Journal of Chemical Ecology, Vol. 15, No. 4, 1989

ALLELOPATHY, CHEMICAL COMMUNICATION, AND PLANT DEFENSE

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(Received March 1, 1988; accepted May 23, 1988)

Abstract—Allelopathy is identified particularly with chemical activity between plants; entomologists refer to allelochemicals in a broader context. Recent work shows that several groups of compounds associated with allelopathy also play a part in communication between plants and other organisms. It is argued that such communication is part of the similarities in plant and animal responses to stress and may contribute to plant defense.

Key Words—Allelopathy, allelochemicals, mitochondria, phagocytosis.

INTRODUCTION

Chemicals are frequently employed in the defense systems of animals, even when physical defenses are well developed (Cogger, 1979). Plants also have physical adaptations for defense and produce a wide spectrum of secondary chemical compounds (Levin, 1976), some of which are active in allelopathy. Several compounds associated primarily with allelopathy, defined as biochemical interactions between plants (including microorganisms traditionally placed in the plant kingdom), appear to have a wider role in plant self-defense (Lovett, 1982a).

Reese (1979) uses the term ''allelochemical'' to describe ''nonnutritional chemicals produced by one organism that affect the growth, health, behavior or population biology of other species''. Biological reaction to such compounds characteristically is one of attraction or stimulation at low concentrations, with the response becoming increasingly one of repellence or inhibition as the concentration increases. The phenomenon of "hormoligosis" (Luckey, 1968), in which toxic insecticides at very low concentrations act as growth stimulants, is analogous.

Plants respond in this manner to many organic and some inorganic chemicals, for example, aluminium (Bennet et al., 1987). Chemicals developed for management of other organisms, for example, insecticides (Chapman and Allen, 1948), will sometimes elicit this type of response in plants.

Monoterpenoids are one group of natural compounds for which such responses have been documented in a range of organisms. Examples include insect larvae (Selander et al., 1974); bacteria and a yeast (Andrews et al., 1980); feeding behavior of mammals (Sheehy and Winward, 1981; Welch and McArthur, 1981; White et al., 1982); and fungal growth (Franich et al., 1982). Similar compounds are allelopathic (Muller, 1966).

Allelochemicals may, therefore, be considered as part of a network of communication in which disparate organisms give similar responses to similar compounds or families of compounds. Plants producing biologically active compounds at relatively high concentrations may be perceived as utilizing chemical defenses.

Plant allelochemicals frequently induce stress in other plants. Such stress may contribute to interference between plants; again, a dimension of defense. We report here on observations of responses to allelopathic stress in some plant species and identify further similarities with responses of other organisms to allelochemicals.

METHODS AND MATERIALS

Linum usitatissimum L. (linseed) seedlings were grown in bioassay (Lovett and Duffield, 1981) over a dilution series of the allelochemical benzylamine, produced in leaf washings of the cruciferous weed *Camelina sativa* L. Crantz (Camelina) (Lovett and Duffield, 1981), with sterile water as the control. Seedlings of *Sinapis alba* L. (white mustard) were grown under similar conditions and exposed to a dilution series of the allelochemicals gramine and hordenine, produced by *Hordeum vulgare* L. (barley) (Overland, 1966). Radicle length of all seedlings was measured after five days of incubation at 24°C in the dark.

The methods of Jones and Varner (1967) and Reeve and Crozier (1975) were used to assess the release and activity of α-amylase in barley, as described by Lovett and Potts (1987).

Thin sections of linseed and white mustard root tips for electron microscopic examination were prepared using a modification of the technique of Lorber and Muller (1976) as described by Levitt et al. (1984).

RESULTS AND DISCUSSION

Radicle length of seedlings of *Linum usitatissimum* L. (linseed) showed the characteristic response to the allelochemical benzylamine (Figure 1). *Sinapis alba* L. (white mustard) showed a similar response to the alkaloids gramine and hordenine produced by *Hordeum vulgare* L. (barley) during germination (Figures 2 and 3).

