PLANT PHOTOSENSITIZERS: A Survey of Their Occurrence in Arid and Semiarid Plants from North America

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Abstract—Various plants native to arid and semiarid habitats throughout the southwestern United States, Baja California, and northern Mexico were bioassayed for phototoxic natural products. Approximately 115 species representing 57 genera and eight plant families were assayed for phototoxic activity by standard antimicrobial techniques using *Escherichia coli* and *Saccharomyces cerevisiae*. Phototoxic constituents were extracted from numerous members in the Asteraceae (Compositae) and occurred with highest frequency among species of the subtribe Pectidinae (tribe Heliantheae). Extracts of *Pectis*, the largest genus in the Pectidinae, had substantial light-activated biocidal action despite the paucity of acetylenic thiophenes, the phototoxins characteristic of most other genera in the subtribe. Leaf resin from the creosote bush [*Larrea tridentata* (Sesse & Mol. ex DC.) Coville; Zygophyllaceae], a dominant desert shrub, possessed potent antimicrobial activity in the absence of light; however, the toxicity of this extract was slightly enhanced in the presence of UVA irradiation. Phototoxic antimicrobials were not detected in extracts of selected species from the Asclepiadaceae, Chenopodiaceae, Hydrophyllaceae, Lamiaceae, Polygonaceae, or Solanaceae.

Key Words—Photosensitizers, arid/semiarid plants, Asteraceae, Zygophyllaceae, Asclepiadaceae, Chenopodiaceae, Hydrophyllaceae, Lamiaceae, Polygonaceae, Solanaceae.

INTRODUCTION

Plant "photosensitizers" or "phototoxins" are chemicals produced by members of at least 30 plant families that adversely affect a wide variety of organisms in the presence of sunlight (Downum, 1986). A partial listing of susceptible organisms includes among others: viruses, phytopathogenic bacteria and fungi, nematodes, and herbivorous insects (see reviews by Towers, 1984, 1986; Downum, 1986; Downum and Rodriguez, 1986; Downum and Nemec, 1987). In addition to these organisms, Campbell et al., (1982) demonstrated that the growth of various non-phototoxin-containing plants could be inhibited by treatment with photosensitizers common to many species of the Asteraceae (Compositae). Such broad-spectrum biological activity suggests that plant phototoxins may be involved with plant defense against a wide range of potentially deleterious or competing organisms in nature.

Although phototoxic phytochemicals have been isolated from a variety of plants, little is known about their occurrence (or biological activity) in species that evolved under high-light conditions where phototoxic action seemingly would provide a most effective plant defense. The present report is an initial effort to establish the prevalence of photosensitizers in plants that grow in environments exposed to high levels of solar irradiation (i.e., the Chihuahuan, Mojave, and Sonoran deserts of North America). Standard antimicrobial techniques were used for these preliminary survey studies, but the broad-spectrum toxicity associated with many of the previously studied plant phototoxins suggests that they may be responsible for a variety of defensive plant responses, in addition to their in vitro antimicrobial effects.

METHODS AND MATERIALS

Plant Material. Bulk collections for extraction and bioassay as well as voucher specimens were collected from various regions of Mexico and the southwestern United States as indicated in Table 1. Plants were air-dried in the field as much as possible and then transported to the laboratory for thorough drying (50°C for five days). Dried, powdered matter (5 g) from each species was extracted with MeOH (50 ml) for 7–10 days at room temperature under darkened conditions. The resulting extracts were filtered and concentrated to approximately 1 ml by rotary evaporation. Concentrated crude extracts were stored at −20°C until they could be bioassayed.

Species of *Pectis* were handled differently to minimize the loss of potential phototoxins, which was reported previously (Downum et al., 1985). These plants were transported from the field on ice and homogenized in MeOH within

TABLE 1. PLANTS FROM ARID AND SEMIARID REGIONS OF UNITED STATES AND MEXICO BIOASSAYED FOR PHOTOTOXIC AND ANTIBIOTIC ACTIVITY WITH *E. coli* AND *S. cerevisiae*[a]

