Intra-specific variation in plant hydraulic sectoriality along a latitudinal gradient

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Introduction

High temperatures and nutrient limitations in deserts challenge plant survival[1]. Large temperature oscillations and droughts typical of cold deserts can result in cavitation[2], the precipitation of dissolved air within a xylem vessel. If xylem vessels are closely packed, then a cavitation event may expand to neighboring vessels, resulting in runaway embolism, and potentially paralyze the vital functions of the plant[3].

Hydraulic sectoriality, where the plant is functionally composed of independent hydraulic units, has been suggested as a strategy to decrease the risk associated with cavitation[4]. This can occur by increasing xylem vessel isolation and/or increasing the physical modularity of the plant. Furthermore, hydraulic sectoriality could enhance a plant's survival in the heterogeneous distribution of resources common to deserts by decreasing the spread of nutrients throughout the plant[4].

Previous work has reported a higher frequency of sectored woody species with aridity[5], but we still lack a basic understanding of how variable this physiological trait is among individuals in the same population and among different populations of the same species. This information is critical for the further consideration of sectoriality as a potentially adaptive trait, since natural selection operates on variation.

Materials and Methods

We explored the degree of hydraulic sectoriality of the desert chamaephyte *Cryptantha flava* (Boraginaceae; fig.1) throughout its range of distribution. We randomly collected caudex (underground stem) samples from 8 individuals of 8 populations ranging 673 km in latitude (Fig. 3). Samples were fixed *in situ* (FAA), mounted in a histological resin, and sliced by the rotary microtome. We measured the perimeter (P), area (A), and diameter of each sample, and used caudex diameter as a proxy to ontogeny. We estimated the degree of sectoriality with three measurements:

① ***C index***[6]: Xylem aggregation

$$C = \frac{\sum_{i=1}^{N}\left[\frac{x_i^2}{\left(x_i^2+\frac{1}{2}y_i^2\right)}\right]}{N}$$

(N= 30 measurements); C > 0.5 → aggregated pattern

x=distance between a random point and the nearest xylem vessel
y=distance between that xylem vessel and its nearest xylem vessel

② ***S index***[5]: Physical fragmentation

$S \propto \text{Fragmentation} = P\cdot\pi^{1/2}/(A^{1/2}\cdot 2\pi)$

③ ***Xylem lumen***

We then correlated *C*, *S* and xylem lumen with plant ontogeny, and explored whether the relationships are population-specific using 2-way ANOVAs and ANCOVAs.

Finally, we calculated differences among the eight populations based on long-term temperature and precipitation data[7], and used principal components analyses to establish whether abiotic factors may affect the degree of sectoriality among populations.