These responses may be termed secondary effects (sensu Winter, 1961) as they reflect primary metabolic disruptions. Interference with the ability of germinating seedlings of linseed (Lovett, 1982b) and *Helianthus annuus* L. (sunflower) (Levitt et al., 1984) to use food reserves has been suggested as an example of such disruption. Reese (personal communication) notes that inhibition of efficiency in converting ingested food is a response of insects to ingested allelochemicals. An example is the response of premature weevils to α-terpineol (Figure 4). In these data of Selander et al. (1974) we note that it is the juvenile form that, like young seedlings, may be most susceptible to biologically active chemicals.

Impaired enzyme activity, identified by Rice (1984) as one primary target for allelopathic activity, may explain a reduced ability to metabolize food reserves such as starch in plants. Recent data indicate that the response of α-amylase, involved in the breakdown of starch, to the allelochemical scopolamine (Lovett et al., 1981) is similar to that observed for gross morphological characteristics such as radicle length (Figure 5). Roshchina et al. (1986) reported

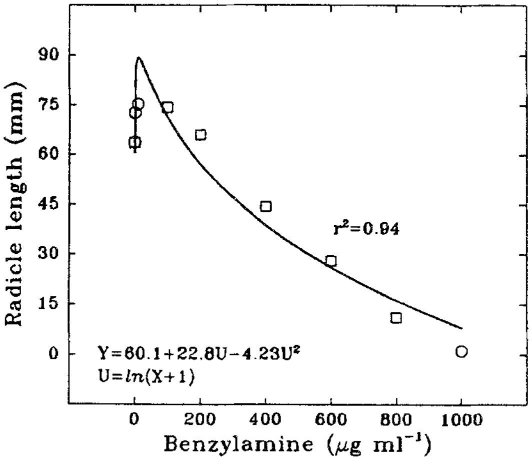

FIG. 1. The response in radicle length of linseed to benzylamine (data from Lovett and Duffield, 1981).

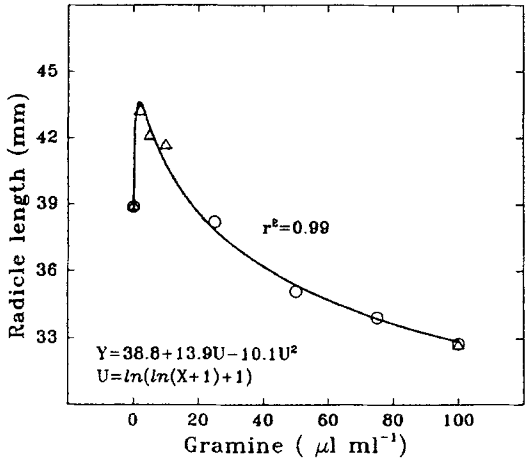

FIG. 2. The response in radicle length of white mustard to gramine (data from Liu and Lovett, 1987).

a similar effect of the alkaloid capsaicine on photosynthetic electron transport in isolated pea chloroplasts. Thus, responses in radicle length or other gross morphological parameters may be explained in terms of similar responses at the level of the cell.

Transmission electron microscopy of linseed and white mustard root tips showed a similar response to allelopathic stress in the root tip cells (Figures 6–

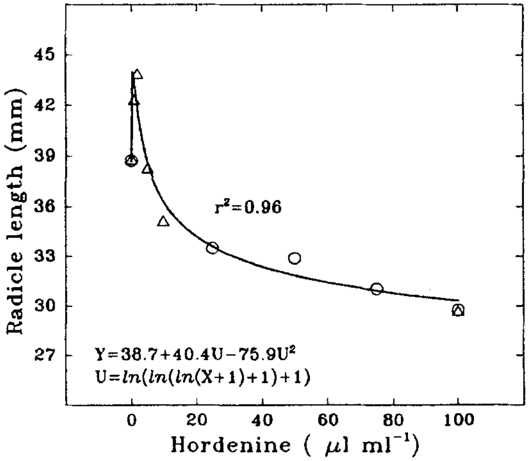

FIG. 3. The response in radicle length of white mustard to hordenine (data from Liu and Lovett, 1987).

