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Communication

Photographic Survey of the Occurrence of Bundle-Sheath Extensions in Deciduous Dicots

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ABSTRACT

In a survey of over 300 nonevergreen dicots in 69 families, many species were found to have translucent patterns attributed to the presence of bundle-sheath extensions (BSE) on the small and ultimate veinlets. The BSE have been shown by others to inhibit transverse air movement within leaves, and it has been suggested that they are important passageways between vascular tissue and the palisade. The only characteristic found to be associated with prominent BSE is that more trees have such features than herbaceous plants. However, many important herbs have them also, including soybeans and sunflowers.

BSE[2] have been described from cross-sections of leaves as plates of compact parenchyma tissue (fibrous bundle-sheaths are found on larger veins) extending in the ordinary case from the small leaf veins or veinlets to the upper and lower epidermises. Wylie (4–8) and Armacost (1) reported that the BSE are particularly common in the leaves of deciduous woody plants and that they are importance as conduits of water between the vascular tissue and the mesophyll via the epidermis. In addition, Meidner (2) and Terashima *et al.* (3) showed that these plates are barriers to the lateral movement of air within the leaf blade.

As is evident in one figure of ref. 7, these extensions, being relatively free of intercellular spaces and of chloroplasts, are much more translucent than the interveinal blade with palisade mesophyll. These "windows" are easily seen (with transmitted light) through a low-powered microscope or hand lens, as a reticulate network of bright lines on a green background. It is possible, therefore, to make a rapid survey of the distribution of the BSE by simple optical examination of fresh leaves. Although it is possible that some BSE may not be detected this way, particularly if they extend to only one epidermis, a typical BSE must be detected.

The present report summarizes a photographic survey of the distribution of BSE patterns in living, deciduous, dicot leaves.

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[2] Abbreviation: BSE, bundle-sheath extension(s).

MATERIALS AND METHODS

Fresh leaves were photographed in transmitted light with a 35-mm single-lens reflex camera attached to a 19-cm bellows extension with a 20-mm, f/3.5 lens, giving about 13× magnification at the film. The leaf sample was pressed against a hole in a metal plate by a microscope slide held in place by clips. The upper (adaxial) surface of the leaf faced the lens.

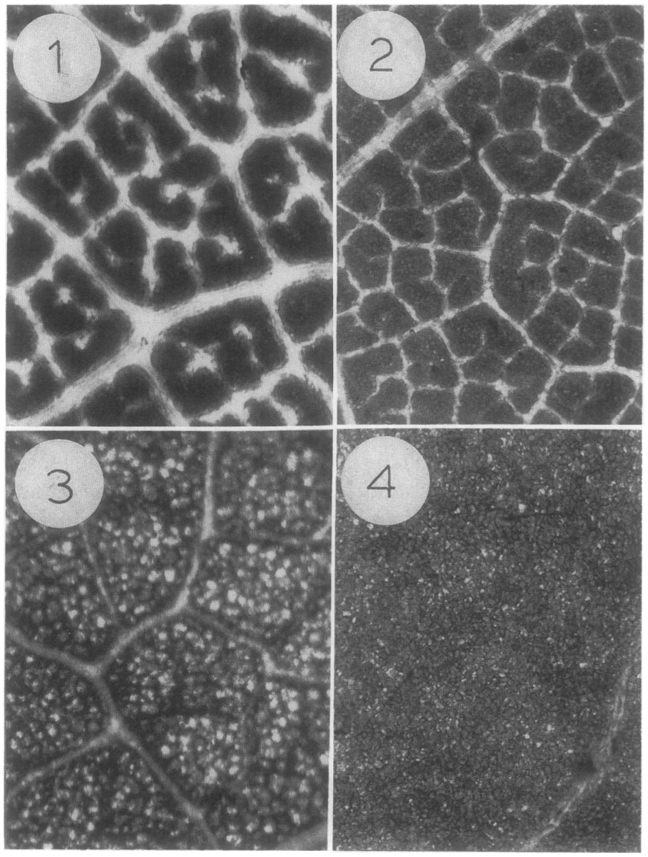
All leaves were from dicots, and were selected from broadleaf, deciduous trees, shrubs, or vines, or from annual or perennial herbs or vines. A few leaves had dark veins instead of bright ones (*Amaranthus* sp., *Gomphrena* sp.), which are presumed to be C-4 leaves. Sampling was of native, cultivated and weedy plants, mostly in southeast Nebraska.