Plants	Collection site	*E. coli*	*S. cerevisiae*
Asclepiadaceae			
Asclepias			
A. subulata Decne.	Baja Calif.	–	–
Asteraceae			
Anthemideae			
Artemisia[b]			
A. dracunculus L.	Baja Calif.	–	–
A. californica Less.	Baja Calif.	–	–
A. tridentata Nutt.	Nevada	–	–
A. ludoviciana Nutt. subsp. *incompta* (Woot.) Keck	Calif.	–	–
A. bigelovii A. Gray in Torr.	Nevada	–	–
Chrysanthemum[b]			
C. coronarium L.	Baja Calif.	–	–
Astereae			
Chrysothamnus[b]			
C. nauseosus (Pall.) Britt. subsp. *consimilis* (Greene) Hall & Clements	Nevada	–	–
C. paniculatus (A. Gray) Hall.	Nevada	–	–
C. viscidiflorus (Hook.) Nutt subsp. *puberulus*	Nevada	–	–
Ericameria[c]			
E. linearifolia (DC.) Urbatsch & Wussow	Baja Calif.	–	–
Hazardia[c]			
H. brickellioides (S.F. Blake) Clark	Nevada	–	–
H. linearifolius DC.	Baja Calif.	–	–
H. squarrosus (H. & A.) Greene var. *grindelioides* (DC.) Clark	Calif.	–	–
Isocoma[c]			
I. acradenia (Greene) Greene	Nevada	–	–
I. veneta (H.B.K.) Greene	Calif.	–	–
Machaeranthera[c]			
M. pinnatifida (Hook.) Shinners subsp. *goodingii* (A. Nels.) Turner & Hartman	Nevada	–	–
M. tortifolia (A. Gray) Cronq & Keck	Arizona	–	–
Lactuceae			
Malacothrix sp.[c]	Calif.	–	–
Eupatorieae			
Hofmeisteria[c]			
H. fasculata (Benth.) Walp. var. *fasciculata*	Baja Calif.	–	–
H. crassifolia S. Wats.	Sonora	–	–

TABLE 1. Continued

Plants	Collection site	*E. coli*	*S. cerevisiae*
Heliantheae			
Ambrosiinae			
Ambrosia[b,d]			
A. ambrosioides (Cav.) Payne	Arizona	+	+
A. camphorata (Greene) Payne	Sonora	+	+, anti
A. chenopodifolia (Benth.) Payne	Baja Calif.	+	anti
A. confertiflora DC.	Sonora	−	−
A. cordifolia Payne	Arizona	+, anti	+
A. deltoides (Torr.) Payne	Arizona	anti	+
A. dumosa (A. Gray) Payne	Sonora	+	+, anti
A. eriocentrata (A. Gray) Payne	Nevada	−	+
A. trifida L.	Arizona	−	−
Dicoria[c]			
D. canescens A. Gray	Baja Calif.	anti	−
Hymenoclea[c]			
H. salsola Torr. & Gray	Baja Calif.	−	−
Parthenice[c]			
P. mollis A. Gray var. *penninsularis* Sauck	Arizona	−	−
Baeriinae			
Eriophyllum[b]			
E. lanatum (Pursh) Forbes	Calif.	−	−
Lasthenia sp.[b,d]	Baja Calif.	−	−
L. coronaria (Nutt.) Ornduff	Baja Calif.	−	−
Chaenactidinae			
Bahia[c]			
B. absinthifolia Benth.	Arizona	−	−
Chaenactis[b,d]			
C. glabriuscula DC.	Calif.	−	−
Hulsea[c]			
H. californica Torr. & Gray	Baja Calif.	−	−
Palafoxia[b,d]			
P. linearis var. *glandulosa* B.L. Turner & M.I. Morris	Baja Calif.	−	−
Coreopsidinae			
Coreocarpus[c]			
C. dissectus (Benth.) S.F. Blake	Baja Calif.	−	−
C. parthenioides Benth. var. *parthenioides*	Baja Calif.	−	−
C. paniculatus (A. Gray) Hall	Calif.	−	−
C. viscidiflorus (Hook.) Nutt.	Calif.	−	−
Thelesperma[b]			
T. filifolium (Hook.) A. Gray	Texas	−	+
T. megapotamicum (Spreng.) O. Ktze.	Arizona	−	+
Ecliptinae			
Encelia[b,e]			
E. ravenii Wigg.	Baja Calif.	−	+
E. farinosa A. Gray var. *farinosa*	Baja Calif.	−	+
E. frutescens (A. Gray) A. Gray	Baja Calif.	−	−
E. ventorum Brandegee	Baja Calif.	−	anti