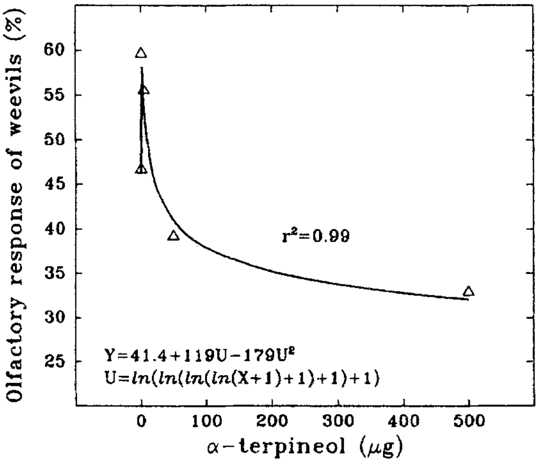

FIG. 4. Olfactory response of weevil larvae to α-terpineol (data from Selander et al., 1974).

8). While control cells showed distinct nuclei, intact organelles, and some small vacuoles (Figures 6 and 8a), increasing concentration of allelochemicals brought about increases in number and size of vacuoles and evidence for phagocytosis (Figures 7 and 8b). Nuclei became less distinct as the concentration of allelochemicals increased and some mitochondria showed evidence of disorganization (Figures 7b–7d and 8b).

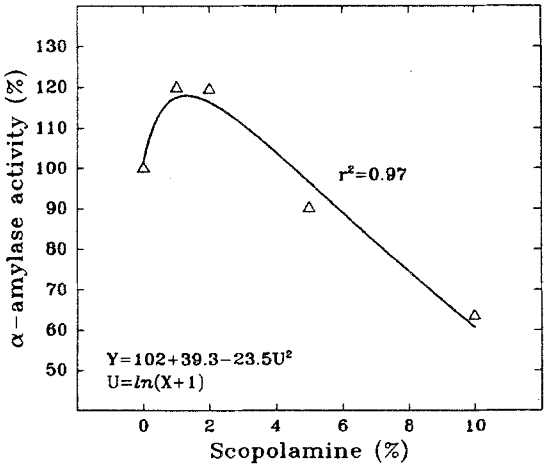

FIG. 5. The response of α-amylase activity to scopolamine.

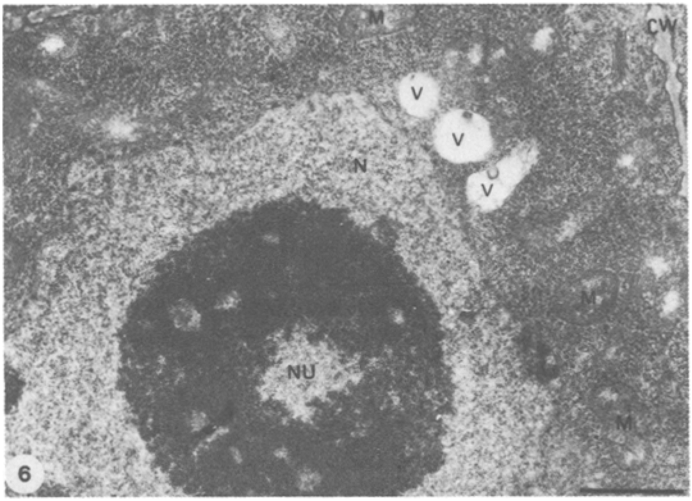

FIG. 6. Linseed root tip, sterile water control. Scale bar = 1 μm. CW = cell wall; V = vacuole; M = mitochondrion; N = nucleus; NU = nucleolus.

Matile (1984) has discussed the detoxification of potentially toxic plant metabolites and highlights the vacuole as a compartment where these toxins may be sequestered. The consistent response of plant root tip cells to allelopathic stress, in which vacuolar development is prominent, shows similarities to those observed in response to other stresses. For example, similar responses occur following invasion by plant parasitic nematodes of root cells of *Apium graveolens* L. (celery) (Bleve-Zacheo et al., 1979) or exposure of *Allium cepa* L. (onion) to heavy metals such as lead (Wierzbicka, 1987). There are close similarities also between the plant vacuoles described here and, for example, autophagic vacuoles in mammals such as the rat (Ahlberg et al., 1982). The limits to which these analogies can be extended is the subject of continuing work in which the roles and relationships of vacuoles, vesicles, endoplasmic reticulum, Golgi apparatus, and mitochondria are being investigated (Lovett et al., 1987; Lovett and Ryuntyu, 1988).