Figure 1. *Cryptantha flava.*

BIOTIC DIFFERENCES

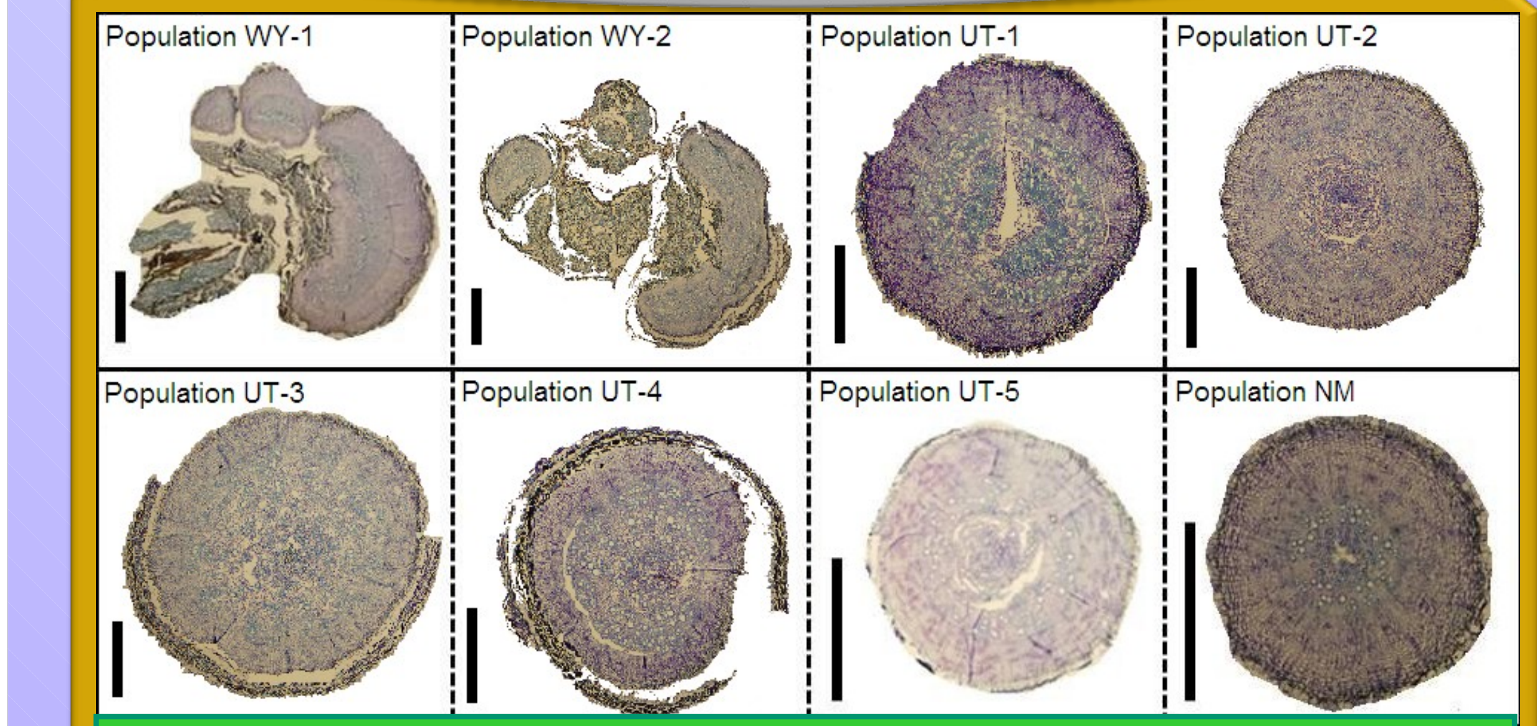


Figure 2. Caudex 5μm cross-sections, organized by decreasing latitude (See fig. 3). Black bar indicates 1 mm.

		C	S	Xylem Lumen
t-test	Diameter	$0.29^{n.s.}$	**7.53*****	**3.44****
2-way ANOVA	Diameter	$1.1^{n.s.}$	**39.63*****	**10.10****
	Population	**3.54****	**2.54***	$1.46^{n.s.}$
	Diameter x Population	$1.35^{n.s.}$	$1.86^{n.s.}$	$1.43^{n.s.}$
ANCOVA	Diameter	**1.11***	**50.76*****	**13.90*****
	Population	$3.33^{n.s.}$	**2.34***	**2.31***

Table 1. *t*-ratios and *F*-ratios of correlations between the degree of sectoriality, plant diameter, and population origin.