TABLE 1. Continued

Plants	Collection site	*E. coli*	*S. cerevisiae*
Heliopsis[b]			
H. parviflora A. Gray var. *rubra* (Fish.) Wigg.	Arizona	–	–
Verbesina[b,d]			
V. dissata A. Gray	Baja Calif.	–	–
V. enceloides (Cav.) A. Gray var. *exauriculata* Robins. & Greenm.	Baja Calif.	–	–
V. palmeri S. Wats.	Baja Calif.	–	–
Zinnia[b]			
Z. grandiflora Nutt.	Arizona	–	–
Gaillardiinae			
Baileya[c]			
B. multiradiata Harv. & Gray	Calif.	–	–
Psilostrophe[c]			
P. cooperi (A. Gray) Greene	Baja Calif.	–	–
Galinsoginae			
Bebbia[c]			
B. juncea (Benth.) Greene var. *juncea*	Baja Calif.	–	–
Helianthinae			
Helianthus[b]			
H. gracilentus A. Gray	Baja Calif.	–	+
H. niveus (Benth.) Brandey. subsp. *niveus*	Baja Calif.	–	–
Heliomeris[c]			
H. multiflora Nutt. var. *nevadensis* (A. Nels.) Yates	Nevada	–	–
Viguiera[f]			
V. deltoidea			
var. *chenopodina* (Greene) S.F. Blake	Baja Calif.	–	+
var. *deltoidea*	Baja Calif.	–	–
V. dentata (Cav.) Spreng.	Sinaloa	–	–
V. laciniata A. Gray	Baja Calif.	–	–
V. microphylla Vasey & Rose	Baja Calif.	–	–
V. purissimae Brandegee	Baja Calif.	–	–
V. tomentosa A. Gray	Baja Calif.	–	–
Madiinae			
Adenothamnus[c]			
A. validus (Brandegee) Keck	Baja Calif.	–	–
Calycadenia[b]			
C. tenella (Nutt.) Torr. & Gray	Baja Calif.	–	–
Hemizonia[b,d]			
H. fasciculata (DC.) Torr. & Gray	Baja Calif.	–	–
Melampodiinae			
Melampodium spp.[b,d]	Texas	–	–
Pectidinae			
Adenophyllum[d,g]			
A. [*Dyssodia*] *porophylloides* A. Gray	Arizona	+	+
Chrysactinia[d]			
C. mexicana A. Gray	Texas	+	+

TABLE 1. Continued

Plants	Collection site	*E. coli*	*S. cerevisiae*
Dyssoida[d,g]			
D. anthemidifolia Benth.	Baja Calif.	+	+
Hymenatherum[d]			
H. acerosum (DC.) A. Gray	Texas	+	+
H. [*Dyssodia*] *pentachaeta* (DC.) B.L. Rob. var. *belenidium* (DC.) Strother[g]	Arizona	+	+
H. tenuilobum DC.	Comm. Source	+	+
Nicolletia[d]			
N. trifida Rydb.	Baja Calif.	+	+
Pectis[h]			
P. canescens H.B.K.	Guerrero	+	+
P. filipes Harv. & Gray var. *subnuda* Fern.	Arizona	+	+
P. imberbis A. Gray	Arizona	+	+
P. linifolia L.			
var. *hirtella* Blake	Michoacan	+	+
var. *linifolia*	Oaxaca	+	+
P. longipes A. Gray (2N)	Arizona	+	+
(4N)	Arizona	+	+
P. luckoviae Keil	Michoacan	+	+
P. multiflosculosa (DC.) Sch. Bip.	Jalisco	+	+
P. multiseta Benth.	Baja Calif.	+	+
P. papposa Harv. & Gray var. *papposa*	Arizona	+	+
P. prostrata Cav.	Arizona	+	+
P. purpurea Bdg. var. *sonorae* Keil	Sinaloa	+	+
P. schaffneri Sch. Bip. ex A. Gray	Oaxaca	+	+
Porophyllum[b]			
P. gracile Benth.	Baja Calif.	+	+
P. ruderale (Jacq.) Cass. var. *macrocephalum* (DC.) Cronq.	Arizona	+	+
P. scoparium A. Gray	Texas	+	+
Peritylinae			
Amauria[c]			
A. rotundifolia Benth.	Baja Calif.	−	−
Perityle[c]			
P. emoryi Torr.	Baja Calif.	−	−
P. microglossa Benth.	Baja Calif.	−	−
P. megalocephalum var. *intricata*	Nevada	+	+
Senecioneae			
Senecio[f]			
S. californicus DC. var. *californicus*	Baja Calif.	−	−
S. douglasii var. *monoensis* (Greene) Jepson	Baja Calif.	−	−
S. salignus DC.	Arizona	−	−
S. vulgaris L.	Calif.	−	−
Chenopodiaceae			
Atriplex sp.	Baja Calif.	−	−