While several metabolic pathways are common to plants and animals, plants differ from animals in important respects, such as lacking a nervous system. We suggest that the evidence presented here points to allelochemicals as important communicators between plants and other organisms. Allelochemicals may attract or repel organisms associated with plants and may contribute to plant

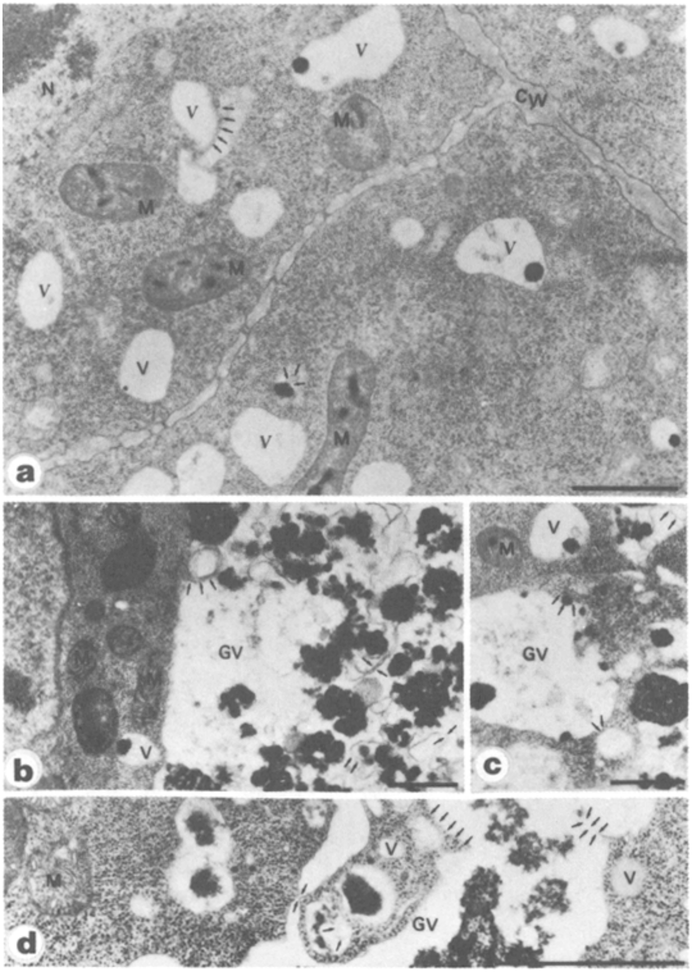

FIG. 7. Linseed root tip, 100 μg/liter benzylamine applied.(a). Linseed root tip, 1000 μg/liter benzylamine applied (b–d). Scale bar = 1 μm. CW = cell wall; V = vacuole; GV = giant vacuole; M = mitochondrion; N = nucleus; arrows indicate phagocytosis.

defense under stress, a role analogous to that of chemicals produced by animals (Edmunds, 1974).

Matile (1975) has drawn attention to the similarities of some lytic phenomena in plants and animals. Autophagic vacuoles are one example and may also

