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NATURAL VARIATION AND REGULATION OF FLORAL ULTRAVIOLET ABSORPTION IN *COREOPSIS* AND *BIDENS*

Ron Scogin

INTRODUCTION

The occurrence of a "bull's-eye" pattern of ultraviolet (UV) wavelength reflectance/absorbance is common among species of Asteraceae (King and Krantz 1975). The phytochemical basis for floral UV absorption in *Bidens* and *Coreopsis* involves anthochlor (flavonoid) compounds (Scogin and Zakar 1976; Scogin, Young, and Jones 1977). These pigments are presented in epidermal cells which are specialized to optimize light absorption by the pigment molecules (Brehm and Krell 1975; Scogin and Rogers 1980). While our understanding of the mechanism of occurrence of UV absorption/reflection is improving (viz., the occurrence of pigments in specialized cells), any understanding of the mechanism *controlling* the expression and extent of UV reflection/absorption is almost nonexistent. In this report, "extent of UV absorption" will mean the percentage of the basal portion of individual ligules which is UV absorptive.

It is assumed for the purposes of this investigation that the occurrence of a UV reflection/absorption pattern in, say, an individual ligule is a result of differential flavonoid synthesis and sequestering (as opposed to controlled translocation of flavonoids from a remote site of synthesis). Various environmental and physiological factors have been demonstrated to influence the rate of flavonoid synthesis including, most notably for the present investigation, plant growth substances (McClure 1975). With this in mind, it was undertaken to determine the effect upon the expression of UV reflection/absorption patterns of exogenously applied growth substances. A necessary preliminary to that investigation was the determination of the extent of naturally occurring intraspecific variation with respect to UV patterning.

MATERIALS AND METHODS

Plants used for hormone application studies were in cultivation at the Rancho Santa Ana Botanic Garden, Claremont, California. Populations of *Coreopsis gigantea* (Kell.) Hall examined for natural variation in UV patterning were located along California Highway 1 between Leo Carrillo State Beach and Point Mugu State Park in Los Angeles and Ventura counties. The studied population of *C. maritima* (Nutt.) Hook. occurred along Monument Road at the U.S.-Mexico border south of San Ysidro, California.

Ligule samples from *Bidens laevis* (L.) BSP were prepared for and examined by scanning electron microscopy using techniques described in Scogin and Rogers (1980).

Hormones were applied repeatedly to maturing buds of experimental plants according to the following protocols:

1. Preparations of indole acetic acid (IAA) and 2,4-dichloro-phenoxyacetic acid (2,4-D) were made by suspending the auxin in heated lanolin to the extent of 100 μg of auxin per mg of lanolin. This preparation was extruded through a syringe onto the peduncle of treated inflorescences.

2. Kinetin solutions of 0.2 mg/ml and 20 mg/ml were prepared in 0.05 M NaOH. These solutions delivered 1 μg and 100 μg of kinetin respectively, with a 5- μl application from an Eppendorf micropipette. Three applications of 5 μl each were made to buds at weekly intervals. A small slit was made in the top of the bud to facilitate hormone entry.

3. A solution containing gibberellic acid (GA) at 20 mg/ml was prepared. The GA was dissolved in a small amount of ethanol and diluted to the appropriate volume with distilled water. Sodium dodecylsulfate was added at 0.01% as a wetting agent to facilitate application. Three applications of 5 μl (100 μg GA) each were made at weekly intervals to slit buds.

The extent of UV absorption was determined by exposure of ligules to ammonia fumes and measuring the extent of characteristic anthochlor color change (Scogin, Young, and Jones 1977).

RESULTS AND DISCUSSION

Natural Variation in UV Patterning

Natural intraspecific variation of UV absorptive extent in ligules.—Abrahamson and McCrea (1977) reported that the results of a comparison of inter- and intrapopulational surveys of UV absorptive extent in ligules among three *Rudbeckia* species were nonuniform. In *Rudbeckia trilobata* L. both inter- and intrapopulational UV absorption variation were low. Intrapopulational variation was low in *R. lacinata* L., but statistically significant differences in interpopulational means were found; whereas *R. hirta* L. exhibited high intrapopulational variation, but statistically nonsignificant differences in interpopulational means. Abrahamson and McCrea concluded that the extent of populational variation with respect to UV absorption patterns is dependent upon the breeding system of the taxon under examination. This conclusion was based upon a comparison of the standard deviations from the means of inter- and intrapopulational samples.

A similar analysis was performed on six natural populations of *Coreopsis gigantea* and yielded results similar to those reported for *Rudbeckia trilobata*; namely, the standard deviation of populational means (3.5) was nested with-

in the range of standard deviations for individual populations (2.3–5.4) (See Table 1). In a more robust test of variation, a one-way analysis of variance was performed on the *Coreopsis* UV absorption populational data, the results of which are shown in Table 2 and which demonstrate that the extent of UV absorption is statistically different among the studied populations.

The range of deviations from the mean among *Coreopsis gigantea* populations is consistent with the conclusion reached by Abrahamson and McCrea that only weak stabilizing selection forces are acting on floral UV patterns. The differences among populational means would be consistent with a clonal origin or high degree of self-fertilization among *C. gigantea* populations. The reproductive biology of *C. gigantea* is poorly known; however, all other *Coreopsis* species tested to date are self-sterile (Crawford 1970, 1971) and apomictic reproduction is not obvious in *C. gigantea*, so the reason for populational distinctions remains obscure.