TABLE 1. Continued

Plants	Collection site	*E. coli*	*S. cerevisiae*
Eurotia			
E. lanata (Pursh) Moq.	Baja Calif.	−	−
Hydrophyllaceae			
Phacelia			
P. distans Benth.	Baja Calif.	−	−
Lamiaceae			
Lepechinia			
L. hastata (A. Gray) Epling	Baja Calif.	−	−
Salvia			
S. columbariae Benth.	Baja Calif.	−	−
Polygonaceae			
Antigonon			
A. leptopus Hook. & Arn.	Sonora	−	−
Solanaceae			
Nicotiana			
N. trigonophylla Dunal	Baja Calif.	−	−
Zygophyllaceae			
Guaiacum			
G. coulteri A. Gray	Sonora	−	−
Kallstroemia			
K. grandiflora Torr. ex A. Gray	Texas	−	−
K. hirsutissima Vail.	Texas	−	−
Larrea			
L. tridentata (Sesse & Moc. ex DC.) Coville	Baja Calif.	+	+
Viscainoa			
V. geniculata (Kell.) Greene var. *geniculata*	Baja Calif.	−	−

[a] Whole plant extracts were concentrated and assayed as described (see Methods and Materials). Presence (+) or absence (−) of inhibitory zones surrounding bioassay disks refers to activity following UV-A (3 hr) and dark incubation for 24 hr. Growth inhibition resulting from antibiotic action (not photoinduced) of an extract is denoted anti.

[b] Acetylenes reported from genus (Bohlmann et al., 1973).

[c] Chemistry unknown.

[d] Thiophenes reported from genus (Bohlmann and Zdero, 1976, 1979; Bohlmann et al., 1973, 1980, 1983; Downum and Towers, 1983; Downum et al., 1985).

[e] Chromenes reported from genus (Proksch and Rodriguez, 1983).

[f] Genus reported to lack polyacetylenes and thiophenes (Bohlmann et al., 1973).

[g] See Downum et al. (1985) for explanation of nomenclatural assignment.

[h] Genus reported to lack acetylenic di- and terthiophenes (Downum and Towers, 1983; Downum et al., 1985).

24 hr of collection. Extracts were bioassayed immediately as their phototoxicity quickly disappeared following homogenization.

Voucher specimens of all species were deposited with Herbaria either at California Polytechnic State University, the University of California at Riverside, or the University of Texas at El Paso.

Microorganisms. Escherichia coli B, a gram-negative bacterium, and *Saccharomyces cerevisiae*, a yeast, were routinely used to bioassay plant extracts for antibiotic and/or phototoxic plant metabolites. Stock cultures of *E. coli* were obtained from the American Type Culture Collection (ATCC 23226); cultures of *S. cerevisiae* were obtained from the laboratory of Dr. G.H.N. Towers (University of British Columbia). Stationary phase cultures (18 hr) grown aerobically at 30°C (*S. cerevisiae*) or 37°C (*E. coli*) were used for all bioassays. *S. cerevisiae* was grown in Sabouraud dextrose broth (Difco) while *E. coli* was inoculated into nutrient broth (Difco).

Bioassay Techniques. Concentrated plant extracts (20–50 μl) were applied to replicate sterile cellulose assay disks and then placed onto lawns of *E. coli* and *S. cerevisiae* as described previously (Downum et al., 1983). Duplicate plates were prepared for all assays. One plate was kept in the dark to determine the antibiotic action of an extract, and UV-A activation or enhancement of biocidal action was determined on a second plate that was irradiated by four horizontal UV-A lamps (Sylvania F40BLB; 18 W/m^2). The level of irradiation used for the bioassays was approximately half that routinely encountered in the desert environment (measured at 365 nm with a Spectroline model DM-365N ultraviolet meter; Spectronics Corp., Westbury, New York).

