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INTRODUCTION

Extrafloral nectaries (EFNs) are glands on a plant, not involved in pollination, that produce solutions containing sugars (and other compounds). Long noted by morphologists, EFNs have recently been observed to be part of ant-plant mutualisms. The function of EFNs appears to be to attract aggressive insects, especially ants, which by disturbing or preying upon herbivores, reduce damage to the plant (Janzen, 1966a,b; Elias and Gelband, 1975; Keeler, 1975, 1977; Bentley, 1976, 1977a,b; Schemske, 1978; Tilman, 1978; Inouye and Taylor, 1979; Pickett ad Clark, 1979). Furthermore, they constitute an unusual plant defense against herbivores: at EFNs plants employ ants as a "bodyguard."

Zimmermann (1932), Schnell et al. (1963) and Elias (1979) have analyzed the distribution of EFNs in flowering plant taxa. From their work, it is clear that EFNs are worldwide and represented in varied vascular plants. At least 73 angiosperm families have species which possess EFNs. A few fern species also have EFNs, apparently an advanced character (see Bentley, 1977a). The number of species with EFNs cannot yet be meaningfully estimated, but 907 are known to me.

This paper reports for the first time the proportion and taxonomic distribution of EFN-bearing plants in the flora of a single area. Only from information about distribution of EFN-bearing species will it be possible to identify the selection pressures affecting the geographic and taxonomic presence or absence of EFNs.

METHODS

The state of Nebraska, about 200, 750 km² in area, lies from 95°25'-104° W, 40°-43° N. Nebraska contains small areas of deciduous forest in the southeast, large areas of tall grass and mixed prairie, a broad area of sandhills prairie in the center of the state and a small amount of coniferous forest in the northwest. Rainfall decreases from 970 mm/year in the southeast to 380 mm/-year in the west. Climate is strongly continental, with a mean annual temperature of 27°C, but annual extremes may range from -34°C to 41°C.

The flora of Nebraska was taken from the Atlas of the Flora of the Great Plains (published by the Great Plains Flora Association, 1977). Species in Nebraska were checked 1) against published lists of plants with EFNs (*e.g.*, Zimmermann, 1932; Schnell et al., 1963; Easu, 1965; Bentley, 1977a), 2) against descriptions in floras that include references to EFNs (especially Metcalfe and

Chalk, 1950; Gleason, 1963; Fernald, 1970; van Bruggen, 1976), 3) in monographs on genera and families, 4) in the field on living specimens and 5) in herbarium specimens.

Nectaries were defined in this study as sites which secrete nectar. Production of nectar (an aqueous sugar solution, sometimes with other compounds present (Baker and Baker, 1973; Bentley, 1977a; Baker et al., 1978) was sufficient to define a nectary, whether or not specialized structures were present. Extrafloral nectaries were distinguished from floral nectaries by the requirement that EFNs not function in attracting or rewarding pollinators. Thus the nectaries of the inflorescence of *Euphorbia (e.g., E. marginata)* or *Asclepias (e.g., A. syriaca)* are floral as defined here, although they are outside the flower. Conversely sepal nectaries, as in *Ipomoea leptophylla*, are considered extrafloral, although morphologically sepals are part of the flower. Species in Nebraska were classified by the above criteria as having or lacking EFNs.

It is impossible to determine whether all species which possess EFNs were detected. The list is conservative and does not include dubious cases. It is hoped that this paper will stimulate others to look for such species.

RESULTS AND DISCUSSION

It proved difficult to determine presence of EFNs. EFNs are rarely mentioned in floras, presumably because they are small and/or poor taxonomic characteristics. Many species in Nebraska are poorly known, so descriptions that might include EFNs are lacking. Many of the EFNs identified are ephemeral, functioning only for a few weeks (*e.g.*, the EFNs on the pods of *Yucca glauca* or the early leaves of *Ipomoea leptophylla*). Such EFNs may easily go unreported.

Of 1620 native or naturalized vascular plant species in Nebraska, 48 or 3.0% were found to have extrafloral nectaries (Table 1). EFNs are much more common in dicotyledonous plants (47 of 1228 species, 3.8%) than in monocotyledonous plants (1 of 392 species, 0.3%). Within the Dicotyledonae, a variety of families are represented. These include members of both relatively primitive and relatively advanced families on diverse phylogenetic lines: there is no simple phylogenetic pattern (see also Zimmerman, 1932; Elias, 1979). The low number of species with EFNs in the Monocotyledonae is, in part, a function of the large number of grasses (Poaceae) and sedges (Cyperaceae) in the Nebraska flora. EFNs are well developed in many orchid genera and in some species of the Iridaceae and Araceae (Zimmermann, 1932; Bentley, 1977a; Elias, 1979; pers obs.); in other regions EFN-bearing plants in the Monocotyledonae may not be so rare.

Patterns of presence and absense of EFNs within genera are dramatic. For example, only two out of 20 species of *Polygonum* in Nebraska *(P. convolvulus* and *P. sepium)* have EFNs. Since congeners occurring in Nebraska are not necessarily closely related, further analysis of patterns within taxa should be approached along phylogenetic lines. However, it should be noted that species in Nebraska with EFNs generally have Nebraskan congeners that lack EFNs.