***P<0.05; **P<0.005; ***P<0.001;** n.s.: P >0.05

ABIOTIC DIFFERENCES

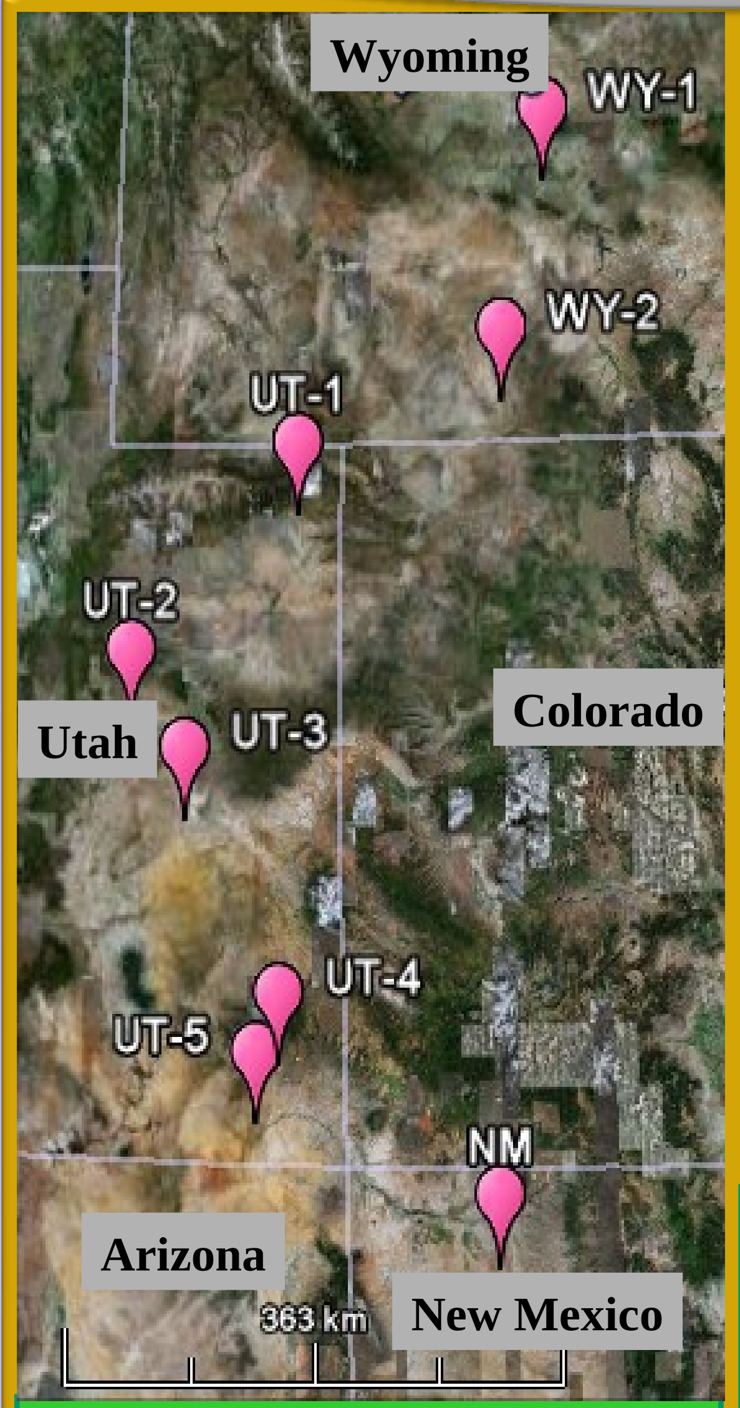


Figure 3. Map of sampled populations of *C. flava*.

