Pacific Science (1985), vol. 39, no. 2

Tissue Elastic Properties of a Mesic Forest Hawaiian *Dubautia* Species with 13 Pairs of Chromosomes[1]

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ABSTRACT: *Dubautia reticulata* grows in a mesic forest habitat in Hawaii and has 13 pairs of chromosomes. The tissue elastic properties of this species are intermediate relative to those of the dry scrub, 13-paired *D. menziesii* and the mesic forest, 14-paired *D. knudsenii*. The tissue elastic modulus near full hydration, for example, is 3.5 MPa in *D. menziesii*, 6.1 MPa in *D. reticulata*, and 18.2 MPa in *D. knudsenii*. As a result of its intermediate tissue elastic properties, *D. reticulata* exhibits an intermediate capacity for maintaining high turgor pressures as tissue water content decreases. These results imply that tissue elastic properties are significantly associated both with the habitat in which a *Dubautia* species grows and with its diploid chromosome number. The latter association is presumably indirect, with the difference in chromosome number serving as a marker for other significant genomic differences.

SIGNIFICANT INTERSPECIFIC VARIATION exists in the tissue elastic properties of the endemic Hawaiian species of *Dubautia* (Compositae). The pattern of variation in these properties appears to be correlated with the pattern of variation in the habitats and diploid chromosome numbers of these species (Robichaux 1984, Robichaux and Canfield 1985). Species that grow in dry habitats and have 13 pairs of chromosomes exhibit significantly lower tissue elastic moduli near full hydration (E_i) than species that grow in mesic to wet habitats and have 14 pairs of chromosomes. Values of E_i range from 2 to 4 MPa among the former species and from 9 to 18 MPa among the latter species. As a result, the capacity for maintaining high turgor pressures as tissue water content decreases is much greater in the 13-paired species from dry habitats than in the 14-paired species from mesic to wet habitats. Since a variety of physiological processes, such as stomatal opening and photosynthetic carbon assimilation, appear to exhibit a significant turgor dependence (Hsiao et al. 1976, Ludlow 1980, Turner and Jones 1980), the former species may be able to tolerate conditions of low moisture availability to a much greater extent than the latter species.

Among the nine *Dubautia* species whose tissue elastic properties have been examined, habitats and diploid chromosome numbers have been correlated. All four 13-paired species have been from dry habitats, while all five 14-paired species have been from mesic to wet habitats (Robichaux 1984, Robichaux and Canfield 1985). Hence, it has not been possible to evaluate the relative importance of these two factors in terms of their association with tissue elastic properties. In this study, I assess their relative importance by examining the tissue elastic properties of *D. reticulata*, a 13-paired species that grows in a mesic habitat (Carr and Kyhos 1981).

MATERIALS AND METHODS

Branches of *Dubautia reticulata* were collected from a population at 1875 m elev. on the east side of Koolau Gap, Haleakala, Maui. The mesic forest at this site is dominated by *Metrosideros polymorpha*, with the arborescent *D. reticulata* occurring as a common

[1] This research was supported by National Science Foundation grant DEB 82-06411 and by a gift from the Atlantic Richfield Foundation. Manuscript accepted 30 November 1984.

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species in the canopy. Annual rainfall is approximately 2000–2500 mm (DLNR 1982).

The tissue elastic properties of *Dubautia reticulata* were analyzed during late May 1984, following the procedures outlined in Robichaux (1984). The tissue elastic modulus (E) is defined as

$$E = \frac{dP}{dR}(R - R_a) \qquad (1)$$

where P is the tissue turgor pressure, R is the tissue relative water content, and R_a is the relative water content of the tissue apoplasm, or the apoplasmic fraction. The finite form of equation (1) was used to calculate the value of E near full hydration (E_i).

A total of six branches from four individuals were analyzed, including duplicate branches from two individuals. Values of E_i in the duplicate branches differed by less than 0.53 MPa. The mean apoplasmic fraction for the four individuals was 0.23 ± 0.01, which is within the range of values reported for the *Dubautia* species (Robichaux 1984, Robichaux and Canfield 1985).

The data for *Dubautia reticulata* are compared in the following analysis with those for *D. menziesii* and *D. knudsenii*. The 13-paired *D. menziesii* grows in a dry scrub habitat on the leeward slopes of Haleakala, where annual rainfall is approximately 1000–1200 mm (DLNR 1982). The 14-paired *D. knudsenii*, in contrast, grows in a mesic forest habitat on Kauai, where annual rainfall is approximately 2000–2500 mm (DLNR 1982). Hence, *D. reticulata* and *D. menziesii* have the same chromosome number but grow in different habitats, while *D. reticulata* and *D. knudsenii* grow in similar habitats but have different chromosome numbers. The data for *D. menziesii* and *D. knudsenii* were obtained from Robichaux and Canfield (1985).

