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Formation of false stems in *Cymopterus longipes*: an uplifting example of growth form change

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Summary. The leaves of *Cymopterus longipes* form prostrate rosettes early in the spring. As the weather warms, these leaves are elevated on a pseudoscape (false stem) which develops below the rosette through the elongation of the caudex (in the region between root and shoot). The effect of this growth form change on the water relations and photosynthesis in *C. longipes* was investigated. Pseudoscape height was not linked to phenology or plant size. Leaf conductance, leaf temperature, and leaf water potential were notably similar between plants with different pseudoscape height growing in different microsites. Experimental manipulation of the microclimate around plants growing naturally allowed us to demonstrate that increased temperature led to an increase in the rate of pseudoscape elongation. By changing the distance above the ground surface of the rosettes of some plants we determined that leaf temperature, leaf to air vapour concentration deficits, leaf conductances, and leaf water potentials were all influenced by pseudoscape height. Leaf conductance in *C. longipes* had a strong negative relationship with ΔW. Since the temperature response of net photosynthesis was extremely flat it was concluded that pseudoscape elongation may be an important morphological means of increasing water use efficiency.

Plants are in general sessile organisms and as such they must endure unfavorable climatic conditions which may occur during their lifetimes. Many morphological plant traits have been shown to be associated with the alleviation of abiotic stresses so that active growth can be extended into less favourable periods. At the leaf level, gradual changes in surface characteristics which change spectral absorption properties have been shown to be important in avoiding excessive leaf temperatures in some desert shrubs (Ehleringer and Werk 1986) and reversible leaf movements are often used to avoid short term stresses (Ehleringer and Forseth 1980; Powles and Björkman 1981). At the canopy level, there are indications that plants can change their position within the microclimatic profile via changes in internodal length. Growth form changes in desert annuals appear to be related to the onset of hot weather (Mulroy and Rundel 1977). These annuals initially grow with prostrate leaves in rosettes, then either grow stems with leaves elevated above the soil surface or simply increase internodal distance.

Cymopterus longipes, a member of the Umbellifereae, demonstrates another mode by which growth form can change over the course of a season. The position of *C. longipes* leaves within the microclimatic profile changes in an unusual manner. Plants initially form a rosette with prostrate leaves which remains close to the ground early in the spring. Instead of losing leaves as the weather warms and replacing them with new cauline leaves, a pseudoscape (false stem) develops below the rosette leaves through the elongation of the caudex (in the region between root and shoot). This process effectively elevates the leaves up off the ground surface. Descriptions of *C. longipes* indicate pseudoscapes can elongate up to 150 mm (Mathias 1930). (Fig. 1).

The consequences of this phenomenon were investigated in this study. The hypothesis investigated was that caudex elongation in *C. longipes* was related to its microsite temperature. It is further suggested that the elevation of the leaves above the ground surface was beneficial to plant performance through the reduction in subsequent water loss and increase in the ratio of assimilation to water loss.

Methods

All measurements were done on naturally occurring plants during 1983. The field site was located in the grassland foothills of the Wasatch Mountains above the University of Utah, Salt Lake City, Utah (latitude 41° N, longitude 112° W).

Measurements of pseudoscape height represent the distance from the soil surface to the underside of the rosette

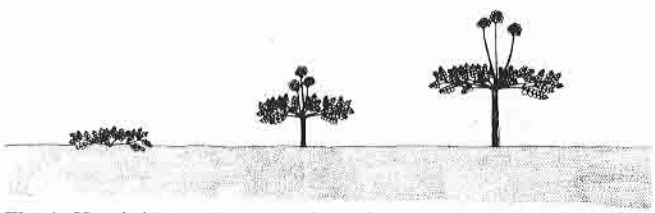

Fig. 1. Hand drawn representation of a *Cymopterus longipes* individual in successive stages of pseudoscape formation. The rosette of leaves is gradually elevated off of the ground as the caudex below it elongates

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of leaves. Several parameters were measured to test for correlations with pseudoscape height. These included leaf temperature, plant size, floral phenology, leaf water potential, and leaf conductance to water vapour. Leaf temperatures were measured with a 36 gage copper/constantan thermocouple connected to a Bat-9 thermocouple meter (Bailey Instruments, Saddle Brook, NJ, USA). Leaf water potential was measured using a pressure chamber (PMS Instruments, Corvallis, OR, USA). Measurements of leaf water potential were made on both overcast day and clear days. Leaf conductance to water vapour was measured using a null balance porometer similar to the one described by Forseth and Ehleringer (1983). Photosynthetic gas exchange was measured on intact leaves under field growth conditions using a null balance gas exchange system (Armstrong Enterprises, Palo Alto, CA, USA), which was similar to that previously described by Field et al. (1982). Phenology was followed throughout the active vegetative cycle and qualitatively scored according to the following index: 1 = pre-flowering; 2 = flower stalks present; 3 = flowers open; 4 = seeds being filled. Intermediate scores were given to plants which met more than one criterion. Plant size was assessed by measuring rosette diameter. Rosette diameter was a very good index of leaf area (leaf area $= 9.69 + 0.001^*$ diameter$^{2.21}$; $r^2 = 0.94$, $n = 31$, $P < 0.01$).

The above mentioned parameters were measured independently of each other on separate plants. In each case, measurements were collected during midday of clear days unless otherwise stated.