Two different methods were used to classify the contact prints. For the first, two lines were placed across the photograph (*i.e.* 48 mm on the film, or about 3.7 mm of the leaf) and the number of sharply visible veins that touched the lines were counted. For convenience in tabulation, these numbers were pooled into six "vein density" groups that had the following designations and ranges: A (28–22 veins/3.7 mm), B (21–16), C (15–12), D (11–8), E (7–4), F (3–0).

The second measure was a subjective assessment ("visual index," ranging from 4 to 0) of the optical importance of the visible veins. This attempted to give credit to the optical contrast between the veins and leaf mesophyll, as well as to the extent of the network. The two measures were highly correlated ($r = 0.85$).

RESULTS AND DISCUSSION

Figures 1 through 4 show representative photographs of the range of leaf patterns found. Wylie (7) shows transverse and paradermal sections of similar variants. More than 300 species in 69 families of dicots were examined. In each of 10 orders (Asterales, Dipsacales, Fabales, Fagales, Lamiales, Polygonales, Ranunculales, Rosales, Salicales, Sapindales; including 20 families and almost two-thirds of the whole set of species), 8 or more species were sampled. When average values were taken, the orders fell in a similar series whether scored by vein density or visual index, but in none of these well-represented orders is there uniformity of structure. Most of the orders with mostly woody representatives have higher values of the average indices. However, herbaceous samples in the Asterales (47 species) and Fabales (23 species) fell in all categories. The remaining 30 orders, taken as a whole,



Figures 1–4. Transmission photographs of leaves showing BSE categories. The short dimension of each photograph is about 1 mm of the leaf. Fig. 1. *Populus deltoides* Marsh. Classes A, 4. Fig. 2. *Abutilon theophrasti* Medic. Classes A, 3. Fig. 3. *Quercus borealis* Michx. f. Seedling shade leaf; note extreme transmissivity of mesophyll, in addition to the BSE. Classes E, 2. Fig. 4. *Taraxacum officinale* Weber. Classes F, 0.

resembled the above 10 orders taken as a whole, but 10 orders had no samples with other than a vein density of F.

Of the trees (75 species), about 59% were scored as A, B, or C (vein density), whereas only 25% of the shrubs (62 species) and 13% of the herbs (176 species) fell in this range. Also, only two examples of the lowest category (F) were found among the trees, whereas about half of the herbs were in this category (see Table I). A list of the species sampled having high values of BSE importance (vein density or visual index) is given in Table II. Some other popular experimental objects, such as tobacco or tomato, appear in the uniformly patternless category. A computer printout of the full data set is available from the author.

Insufficient replication was obtained for good statistical analysis, but no indication was found of environmental association with these anatomical differences, except for the well-known differences between sun and shade leaves. Here, the thinner shade leaves were much more translucent, making the contrast between BSE and mesophyll less clear, and the visible veins were somewhat farther apart. Thicker evergreen leaves have less prominent BSE (8).

The presence or absence of the BSE must have physiological significance for photosynthesis, water relations, and/or other functions, but further discussion would be merely speculative at this time.

ACKNOWLEDGMENT

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Table I. *Distribution of 313 Samples among Vein-Density Groupings*

	A	B	C	D	E	F	No.
				%			
Trees	13	21	25	23	15	3	75
Shrubs	3	6	16	21	24	29	62
Herbs	3	4	6	11	20	56	176
Total	5	9	13	16	20	38	313

Table II. *List of Species with Prominent Visible BSE*
Vein density is A or B; and/or visual index is 4 or 3.