The sites of EFNs on the plant vary greatly (Table 1). The most common single site is on the foliage (35/48, 73%). EFNs associated with vegetative part

Table 1. Angiosperms in Nebraska Known to Have Extrafloral Nectaries. Key to site of nectary: 1 on leaf; 2 on petiole; 3 on stipules; 4 on stems; 5 on pedicels, peduncles and stems in inflorescence; 6 on sepals and calyx; 7 on bracts; 8 on fruit, capsule or pod. NB: function of nectaries at sites 5-7 is not in attracting or rewarding pollinators.

ASTERACEAE
Centaurea cyanus 1
Helianthus annuus 1,7
H. grosseserratus 1,7
H. maximiliani 1,7
H. petiolaris 1,7
BALSAMACEAE
Impatiens bicolor 1
I. pallida 1
BIGNONIACEAE
Campsis radicans 1,5,6,8
Catalpa speciosa 1,5,8
CONVOLVULACEAE
Ipomoea leptophylla 1,5
I. pandurata 1,5
EUPHORBIACEAE
Croton glandulosus 2
FABACEAE
Cassia fasciculata 2
C. marilandica 2
Desmanthus illinoensis 1
Glycyrrhiza lepidota 1
Vicia glauca 3
LILIACEAE
Yucca glauca 8
ONAGRACEAE
Oenothera albicaulis 1
O. nuttallii 5, 8
O. pallida 1
POLYGONACEAE
Polygonum convolvulus 2
P. scandens 2
ROSACEAE
Prunus americana 1
P. angustifolia 1
P. besseyi 1
P. hortulana 1,6
P. serotina 1,6
P. virginiana 7
Rosa acicularis 2,3
R. blanda 3
R. multiflora 3
R. setigera 2, 3, 5
R. woodsii 3
SALICACEAE
Populus angustifolia 1
P. balsamifera 1
P. deltiodes 1
P. tremuloides 1
Salix alba 1,2
S. amygdaloides 1
S. caroliniana 1
S. exiqua 1
S. fragilis 1,2
S. lucida 1,2
S. petiolaris 1
S. rigida 1
SIMARUBACEAE
Ailanthus altissima 1
SOLANACEAE
Solanum nigrum 1,2,4

(leaves, stems, 46/48, 96%) are more common than those associated with buds, the outsides of flowers, or fruit (14/48, 29%). Note that the average plant with EFNs has them at 1.5 different sites (72/48) *i.e.*, plants tend to have more than one EFN system. The reason for this tendency is not obvious. Perhaps where one set of nectaries is advantageous, additional nectaries are also advantageous.

Frequency of EFNs in herbs in Nebraska was compared to frequency in woody plants. Of the 1572 species in the state without EFNs, 80 (6.0%) are woody, the rest herbaceous. Forty-eight species have EFNs: 28 (58.3%) are woody. This difference is statistically significant ($x^2 = 215.7$, $p < 0.001$, d.f. = 1).

The flora of Nebraska includes 45 vines. Of these, four (*Campsis radicans, Ipomoea pandurata*, and the two species of *Polygonum*) have extrafloral nectaries. The frequency (4/45, or 8.9%) is considerably higher than the frequency of species with EFNs in the state as a whole. The number is, however, much too small to test statistically.

The frequency of plants with EFNs among the species in the flora that are introduced but naturalized is 5/142 (3.5%). This is not significantly different from the frequency in native species (43/1435), ($x^2 = 0.172$, df = 1, $0.10 > p > 0.25$).

Arranging the species known to have EFNs by habitat there is no obvious pat-

tern: all the major ecosystems have some species with EFNs. There are 13 tall grass prairie species with EFNs, 11 sandhills prairie species, 22 forest species, 5 riparian species not found in other habitats, and 3 introduced species of disturbed sites only. If biogeographic patterns of the distribution of EFNs exist, apparently they must be looked for on either a larger (*e.g.*, temperate vs. tropical) or smaller (communities within a biome) scale.

Since no similar analysis has been done for a tropical flora, it is difficult to say whether the assertion that EFNs are more common in the tropics is valid (Gilbert in Orians, 1974; Bentley, 1977a). However, it seems likely that if the values for floras are as high as those for transects (Bentley, 1976; Keeler, 1979a) then indeed the frequency of temperate plants with EFNs is less, at least in Nebraska, as compared to Costa Rica. However, there also appear to be tropical habitats at moderate elevations which completely lack species with EFNs (Keeler, 1979a) while EFNs are known from high elevations in the Rocky Mountains (Inouye and Taylor, 1979). Considerably more data is required to settle this point.

Extrafloral nectaries have been shown to be involved in a mutualism with ants in the few cases studied to date. Some of these studies are tropical (Janzen, 1966a,b; Bentley, 1977b; Keeler, 1977; Schemske, 1978; Pickett and Clark, 1979). Temperate plants have also been shown to be protected by extrafloral nectary visitors. These include Nebraskan species *Prunus serotina* (Tilman, 1978), *Campsis radicans* (Elias and Gelband, 1975) and *Ipomoea leptophylla* (Keeler, 1979b), plus the Rocky Mountain sunflower, *Helianthella quinquenervis* (Inouye and Taylor, 1979). For these three species, mutualism with ants at extrafloral nectaries is expected in Nebraska. The other species with EFNs should be investigated for ant-plant mutualism.

Ants are found in all Nebraska ecosystems. Consequently, the possibility of mutualism with ants does not explain the peculiar distribution of extrafloral nectaries among Nebraskan plant species: the presence of EFNs on some species of a genus and not in others, how the different sites of the nectaries affect their activity and why there is a correlation with woodiness. These results require further investigation.

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