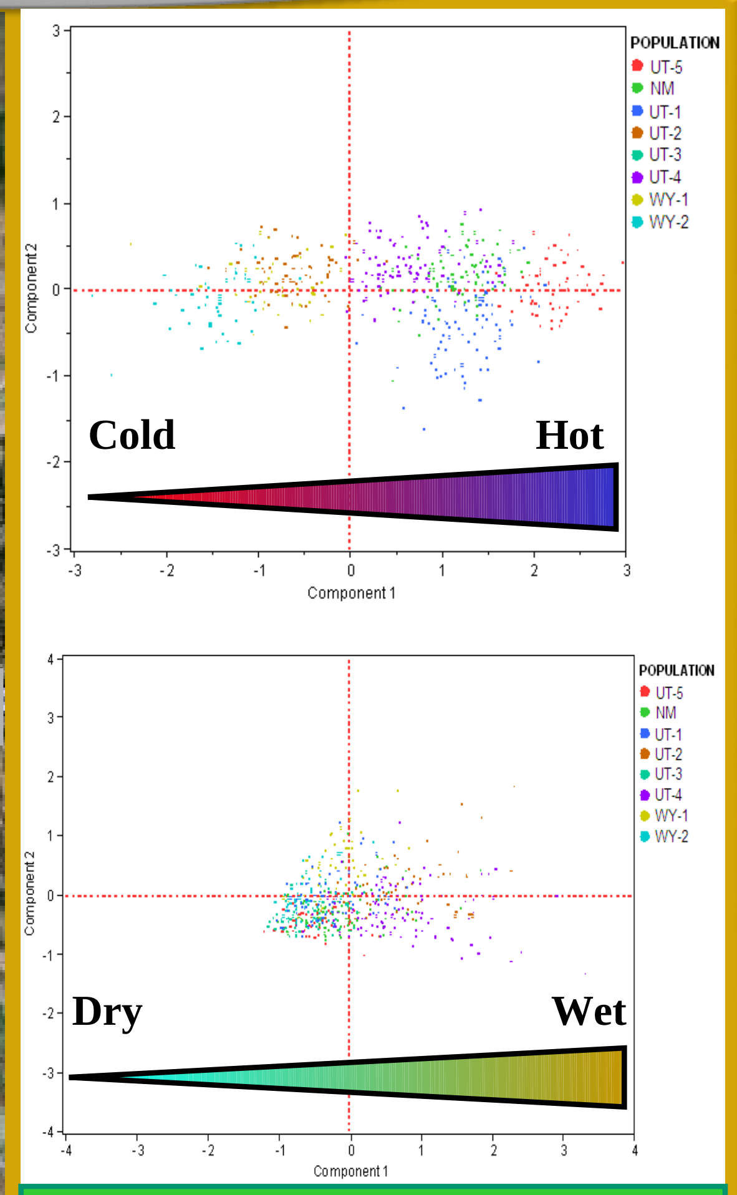
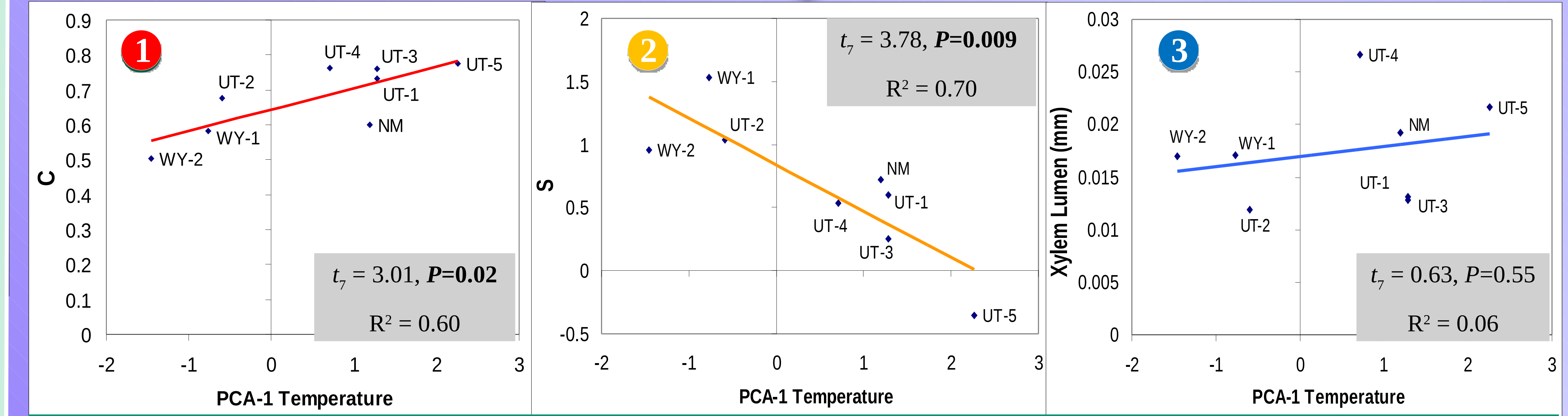


Figure 4. Principal component analyses for the sampled populations based on their long-term monthly average temperature (top) and monthly total precipitation (bottom).

Does climate explain differences in hydraulic sectoriality among populations?



$t_7 = 3.01$, $\boldsymbol{P=0.02}$; $R^2 = 0.60$

$t_7 = 3.78$, $\boldsymbol{P=0.009}$; $R^2 = 0.70$

$t_7 = 0.63$, $P=0.55$; $R^2 = 0.06$

Figure 5. Correlations of the various indexes of sectoriality with differences in temperature among populations (Axis PCA-1, fig. 4, top).

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Citations: [1]**Ehleringer, J. 1980**. In *Adaptations of plants to water and high temperature stress*. [2]**Davis SD et. al. 1999.** *American Journal of Botany*. [3]**Orians CM et. al. 2005.** In *Vascular transport in plants*. [4]**Schenk HJ. 1999**. *Plant Ecology*. [5]**Schenk HJ et. al. 2008.** *PNAS*. [6]**Gibson DJ. 2002**. *Methods in comparative plant population ecology*. [7]http://www.wrcc.dri.edu/index.html.