Species	Family	Species	Family
Herbs		*Acer saccharinum* L.	Aceraceae
Abutilon theophrasti Medic.	Malvaceae	*Acer saccharum* L. (2)	Aceraceae
Amphicarpa bracteata (L.) Fern.	Fabaceae	*Aesculus glabra* Willd.	Hippocas-tanaceae
Asclepias syriaca L.	Asclepiadaceae		
Baptisia bracteata Muhl. ex Ell.	Fabaceae	*Ailanthus altissima* (P. Mill.) Swingle	Simaroubaceae
Desmodium illinoense A. Gray	Fabaceae		
Eupatorium rugosum Houtt.	Asteraceae	*Alnus rubra* Bong. (2)	Betulaceae
Fragaria sp.	Rosaceae	*Betula lutea* Michx.	Betulaceae
Glycine max (L.) Merr. (2)[a]	Fabaceae	*Carya cordiformis* (Wang.) K. Koch	Juglandaceae
Grindelia squarrosa (Pursh) Dun.	Asteraceae	*Catalpa speciosa* Warder	Bignoniaceae
Helianthus annuus L.	Asteraceae	*Celtis occidentalis* L. (2)	Ulmaceae
Helianthus tuberosus L.	Asteraceae	*Cercis canadensis* L. (2)	Caesalpiniaceae
Potentilla arguta Pursh	Rosaceae	*Cladastris lutea* (Michx. f.) K. Koch	Fabaceae
Psoralea tenuiflora Pursh	Fabaceae	*Fraxinus pennsylvanica* Marsh. (3)	Oleaceae
Silphium integrifolium Michx. (2)	Asteraceae	*Gymnocladus dioica* (L.) K. Koch	Caesalpiniaceae
Silphium laciniatum L.	Asteraceae	*Juglans nigra* L.	Juglandaceae
Silphium perfoliatum L.	Asteraceae	*Koelreuteria paniculata* Laxm.	Sapindaceae
Solidago gigantea Ait. (2)	Asteraceae	*Morus rubra* L.	Moraceae
Solidago rigida L. (4)	Asteraceae	*Ostrya virginiana* (P. Mill.) K. Koch	Betulaceae
Verbena stricta Vent.	Verbenaceae	*Platanus occidentalis* L.	Platanaceae
Xanthium strumarium L. (2)	Asteraceae	*Populus deltoides* Marsh. (2)	Salicaceae
Shrubs		*Prunus persica* (L.) Batsch.	Rosaceae
Amorpha canescens Pursh	Fabaceae	*Quercus macrocarpa* Michx.	Fagaceae
Amorpha fruticosa L.	Fabaceae	*Quercus palustris* Muench.	Fagaceae
Ceanothus herbaceus Raf.	Rhamnaceae	*Quercus borealis* Michx. f.	Fagaceae
Cotinus coggygria Scop.	Anacardiaceae	*Robinia pseudoacacia* L. (2)	Fabaceae
Prunus americana Marsh. (2)	Rosaceae	*Salix amygdaloides* Anderss. (2)	Salicaceae
Rhus glabra L.	Anacardiaceae	*Sophora japonica* L.	Fabaceae
Rosa arkansana Porter	Rosaceae	*Tilia americana* L. (2)	Tiliaceae
Salix nigra Marsh.	Salicaceae	*Tilia europaea* L.	Tiliaceae
Spiraea vanhouttei (Briot.) Zabel	Rosaceae	*Ulmus americana* L.	Ulmaceae
Staphylea trifolia L.	Staphyleaceae	Vines	
Trees		*Humulus lupulus* L.	Cannabaceae
Acer grandidentata Nutt.	Aceraceae	*Sicyos angulatus* L.	Cucurbitaceae
Acer macrophyllum Pursh	Aceraceae	*Toxicodendron radicans* (L.) O. Ktze.	Anacardiaceae
Acer negundo L.	Aceraceae		
Acer platanoides L.	Aceraceae	*Wisteria macrostachya* Nutt.	Fabaceae

[a] Numbers in parentheses denote numbers of specimens if more than one.