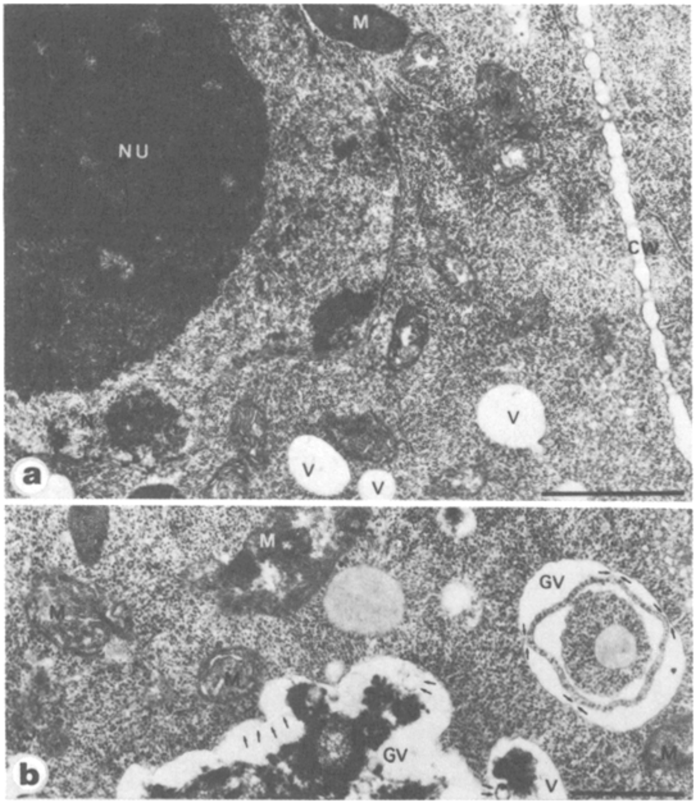

FIG. 8. White mustard root tip, sterile water control (a). White mustard root tip, 100 μg/liter hordenine applied (b). Scale bar = 1 μm. CW = cell wall; V = vacuole; GV = giant vacuole; M = mitochondrion; NU = nucleolus; arrows indicate phagocytosis.

be part of a common response to stress, suggesting that further analogies will become apparent as the combined disciplines of morphology, cytology, and biochemistry are brought to bear on allelopathic phenomena.

Acknowledgments—We thank the Australian Research Grants Scheme and the University of New England for financial support.

REFERENCES

AHLBERG, J., HENELL, F. and GLAUMANN, H. 1982. Proteolysis in isolated autophagic vacuoles from rat liver. Effect of pH and of proteolytic inhibitors. *Exp. Cell Res.* 142:373–383.

ANDREWS, R.E., PARKS, L.W., and SPENCE, L.D. 1980. Some effects of Douglas fir terpenes on certain micro-organisms. *Appl. Environ. Microsc.* 40:301-304.

BENNET, R.J., BREEN, C.M., and FEY, M.V. 1987. The effects of aluminium on root cap function and root development in *Zea mays* L. *Environ. Exp. Bot.* 27:91-104.

BLEVE-ZACHEO, T., ZACHEO, G., LAMBERTI, F., and ARRIGONI, O. 1979. Cell wall protrusions and associated membranes in roots parasitized by *Longidorus apulus. Nematologia* 25:62-66.

CHAPMAN, R.K., and ALLEN, T.C. 1948. Stimulation and suppression of some vegetable plants by DDT. *J. Econ. Entomol.* 41:616-623.

COGGER, H.G. 1979. Reptiles and Amphibians of Australia. Reed, Sydney.

EDMUNDS, M. 1974. Defence in Animals. Longman, Harlow, U.K.

FRANICH, R.A., GASKIN, R.E., WELLS, L.G., and ZABKIEWICZ, J.A. 1982. Effect of *Pinus radiata* needle monoterpenes on spore germination and mycelial growth of *Dothistroma pini* in vitro in relation to mature tree resistance. *Physiol. Plant Pathol.* 21:55-63.

JONES, R.L., and VARNER, J.E. 1967. The bioassay of gibberellins. *Planta* 72:155-161.

LEVIN, D.A. 1976. The chemical defences of plants to pathogens and herbivores. *Annu. Rev. Ecol. Syst.* 7:121-159.

LEVITT, J., LOVETT, J.V., and GARLICK, P.R. 1984. *Datura stramonium* allelochemicals: Longevity in soil and ultrastructural effects on root tip cells of *Helianthus annuus* L. *N. Phytol.* 97:213-218.

LIU, D.L., and LOVETT, J.V. 1987. Crop allelochemical interference with weed seed germination. *Proceedings of a Workshop on Weed Seed Biology.* Orange, New South Wales, pp. 116-119.

LORBER, P., and MULLER, W.H. 1976. Volatile growth inhibitors produced by *Salvia leucophylla:* Effects on seedling root tip ultrastructure. *Am. J. Bot.* 63:196-200.

