<i>Iberis sp.</i> MI (39), PA
	<i>Lobularia maritima</i> Desv. MI (39)
<i>Barbarea vulgaris</i> L.	NY
	<i>Lunaria rediviva</i> L. MA (40)
<i>Brassica nigra</i> (L.) Koch.	NY
	<i>Raphanus sativus</i> L. NY (38)
<i>B. oleracea</i> L.	NY (46)
	PLATANACEAE
<i>Platanus occidentalis</i> L.	PA
	HAMAMELIDACEAE
<i>Liquidambar styraciflua</i> L. ^c	PA
	SAXIFRAGACEAE
<i>Astilbe sp.</i>	PA
	<i>Philadelphus coronarius</i> L. var. <i>aureus</i>
<i>Deutzia scabra</i> Thunb.	
	Rehd. MA (40)
(= <i>crenata</i> Sieb. & Zucc.)	MA (40), Ont. ^e
<i>D. sp.</i>	OH (71), NY (38), RI (USNM), (24)
	(13), OH (71), Ont. (47), NY (17, 38, 49)
<i>Hydrangea paniculata</i> Sieb.	MA (40), ME (45)
	<i>Saxifraga umbrosa</i> L. NY (38)

Table 1. (Continued)

Host, ^a Locality, and Reference ^b	
ROSACEAE	
<i>Alchemilla vulgaris</i> L. PA	<i>Prunus triloba</i> Lindl. PA
<i>Geum laciniatum</i> Murr. PA	<i>Pyrus communis</i> L. IN (73)
<i>Malus sylvestris</i> Miller ^f PA	<i>Rosa</i> sp. NY (17), WI (1)
<i>Physocarpus opulifolius</i> (L.) Maxim. PA	<i>Rubus</i> sp. NY (35), NY, PA
<i>Potentilla recta</i> L. PA	
LEGUMINOSAE	
<i>Lathyrus odoratus</i> L. NY (38)	<i>Pisum sativum</i> L. NY (38)
<i>Lupinus</i> sp. CT (9), NY (26)	<i>Trifolium agrarium</i> L. PA
<i>Medicago lupulina</i> L. PA	<i>T. hybridum</i> L. PA
<i>M. sativa</i> L. NY (53, 33), PA	<i>T. pratense</i> L. NY, PA
<i>Melilotus alba</i> Desr. NY, PA	<i>T. sp.</i> MA (28), NY (38)
<i>M. officinalis</i> (L.) Lam. NY, PA	<i>Vicia caroliniana</i> Walt. PA
<i>Phaseolus vulgaris</i> L. NY (35)	
GERANIACEAE	
<i>Pelargonium</i> × <i>hortorum</i> L. Bailey. NJ (69), NY (38), PA ^g	<i>P. limoneum</i> Sweet MA (40)
SIMAROUBACEAE	
<i>Ailanthus altissima</i> Swingle. PA	
ANACARDIACEAE	
<i>Rhus radicans</i> L. PA	<i>R. sp.</i> NY (17)
<i>R. typhina</i> Torner PA	
ACERACEAE	
<i>Acer ginnala</i> Maxim. NY (32)	<i>A. japonicum</i> Thunb. MA (40)
BALSAMINACEAE	
<i>Impatiens capensis</i> Meerb. PA	
AQUIFOLIACEAE	
<i>Ilex aquifolium</i> L. PA	
CELASTRACEAE	
<i>Euonymus atropurpureus</i> Jacq. NY (17)	
VITACEAE	
<i>Parthenocissus quinquefolia</i> Planch. NY, PA	<i>Vitis</i> sp. Fr.-Amer. hybrid cv 'Verdelet' PA
MALVACEAE	
<i>Hibiscus syriacus</i> L. MA (40)	<i>H. sp.</i> CT (9), PA
ELAEAGNACEAE	
<i>Elaeagnus umbellata</i> Thunb. PA	
VIOLACEAE	
<i>Viola</i> sp. PA	
CUCURBITACEAE	
<i>Cucumis sativus</i> L. NY (38)	<i>Cucurbita</i> sp. NY (38)
<i>C. sp.</i> , melon SD (64)	
LYTHRACEAE	
<i>Lythrum salicaria</i> L. NY	
ONAGRACEAE	
<i>Circaea quadrisulcata</i> (Maxim.) Franchet & Oenothera biennis L. NJ (15), NY, PA	

