Comparative anatomy of the leaves and stems of Encelia (Asteraceae: Heliantheae)

Scott R. Koukol and Curtis Clark

Biological Sciences, California State Polytechnic University, Pomona CA 91768, and Rancho Santa Ana Botanic Garden, Claremont CA 91711

Introduction

It is well-established that internal anatomy may reflect adaptation to environmental constraints; the suites of features that characterize xeromorphic and hydromorphic leaves, for example, are standard fare in basic botany courses. It is also well-known that internal anatomy may reflect phylogeny, and in fact anatomical features are commonly used in phylogenetic reconstruction. In Encelia, adaptation and phylogeny are not precisely aligned. The genus resolves into two major clades (called the californica clade and the frutescens clade) using either a suite of phenotypic features or sequences of the internal transcribed spacer (ITS) of nrDNA. Each of these clades contains species with dense leaf pubescence that shades the leaf and thus reduces midday leaf temperatures, and other species with effectively glabrous leaves, that either rely on transpirational cooling or are drought-decidual. The purpose of this study is to examine the anatomy of leaf blades and petioles, peduncles, and young and older vegetative stems, to determine if the anatomy reflects phylogeny, adaptation, both, or neither. This poster reports on leaf blades and petioles only.

Materials and Methods

Samples were collected from plants growing in containers outdoors on the roof of a building at California State Polytechnic University, Pomona. Tissues were fixed in FAA (formalin, propionic acid, ethanol) and dehydrated in a TBA (tertiary butyl alcohol) series before paraffin embedding. Prior to sectioning, embedded tissues were softened in a 10:3:90 solution (by volume) of Aerosol OT, glycerine and water. After sectioning, specimens were stained in a series of solutions of zinc chloride, safranin, orange G, tannic acid mixture, tannic acid and iron alum (Sharman, 1943), mounted on microscope slides, and photographed.

Results

E. farinosa var. radians

E. exsiccans

E. californica

E. ventorum

E. asperifolia (Stabilized hybrid of E. frutescens and E. californica)

Discussion

This study has clarified the status of a phylogenetically significant anatomical difference pointed out in previous studies: resin ducts are present in the frutescens clade, at least in E. actoni. This observation actually strengthens the observed differences in secondary chemistry between the clades: they can no longer be attributed simply to the lack of resin ducts in one clade. Leaf petioles are most likely to show phylogenetic differences rather than adaptive differences: in Encelia they are of similar size and texture among the species, and would be expected to be differentially adapted only for drought-deciduousness. In fact, the petioles show little difference among the species examined.

Leaf blades, on the other hand, show strong differences in their external anatomy that relate to differing approaches to dealing with water stress and other environmental factors. Thus it would be expected that internal anatomy might better reflect adaptation than phylogeny.

Despite the clear external differences among the leaves of the species studied, the internal differences are minor. The greatest difference is seen in E. ventorum, where the highly dissected leaf forms cylinders of somewhat succulent mesophyll around groups of vascular bundles.

Internal differences in stem anatomy are expected: all members of the frutescens clade and some of the californica clade have thick bark on older stems, but E. farinosa has stems with a thin bark and a thick active secondary phloem that evidently serves as a site of food storage. Data are not yet available to address these differences, nor possible differences in peduncles.

Conclusions

These preliminary studies suggest that internal leaf anatomy does not strongly differentiate the species of Encelia, and thus does not clearly conform to either adaptation or phylogeny. Several other lines of evidence, including interfertility and little differentiation in ITS sequences, suggest that the species are recently evolved, and internal anatomy is consistent with that hypothesis. This serves to make the adaptations of the individual species even more remarkable, as they are all based on a common architecture.

Acknowledgments

We would like to thank Travis Columbus, Doug Moore, Maria Elena Siqueiros, and Victor Steinmann for countless courtesies extended in the anatomy lab of Rancho Santa Ana Botanic Garden. Bob Koukol provided assistance in the field.

Literature Cited

Sharman, B.C. 1943. Tannic acid and iron alum with safranin and orange G in studies of the shoot apex. Stain Technology 3:105-111.