Interspecific variation in UV absorptive proportions.—A single, natural population of *Coreopsis maritima* was examined ($n = 35$) and its extent of floral UV absorption was not significantly different from that of *C. gigantea* (two-tailed *t*-test at the 1% level). Since the UV absorption/reflection pattern of these two *Coreopsis* species are statistically (and, most likely, biologically) indistinguishable, UV patterning plays little role in their reproductive isolation and maintenance of their specific integrities.

Genetic control of the extent of ligular UV absorption.—The genetic basis for the biogenesis of corolla pigments (especially phenolics) is now well established (Harborne 1967). By contrast, any understanding of the genetic control of intrafloral pigment expression in nectar guides, corolla blotches, and UV absorption/reflection patterns is very rudimentary. The present data demonstrating different UV absorptive proportions among *Coreopsis gigantea* populations suggest a genetic component regulating pigment extent in the ligule. Controlled genetic-cross studies involving helianthoid taxa and examining the extent of visual (anthocyanin) pigmentation have been performed on *Helianthus annuus* L. (Fick 1976) and on *Coreopsis tinctoria* Nutt. (Smith and Parker 1971). Crosses between noncyanic ("nonred") and wholly or partially cyanic flowers of both taxa yielded progeny in which all members of the F_1 generation exhibited a "bulls-eye" or "gaillardia" cyanic pigmentation pattern. The second filial generations yielded mixed results between the two taxa. In *Helianthus* the completely red and "gaillardia" patterns of the F_2 generation were not distinguished, but lumped together as "red" and therefore precluded a more detailed genetic analysis. In *Coreopsis*, five graded classes of pigment extent were reported (ranging from noncyanic to 50% of the ligule length pigmented). The authors of both studies concluded that a digenic (two locus) model best described the genetic regulation of pigment extent in ligules.

Table 1. Natural variation in extent of floral UV absorption in *Coreopsis gigantea* and *C. maritima*.

Population	Number of plants sampled	Percentage of ligule absorptive	Standard deviation
<i>C. gigantea</i>			
1	38	37	5.4
2	32	44	3.1
3	12	45	2.3
4	5	40	3.6
5	20	37	2.5
6	26	38	3.9
Mean		39.7	3.5
<i>C. maritima</i>	35	40.5	6.6

Table 2. Analysis of variance in floral UV absorption extent among *Coreopsis gigantea* populations.

	Degrees of freedom	Sum of squares	Mean squares	F-ratio
Among populations	5	1320	264	20.6
Within populations	127	1629	12	

Table 3. The effect of hormone treatment on extent of ligule UV absorption.

Hormone treatment	<i>Coreopsis gigantea</i>		<i>Bidens laevis</i>	
	Sample size	Percent change	Sample size	Percent change
IAA	13	+16	26	+3
2,4-D	18	+31	nd	nd
GA	21	-7	28	-9
Kinetin				
1 μ g	5	-2	20	0
100 μ g	8	+30	nd	nd

nd: not determined.

Effect of Hormone Treatments

Plant growth substances are known to affect many plant characters, both morphological and biochemical. Since they have been shown to have both stimulatory and inhibitory influences on flavonoid biosynthesis in various circumstances (McClure 1975), it was determined to test their effect on the biochemical, as well as morphological, aspects of floral UV pattern production.

Macromorphological effects.—The influence of growth substances on floral development is well documented. The effects on *Bidens* and *Coreopsis* included doubling and trebeling of ligule whorls with auxin applications and elongation of ligules and phyllaries in buds treated with gibberellic acid. Hormone treatment also qualitatively affected the anthochlor color reaction (and therefore the congruent UV absorption pattern). Application of kinetin caused the least modification of the anthochlor reaction compared with untreated plants. The color reaction appeared normal in intensity and the definition of the absorptive/reflective interface. In auxin-treated plants the anthochlor color reaction appeared much weaker and more diffuse and the demarkation between absorptive and reflective ligule portions was much less distinct. Gibberellic acid-treated plants produced anthochlor reactions similar to those treated with auxins, but the interface location was more obscure. Qualitatively similar results were seen in photographs of treated flowers which were photographed through an 18A filter.

Micromorphological effects.—A dimorphism occurs in epidermal petal papillae of the two taxa under examination, between the conical, UV-absorptive cells at the basal portion of the ligule and the rounded, UV-reflective cells at the tip (Scogin and Rogers 1980). The epidermal surface of IAA-treated ligules of *Bidens laevis* was examined by scanning electron microscopy to determine whether auxins caused micromorphological changes related to the anthochlor color changes noted above. Rather unexpectedly, no micromorphological differences could be detected between treated and untreated plants with respect to basal or apical ligule epidermal micromorphologies. The papillae dimorphism noted in untreated ligules also occurs in hormone-treated ligules and any micromorphological changes attributable to hormone treatment were undetectable.

Extent of UV absorption.—The effects of four hormones in three growth regulator classes upon the extent of UV absorption in ligules was determined and the results are summarized in Table 3. Qualitatively consistent results were obtained between the two test species. Gibberellic acid slightly reduced the UV absorption extent, whereas kinetin and auxins significantly increased the absorption extent when applied in sufficient amounts. These results provisionally implicate hormone levels as one factor involved in determining the extent of ligular UV absorption. Additional studies will be required to further elucidate the complete role of plant growth regulators in the control of floral UV absorption.

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