Table 1. (Continued)

Host, ^a Locality, and Reference ^b	
Savatier. PA, WV	<i>O. fruticosa</i> L. PA <i>O. sp.</i> CT (5)
CORNACEAE	
<i>Cornus alternifolia</i> L. PA	<i>C. mas</i> L. PA
ARALIACEAE	
<i>Acanthopanax sieboldianus</i> Makino (74)	<i>A. sp.</i> MA (59)
<i>Aralia spinosa</i> L. MA (40), WV	<i>Hedera helix</i> L. NJ (69)
UMBELLIFERAE	
<i>Cryptotaenia canadensis</i> (L.) DC. NY, PA	<i>Pastinaca sativa</i> L. and var. <i>syvestris</i> DC.
<i>Daucus carota</i> L. NY, PA	IL (37), NY, PA
ERICACEAE	
<i>Rhododendron</i> spp., deciduous & evergreen, azaleas. PA	
PRIMULACEAE	
<i>Lysimachia ciliata</i> L. NY	<i>Primula sp.</i> PA
<i>L. clethroides</i> Duby MA (40)	
OLEACEAE	
<i>Forsythia intermedia</i> Zabel PA	<i>F. sp.</i> CT (11), MA (63), NJ (69), NY (62)
LOGANIACEAE	
<i>Buddleia sp.</i> NJ (68), PA	
APOCYNACEAE	
<i>Vinca minor</i> L. MA (61), PA	
ASCLEPIADACEAE	
<i>Asclepias syriaca</i> L. NY	
RUBIACEAE	
<i>Galium boreale</i> L. MA (40)	<i>Gardenia jasminoides</i> Ellis. MI (39)
<i>G. mollugo</i> L. NY, PA	
POLEMONIACEAE	
<i>Phlox paniculata</i> L. PA	<i>P. sp.</i> IN (14)
<i>P. carolina</i> L. (as <i>P. suffruticosa</i>). MA (40)	<i>Polemonium reptans</i> L. MA (40)
CONVOLVULACEAE	
<i>Convolvulus sp.</i> , bindweed PA	<i>Ipomoea sp.</i> NY (38)
BORAGINACEAE	
<i>Borago officinalis</i> L. PA	<i>Heliotropium arborescens</i> L. CT (11), MA (40)
<i>Hackelia virginiana</i> (L.) M. Johnston. PA	<i>Symphytum officinale</i> L. PA
VERBENACEAE	
<i>Aloysia triphylla</i> Britt. NY (26)	<i>V. sp.</i> CT (10), IN (4), NY (49)
<i>Clerodendrum trichotomum</i> Thunb. PA	<i>Vitex negundo</i> L. PA
<i>Verbena hastata</i> L. NY	
LABIATAE	
<i>Ajuga sp.</i> PA	<i>M. rotundifolia</i> Huds. PA
<i>Coleus sp.</i> MI (39), NJ (69)	<i>M. spicata</i> L. CT (6), PA
<i>Glechoma hederacea</i> L. NY, PA	<i>M. sp.</i> MI (64), Ont. (47)
<i>Hyssopus officinalis</i> L. PA	<i>Nepeta cataria</i> L. MI (56), NY, PA, WV
<i>Lavandula latifolia</i> Vill. NY	<i>N. × faassenii</i> Bergmans. NY
<i>L. officinalis</i> Chaix. NY	<i>N. mussinii</i> Spreng. NY, PA

Table 1. (Continued)