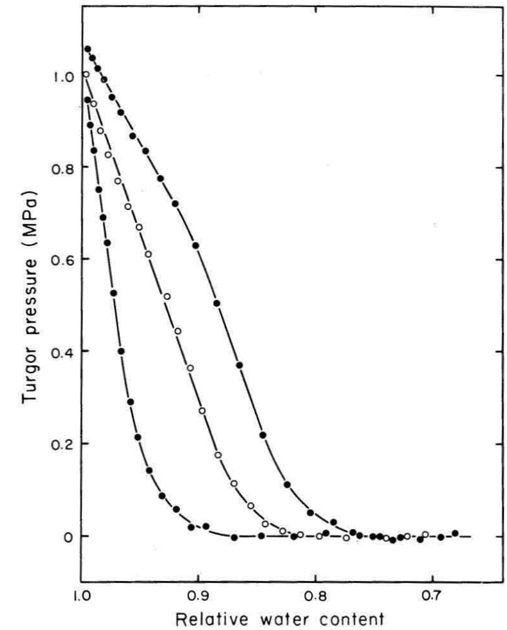

FIGURE 1. Relationship between tissue turgor pressure and tissue water content for *Dubautia reticulata* (open symbols), *D. menziesii* (closed symbols, upper curve), and *D. knudsenii* (closed symbols, lower curve). Data for *D. menziesii* and *D. knudsenii* are from Robichaux and Canfield (1985).

RESULTS

The tissue elastic modulus near full hydration in *Dubautia reticulata* is intermediate relative to that in *D. menziesii* and *D. knudsenii*. The value of E_i in *D. reticulata* is 6.07 ± 0.99 MPa (mean $\pm$ 1 SD, $n = 4$). For comparison, values of E_i in *D. menziesii* and *D. knudsenii* are 3.51 ± 0.67 MPa ($n = 5$) and 18.23 ± 1.02 MPa ($n = 6$), respectively (Robichaux and Canfield 1985). The differences in E_i among the various species are all statistically significant at $p < 0.05$.

The large differences in E_i among the three species are related directly to large differences in their capacities for maintaining high turgor pressures as tissue water content decreases (Figure 1). Maximal values of turgor pressure in the three species are similar, reflecting the fact that their tissue osmotic potentials at full hydration are not significantly different (-1.12 ± 0.04 MPa in *D. menziesii*, -1.10 ± 0.01 MPa in *D. reticulata*, and -1.07 ± 0.05 MPa in *D. knudsenii*). However, the initial rates at which turgor pressure declines with decreasing tissue water content differ markedly, with *D. reticulata* exhibiting an intermediate rate relative to the other two species. These differences are reflected in the intermediate value of E_i in *D. reticulata*. The effect of these differences on the magnitude of tissue turgor pressure at moderate tissue water contents is very pronounced. At a relative water content of 0.90, for example, the value of turgor pressure is 0.61 MPa in *D. menziesii*, 0.30 MPa in *D. reticulata*, and 0.02 MPa in *D. knudsenii*. The differences in E_i also influence the relative water contents at which zero turgor pressure is reached in the three species. These values are 0.76 in *D. menziesii*, 0.82 in *D. reticulata*, and 0.87 in *D. knudsenii*.

DISCUSSION

Tissue elastic properties appear to be significantly associated both with the habitat in which a *Dubautia* species grows and with its diploid chromosome number. The association with habitat is apparent in the comparison between *D. reticulata* and *D. menziesii*, since these two species have the same chromosome number but grow in different habitats. In this instance, the species from the more mesic habitat has the higher tissue elastic modulus near full hydration. This difference presumably reflects genotypic rather than phenotypic differentiation, since the degree of phenotypic variation in the tissue elastic properties of the 13-paired *Dubautia* species appears to be very limited (Robichaux 1984)

The association with diploid chromosome number is apparent in the comparison between *Dubautia reticulata* and *D. knudsenii*, since these two species grow in similar habitats but have different chromosome numbers. In this instance, the species with the higher chromosome number has the higher tissue elastic modulus near full hydration. This association is presumably indirect, with the difference in chromosome number serving as a marker for other significant genomic differences.

The difference in tissue elastic properties between *Dubautia reticulata* and *D. knudsenii* may be an example of the influence of phylogenetic constraint (Gould and Lewontin 1979). All twelve 14-paired *Dubautia* species grow in mesic to wet habitats, while seven of the nine 13-paired species grow in dry habitats (Carr 1978, Carr and Kyhos 1981). The 13-paired species appear to have evolved as a monophyletic group from a 14-paired ancestor (Carr and Kyhos 1981), with the arborescent *D. reticulata* representing a specialized development among the 13-paired species. *Dubautia reticulata* may thus exhibit certain physiological constraints associated with its having evolved from a lineage of dry habitat, 13-paired species. As a result, even though it grows in a mesic habitat, *D. reticulata* may be precluded from acquiring tissue elastic properties similar to those of *D. knudsenii*, which evolved from a lineage of mesic to wet habitat, 14-paired species.

ACKNOWLEDGMENTS

I thank G. Carr and D. Kyhos for sharing their knowledge of the ecology and evolutionary biology of the Hawaiian *Dubautia* species. I also thank A. Holt and T. Quisenberry of the Nature Conservancy of Hawaii for generous access to Waikamoi Preserve; B. Cooper, R. Nagata, and L. Loope of Haleakala National Park for important logistical support; and A. Medeiros, L. Stemmermann, and E. Funk for invaluable field assistance.

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