RESULTS AND DISCUSSION

Extracts of many plants belonging to the sunflower family (Asteraceae) inhibited the growth of *E. coli* and *S. cerevisiae* cultures as did the leaf extract from the creosote bush *Larrea tridentata* (Zygophyllaceae) (Table 1) when exposed to UV-A irradiation. Several of these plant extracts also inhibited the growth of the bioassay organisms without light activation; however, this activity was less pronounced than the phototoxic activity. A limited number of extracts from species representing the Asclepidaceae, Chenopodiaceae, Hydrophyllaceae, Lamiaceae, Polygonaceae, and Solanaceae failed to elicit any kind of biological activity toward *E. coli* or *S. cerevisiae*.

Plants belonging to the Asteraceae were given preference in our survey because they represent a quantitatively important component of most arid and/or semiarid habitats in North America and because UV-mediated antibiotic activity has been associated with many plants from this large family (Camm et al., 1975). Extracts from approximately 35% of the species surveyed elicited

phototoxic responses from the bioassay organisms. Several species also contained effective antimicrobial agents that did not require light activation; these included five species of *Ambrosia*, one species of *Dicoria*, and one species of *Encelia*. The greatest number of phototoxin-containing plants belonged to the tribe Heliantheae [as revised by Robinson (1981)]. Nearly 50% of the plant extracts from members of this tribe tested positive for light-activated toxins. The Pectidinae, a subtribe within the Heliantheae, is of particular note because extracts from all of the plants in this taxonomic grouping were phototoxic toward both *E. coli* and *S. cerevisiae*.

Various polyacetylenic or thiophenic metabolites are most likely responsible for the phototoxicity of extracts from many members of the Asteraceae. Such chemicals are widely distributed in the family (Bohlmann et al., 1973) and many are potent photosensitizers (McLachlan et al., 1984, 1986; Marchant and Cooper, 1987). Thiophenes, which are biosynthetically derived from acetylenic precursors by sulfide addition (Bohlmann et al., 1973), are also powerful phototoxins (Downum et al., 1982, 1983). Although these phototoxic metabolites occur sporadically throughout the Asteraceae (Bohlmann et al., 1973), they are particularly characteristic of genera in the subtribe Pectidinae (Bohlmann et al., 1973; Downum and Towers, 1983; Downum et al., 1985). *Pectis*, the largest genus in this subtribe, is, however, phytochemically distinct from the remainder of the genera in this taxonomic grouping in that thiophenes have yet to be detected in the 20 or so species examined thus far (Downum and Towers, 1983; Downum et al., 1985). The identity of the chemical constituents responsible for the phototoxicity of *Pectis* extracts remains in question.

Leaf extracts from the creosote bush, *Larrea tridentata* (Zygophyllaceae), contained constituents that were effective biocidal agents in the absence of UV-A. The antimicrobial activity of this extract was enhanced slightly on exposure to UV-A. The creosote bush was the only plant outside of the Asteraceae to elicit both dark and UV-A-enhanced biological activity against *E. coli* and *S. cerevisiae*. Several other Zygophyllaceae genera were also bioassayed (e.g., *Guaiacum, Kallistroemia*, and *Viscanoa*), but antimicrobial activity similar to that mediated by *Larrea* extracts was not observed.

Isolation, identification, and bioactivity studies of the toxic chemicals from *Pectis* spp. and *L. tridentata* are currently underway.

This preliminary study suggests that phototoxic phytochemicals are fairly common among taxonomically diverse members of the Asteraceae. Light-enhanced biocidal activity was also associated with extracts of *Larrea tridentata*, a dominant shrub throughout the Chihuahuan, Mojave, and Sonoran deserts. The presence of light-activated antimicrobial agents in plants that typically grow under high levels of solar irradiation suggests that such allelochemicals may mediate important interactions between photosensitizer-containing plants and potentially deleterious organisms in these environments. The prev-

alence of phototoxic phytochemicals in other high-light environments (e.g., tropical and subtropical habitats) is currently being investigated.

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