Host, ^a Locality, and Reference ^b	
<i>L. sp.</i> NY (26)	<i>Origanum vulgare</i> L. PA
<i>Leonurus cardiaca</i> L. NY, PA	<i>Salvia officinalis</i> L. CT (5), NH (USNM), NY (38), Ont. (19), PA
<i>Melissa officinalis</i> L. NY, PA	<i>Stachys olympica</i> Poir. PA
<i>Mentha citrata</i> Ehrh. PA	<i>Teucrium canadense</i> L. PA
<i>M. piperita</i> L. WV (USNM)	
SOLANACEAE	
<i>Atropa belladonna</i> L. PA (54)	<i>N. tabacum</i> L. Can. (3)
<i>Capsicum frutescens</i> L. CT (11)	<i>Physalis alkekengi</i> L. CT (11), PA
<i>Datura stramonium</i> L. NY	<i>P. subglabrata</i> MacKenzie & Bush PA
<i>Lycium halimifolium</i> Mill. NY, WV	<i>Solanum carolinense</i> L. PA
<i>Lycopersicon esculentum</i> Mill. MA (58)	<i>S. dulcamara</i> L. NY (17), NY, PA
<i>Nicotiana glauca</i> Link & Otto (= <i>affinis</i>). NY (49)	<i>S. tuberosum</i> L. MD (25), ME (44), N.S. (52), NY (16), Ont. (20), PA, WI (USNM)
SCROPHULARIACEAE	
<i>Antirrhinum majus</i> L. NJ (68), NY (17), Ont. (19)	<i>V. thapsus</i> L. NY, PA, WV
<i>Linaria vulgaris</i> J. Hill. Can. (51), NY, PA	<i>V. sp.</i> MI (66), MI (21), NY (26)
<i>Penstemon digitalis</i> Nutt. PA	<i>Veronica chamaedrys</i> L. PA
<i>Scrophularia lanceolata</i> Pursh. PA	<i>V. spicata</i> L. PA
<i>Verbascum blattaria</i> L. PA	<i>V. sp.</i> NY (26), OH (31)
BIGNONIACEAE	
<i>Campsis radicans</i> Seem. OH (31)	<i>C. ovata</i> Don ^c PA
<i>Catalpa bignonioides</i> Walt PA	
PLANTAGINACEAE	
<i>Plantago lanceolata</i> L. PA	<i>P. sp.</i> MA (28), NY (38)
<i>P. rugelii</i> Dcne. NY, PA	
CAPRIFOLIACEAE	
<i>Kolkwitzia amabilis</i> Graebn. PA	<i>V. dilatatum</i> Thunb. PA
<i>Lonicera japonica</i> Thunb. CT (11), NJ (68), PA	<i>V. opulus</i> L. 'Nanum'. PA
<i>L. sp., morrowi</i> Gray or <i>canadensis</i> Bartr. PA	<i>V. plicatum</i> Thunb. 'Tomentosum'. PA
<i>L. tatarica</i> L. PA	<i>V. rhytidophyllum</i> Hemsl. PA
<i>L. sp.</i> MA (59)	<i>V. sargentii</i> Koehne 'Onondaga'. PA
<i>Sambucus canadensis</i> L. PA	<i>V. sp.</i> NY (65)
<i>S. nigra</i> L. var. <i>aurea</i> Sweet. MA ^h	<i>Weigela floribunda</i> Mey. PA
<i>S. sp.</i> OH (31)	<i>W. sp.</i> MD (24), NY (17), OH (71), Ont. (19), RI (60)
<i>Viburnum carlesii</i> Hemsl. PA	
VALERIANACEAE	
<i>Valeriana officinalis</i> L. MA (40), PA	
DIPSACEAE	
<i>Dipsacus sylvestris</i> Huds. NY, PA	<i>Scabiosa</i> sp. NY (26)
CAMPANULACEAE	
<i>Campanula persicifolia</i> L. MA (40)	
COMPOSITAE	
<i>Achillea millefolium</i> L. PA	<i>Erigeron canadensis</i> L. PA
<i>A. sp.</i> CT (9), MA (40)	<i>E. philadelphicus</i> L. NY

Table 1. Plants serving as hosts of or damaged by *Poeciloscopus lineatus*.