LOVETT, J.V. 1982a. Allelopathy and self-defence in plants. *Aust. Weeds* 2:33-36.

LOVETT, J.V. 1982b. The effects of allelochemicals on crop growth and development, pp. 93-110, *in* J.S. McLaren (ed.). Chemical Manipulation of Crop Growth and Development. Butterworths, London.

LOVETT, J.V., and DUFFIELD, A.M. 1981. Allelochemicals of *Camelina sativa. J. Appl. Ecol.* 18:283-290.

LOVETT, J.V., and POTTS, W.C. 1987. Primary effects of allelochemicals of *Datura stramonium* L. *Plant Soil* 98:137-144.

LOVETT, J.V. and RYUNTYU, M.Y. 1988. Vacuolar activity and phagocytosis as responses to allelopathic stress. *Inst. Phys. Conf. Series* 93:103-104.

LOVETT, J.V., LEVITT, J., DUFFIELD, A.M. and SMITH, N.G. 1981. Allelopathic activity of *Datura stramonium* L. (thorn-apple). *Weed Res.* 21:165-170.

LOVETT, J.V., RYUNTYU, M.Y., and GARLICK, P.R. 1987. Allelopathic effects of thornapple *Datura stramonium* L. Proceedings 8th Australian Weeds Conference. Sydney, pp. 179-181.

LUCKEY, T.D. 1968. Insecticide hormoligosis. *J. Econ. Entomol.* 61:7-12.

MATILE, Ph. 1975. The Lytic Compartment of Plant Cells. Cell Biology Monographs 1, Springer-Verlag, Vienna.

MATILE, Ph. 1984. Das toxische Kompartiment der Pflanzenelle. *Naturwissenschaften* 71:18-24.

MULLER, C.H. 1966. The role of chemical inhibition (allelopathy) in vegetational composition. *Bull. Torrey Bot. Club* 93:332-351.

OVERLAND, L. 1966. The role of allelopathic substances in the "smother crop" barley. *Am. J. Bot.* 53:423-432.

REESE, J.C. 1979. Interactions of allelochemicals with nutrients in herbivore food, pp. 309-330, *in* G.A. Rosenthal and D.H. Janzen (eds.). Herbivores: Their Interaction with Secondary Plant Metabolites. Academic Press, New York.

REEVE, J.C., and CROZIER, A. 1975. Gibberellin bioassays, pp. 35-64, *in* H.N. Krishnamoorthy (ed.). Gibberellins and Plant Growth. Wiley, New York.

RICE, E.L. 1984. Allelopathy, 2nd ed. Academic Press, Orlando, Florida.

ROSHCHINA, V.V., RUZIENA, R.Kh., and MUKHIN, E.N. 1986. Capsaicine from the fruits of red pepper *Capsicum annuum* L. as a regulator of photosynthetic electron transport. *J. Biochem. Microb.* 22:403–409.

SELANDER, J., KALO, P., KANGAS, E., and PERTUNNEN, V. 1974. Olfactory behaviour of *Hylobium abietis* L. (Col., Curculionidae). I. Response to several terpenoid fractions isolated from Scots pine phloem. *Ann. Entom. Fenn.* 40:108–115.

SHEEHY, D.P., and WINWARD, A.H. 1981. Relative palatability of seven *Artemisia* taxa to mule deer and sheep. *J. Range Manage.* 34:397–399.

WELCH, B.I., and MCARTHUR, E.D. 1981. Variation of monoterpenoid content among subspecies and accessions of *Artemisia tridentata* grown in a uniform garden. *J. Range Manage.* 34:380–384.

WHITE, S.M., WELCH, B.L., and FLINDERS, J.T. 1982. Monoterpenoid content of pygmy rabbit stomach ingesta. *J. Range Manage.* 35:107–109.

WIERZBICKA, M. 1987. Lead accumulation and its translocation barriers in roots of *Allium cepa* L.—autoradiographic and ultrastructural studies. *Plant Cell Environ.* 10:17–26.

WINTER, A.G. 1961. New physiological and biological aspects in the interrelations between higher plants. *Soc. Exp. Biol. Symp.* 15:229–244.