Results

- Xylem lumen and physical modularity (*S*) correlated positively with ontogeny, but xylem aggregation (*C*) did not.
- The rates with which individuals become more sectored through ontogeny (slope of sectoriality index-diameter correlations, table 1) were not different among populations, but the mean degree of sectoriality (intercept) was population-specific.
- The sampled populations were more distinct based on temperature (PCA-1 T: 64.5%; fig. 4 top), than on precipitation (PCA-1 P: 24.5%; fig. 4 bottom) or elevation (not shown).
- Xylem aggregation (*C*) correlated positively with temperature, while physical modularity (*S*) correlated negatively with temperature (Fig. 5). Although xylem lumen was population-specific, differences in T, P or elevation did not satisfactorily explain such differences.

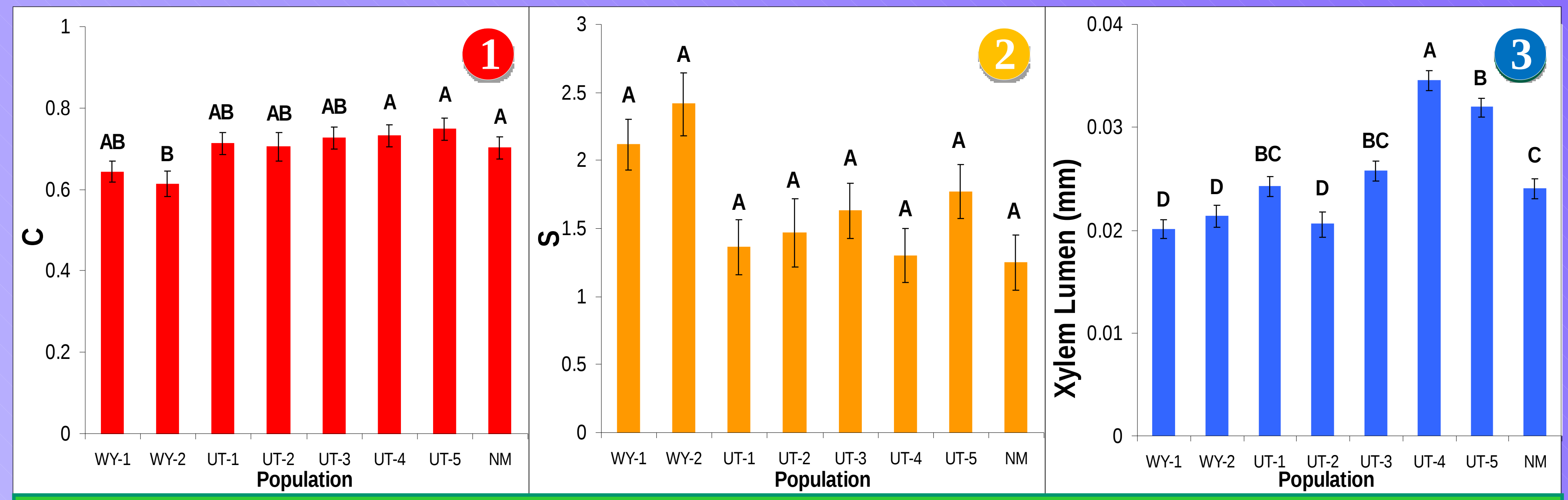

Figure 6. Tukey-Kramer HSD tests for the degree of sectoriality in each population as explained by differences in temperature among populations (Axis PCA-1, fig. 4 top). Populations are ranked from left to right by decreasing latitude (Fig. 3).

Discussion

We found significant intra-specific differences in the degree of hydraulic sectoriality for several populations of the desert chamaephyte *Cryptantha flava*. Such differences correlated with temperature, but not with precipitation or elevation (not shown). Our findings suggest that there are multiple abiotic factors –not only precipitation, as previously suggested[5]– to consider when evaluating the shaping forces behind plant sectoriality.

We suggest that the development of physical modules and xylem aggregation through the ontogeny of *C. flava* may have habitat-specific complementary roles. Physical modularity may satisfactorily isolate cavitation events within a single module, which can in turn be sacrificed without endangering the rest of the individual. Because the degree of physical modularity is greater in colder habitats, this trait may be of particular importance for coping with freeze-thaw cavitations. On the other hand, xylem aggregation may be more advantageous for individuals in temperature-induced drought habitats since the degree of xylem aggregation is greater in hotter habitats.

The abiotic factors behind the population-level variation in xylem lumen remain unanswered – neither temperature, precipitation, nor altitude explains the pattern.