Host, ^a Locality, and Reference ^b	
<i>Ageratum</i> sp. CT (7), MI (39), NY (26)	<i>Eupatorium fistulosum</i> Barratt. PA
<i>Ambrosia</i> sp. NY (35)	<i>E. maculatum</i> L. NY
<i>Arctium minus</i> (Hill) Bernh. MA (28), MI (USNM), NY (49), NY, PA (75), PA	<i>E. perfoliatum</i> L. MA (USNM), NY, PA
<i>Artemisia absinthium</i> L. PA	<i>Gaillardia</i> sp. CT (10), Ont. ^e , PA
<i>A. pontica</i> L. PA	<i>Helenium</i> sp. NY (26)
<i>A. schmidtiana</i> Maxim. PA	<i>Helianthus tuberosus</i> L. NY, PA
<i>A. vulgaris</i> L. PA	<i>H. sp.</i> CT (9), NY (70)
<i>A. sp.</i> NY (26), WI (USNM)	<i>Heliopsis</i> sp. (74)
<i>Aster</i> sp. CT (11), MI (39), Ont. (22)	<i>Hieracium pratense</i> Tausch. NY
<i>Bidens</i> sp. NY (35), PA	<i>Lactuca sativa</i> L. NY (38), PA
<i>Carduus nutans</i> L. SD (43)	<i>L. scariola</i> L. NY
<i>Centaurea cyanus</i> L. NY (26), WV	<i>Liatris spicata</i> Willd. PA
<i>Chrysanthemum leucanthemum</i> L. NY, PA	<i>Prenanthes alba</i> L. NY
<i>C. maximum</i> Ramond. NY (26), PA	<i>Rudbeckia hirta</i> L. Ont. ^e , PA
<i>C. morifolium</i> Ramat. PA	<i>R. laciniata</i> L. NY (26)
<i>C. parthenium</i> Pers. MI (39), PA	<i>Senecio vulgaris</i> L. PA
<i>C. spp.</i> CT (6), DC (USNM), OH (41), NY (38), Ont. (48)	<i>Solidago graminifolia</i> (L.) Salisb. NY
<i>Cichorium intybus</i> L. NY, PA, WV	<i>S. sp.</i> PA
<i>Cirsium arvense</i> (L.) Scop. NY (49), NY, PA	<i>Tanacetum vulgare</i> L. MA (40), NY (17), WI (USNM)
<i>Coreopsis</i> sp. CT (9), NY (26), Ont. (48)	<i>Taraxacum officinale</i> Weber. NY (49), NY, PA
<i>Dahlia pinnata</i> Cav. NY (17), Ont. (19), PA	<i>Tussilago farfara</i> L. NY, PA
<i>Echinops ritro</i> L. PA	<i>Verbesina alternifolia</i> (L.) Britton ex Kearney WV
	<i>Zinnia</i> sp. MA (61), Ont. (23)
	LILIACEAE
<i>Hemerocallis</i> sp. NY (38)	<i>Hosta undulata</i> Bailey PA
	IRIDACEAE
<i>Gladiolus</i> sp. NJ (69)	

^aFor commonly recorded hosts such as currants and gooseberries, generally only the older references are cited for a particular state.

^bPlants followed only by a state abbreviation are those on which we have observed nymphs or damage.

^cFeeding limited to sucker shoots or water sprouts.

^dU.S. National Museum of Natural History collection.

^eLetter dated 23 Nov. 1893 from D. W. Beadle, Toronto, Ont., to M. V. Slingerland.

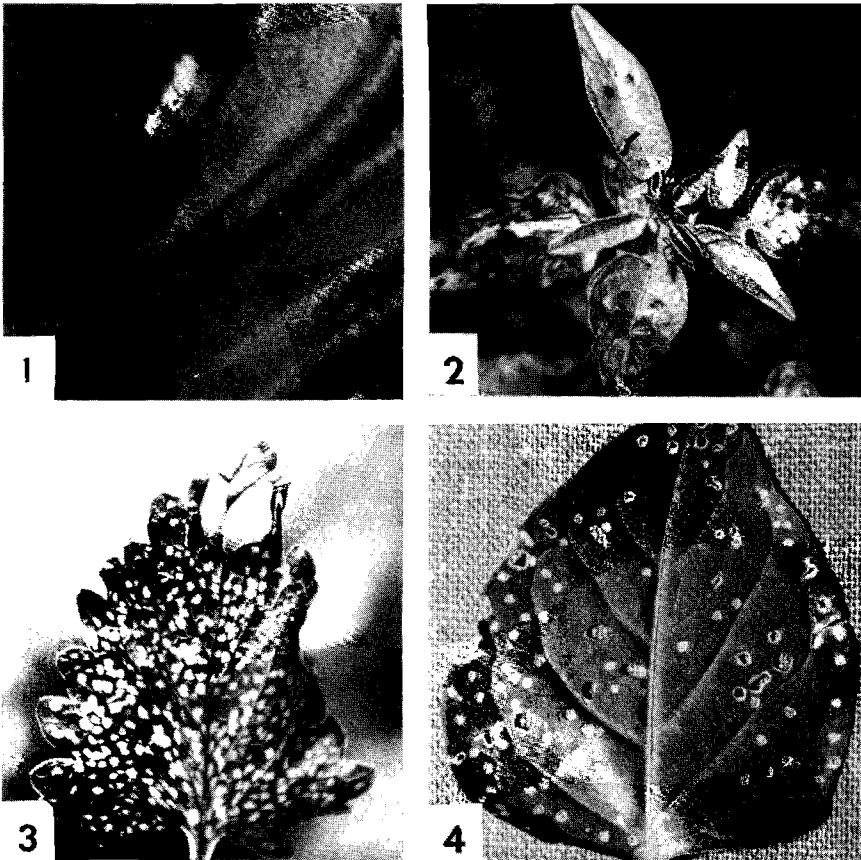
^fDamage to grafts of first season; letter dated 1 Dec. 1893 from Theodore Day, Dyberry (Wayne Co.), Pa., to M. V. Slingerland.

^gIn greenhouse.

^hLetter dated 15 Dec. 1893 from W. H. Manning, Brookline, MA, to M. V. Slingerland.

FEEDING PROCESS AND PLANT RESPONSE

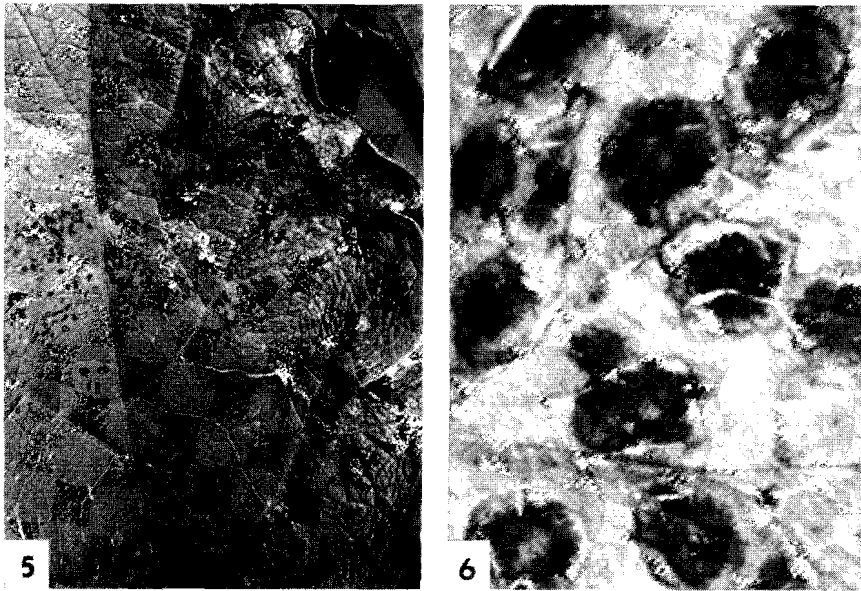
Symptoms of feeding by fourlined plant bug are well known, Slingerland (1893) having noted "minute semi-transparent darkish spots" on new growth of currant. Others described injury in terms of round, depressed, water-soaked lesions. This description of damage is in many cases accurate, but the visible effects of feeding take on different forms depending on leaf shape, texture, pubescence, and venation. On leaves of bittersweet (Fig. 2) and for-



Figs. 1-4. *Poecilocapsus lineatus*. (1) Eggs inserted in stem of *Lythrum salicaria*; deposited flush with the stem surface, eggs are pushed out with growth of plant. (2) Adults and injury on *Solanum dulcamara*. (3) Transparent feeding areas on *Nepeta cataria*. (4) Holes in leaf of *S. dulcamara*.

sythia which are relatively broad, thin, and smooth, feeding by *P. lineatus* produces discrete, nearly round spots. Injured areas may become transparent (Fig. 3), and after several weeks, dead tissue may drop from feeding sites, leaving tiny holes (Fig. 4). Such damaged leaves of bittersweet and other plants (particularly Solanaceae) harboring populations of alticine chrysomelids appear as though fed on by flea beetles. Feeding on red clover leaves produces irregular rather than roundish spots, the feeding sites soon turning blackish and conforming to the pattern of venation. Burdock leaves show a reticulate pattern of tiny, irregular spots (Fig. 5). On strongly pubescent foliage even heavy plant bug feeding causes little visible injury. For example, on common mullein (*V. thapsus*) the dense wool on the thick leaves nearly obscures feeding damage, while on moth mullein (*V. blattaria*) the thinner, glabrous leaves show more typical symptoms. Feeding may cause severe withering of the tips, or even entire leaves, on plants having linear or dissected foliage (*Artemisia*, *Daucus*, *Dianthus*, *Galium*).

It is the physiological basis of feeding rather than external symptoms that offers a challenging area for further study. Although there exist numerous accounts of the damage



Figs. 5-6. *Poecilcapsus lineatus* injury. (5) Reticulate pattern on leaf of *Arctium minus*. (6) Circular lesions (ca. 2 mm diam.) appearing immediately after penetration of stylets.

inflicted by the fourlined plant bug, reports are vague concerning the length of time required for expression of symptoms. Indeed, it is implied in most descriptions of damage that a time lag occurs between initial penetration of the stylets and the appearance of local lesions. Lintner (1882) mentioned that semitransparent spots became evident within one or two days after extraction of parenchyma, and Slingerland (1893) noted that after *P. lineatus* withdraws "interior pulp" from leaf tissue, the layers soon collapse.

Plant response to feeding by *P. lineatus*, however, is immediate. As soon as the stylets touch the leaf surface, a violent clearing of tissues begins at the point of penetration and radiates to form a roughly circular spot of almost 2 mm diameter (Fig. 6). Formation of the lesion is most readily apparent on thin, glabrous leaves and takes place so rapidly (< 1 sec.) that it gives the appearance of being instantaneous. The bug then begins to feed without removing its stylets from the leaf, and fluids can be seen being taken up from the lesion.

Lygus bugs and related mirids of the subfamily Mirinae (to which *P. lineatus* belongs) are known to feed by the lacerate-flush method (Miles 1972), penetrating both intra- and inter-cellular spaces (Flemion et al. 1954). They induce various phytotoxemias as a result of stylet penetration and withdrawal, coupled with injection of enzymatic and non-enzymatic salivary secretions (see Tingey and Pillemer [1977] for a review of pertinent literature). In intensive studies on the feeding habits of *Lygus disponsi* Linnavuori, Hori (1971) found that external evidence of leaf feeding did not appear for several hours. More rapid response to mirid feeding has been described for the bryocorine mirid *Helopeltis bergrothi* Reuter, which within an hour of stylet penetration produces well-defined, water-soaked areas on stems of tea (Leach and Smee 1933). The cacao capsid (mirid) *Sahlbergella singularis* Haglund, another bryocorine, causes lesions to develop while feeding is still taking place (Carter 1973).

To our knowledge, however, no mirid except *P. lineatus* has been shown to induce an immediate histolysis of plant tissues. It seems probable that this mirid injects a potent lipid enzyme which causes a violent breakdown of plant substances. In future biochemical

studies an attempt will be made to determine the biologically active constituents in the salivary secretions of *P. lineatus*.

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