An experiment was performed to assess the effect of microclimate temperature on caudex elongation. In order to test whether increased temperature would increase the rate of elongation, translucent polymethylpentene covers were placed over 8 individual *C. longipes* plants growing in the grassland. To prevent excessive CO_2 and/or water vapour gradients from being established, small holes were cut in the tops of these covers. Beginning on the day the covers were put in place and periodically thereafter, the pseudoscape height of each experimental plant and its nearest neighbouring *C. longipes* were recorded. Midday air temperatures under the covers and in the open at leaf height were recorded as well.

The short-term effects of an elongated pseudoscape on the leaf temperature and water relations of *C. longipes* were compared to one which would have remained at the soil surface. This was accomplished by measuring the diurnal course of leaf temperatures, leaf to air vapour concentration deficits, leaf conductance to water vapour, transpiration, and leaf water potential of 8 individuals growing in the field. After the first set of measurements were made in the morning, 4 of these individuals were chosen at random and rocks were piled underneath until their leaves were effectively at the ground surface. All plants were within a 20 m^2 area of very rocky substrate. Thus the main difference between the control and the experimental plants was the distance from the rocky surface to the leaves. Techniques used for the measurements were the same as discussed above.

Results and discussion

None of the parameters measured, leaf temperature, plant size, floral phenology, leaf water potential, or leaf conductance, were found to be correlated with pseudoscape height. This was a very significant result since it eliminated the possibility that caudex elongation was a simple and obligatory developmental process. Pseudoscape height was not linked with flowering phenology. All plants which had begun to lift above the soil surface had already initiated flowering. Also, we observed the contrasting pattern that plants may set seed before elongation of the pseudoscape above the soil surface. There was no correlation between height above the ground and index of phenology ($r^2 = 0.01$, $n = 56$, $P \gg 0.1$).

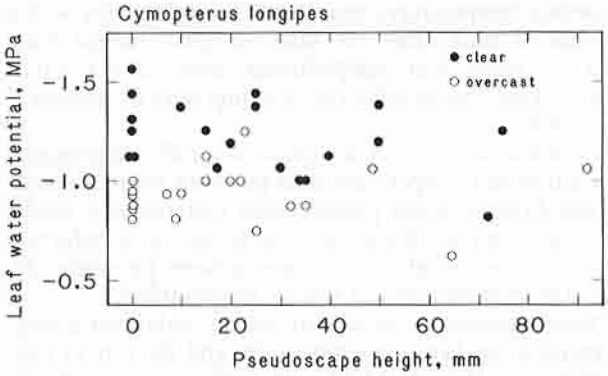

Fig. 2. Leaf water potential in relation to pseudoscape height, measured on a clear day (closed dots), and on an overcast day (open dots). There was very little variation in leaf water potential and it was independent of pseudoscape height ($n = 20$, $r^2 = 0.09$ clear day; $n = 20$, $r^2 = 0.0002$ overcast day)

Pseudoscape height was also independent of plant size ($r^2 = 0.05$, $n = 56$, $P \gg 0.1$). There is no minimum plant size which must be attained before caudex elongation begins. Individual plants which had not yet developed a pseudoscape spanned the entire range of plant sizes measured.

Pseudoscape height was not correlated with midday leaf water potential (Fig. 2) (clear day: $r^2 = 0.09$, $P > 0.1$; overcast day: $r^2 = 0.0002$, $P \gg 0.1$). Although midday water potentials measured under conditions of low transpirational demand (overcast day) were generally more favorable than those measured under clear days, in both cases the leaf water potential was almost constant despite differences in plant height above the soil surface.

Plants which had long pseudoscapes were experiencing the same midday water potentials as those on the soil surface. This can be related to the observation that leaf conductance and leaf temperature were also independent of pseudoscape height (conductance $r^2 = 0.08$; temperature $r^2 = 0.037$, $P \gg 0.1$) (Fig. 3A, B). It was also seen that leaf conductance and temperature spanned a small range even though pseudoscape height ranged from 0–70 mm above the soil surface.

We suggest that the similarities in leaf temperature, conductance, and water potential resulted from a correlation between microsite air temperature and caudex elongation. In sparse vegetation situations, such as grasslands in which *C. longipes* typically occurs, daytime microclimate profiles of air temperature decrease with height and particularly steep air temperature gradients occur near the surface (Campbell 1977). Thus, at a warm microsite we might expect to find longer pseudoscapes than at cooler microsites since the air would be warmer close to the soil surface; pseudoscape height appears to roughly balance microsite temperature. There was considerable microsite heterogeneity in the areas where measurements were collected. Midday

soil surface temperatures beneath *C. longipes* plants within 3 meters of each other on May 26, 1983 ranged from 46–55° C, while leaf temperatures were 29.3° C ± 0.66 ($x \pm$ s.e.). Leaf conductances at this time were 0.2 mol m^{-2} s^{-1} ± 0.008.

If caudex elongation takes place at a rate which is proportional to leaf temperature then plants in warmer microsites should grow longer pseudoscapes than plants at cooler sites. The result of this elongation would be a reduction of the variation in leaf temperatures between microsites despite large variations in soil surface temperatures.

Plants enclosed in translucent covers, exhibited a positive relationship between temperature and the rate of caudex elongation (Fig. 4). Midday air temperatures inside the polymethylpentene enclosures were 3–5° C warmer than the air temperature at the same height outside them (for example, May 7, 1983: 19.7° C ± 0.45 outside, 22.8° C ± 0.17 inside). At the beginning of the experiment on April 22, 1983 all of the plants were prostrate on the soil surface. Four days later the covered plants were extending pseudoscapes while their nearest neighbors were still prostrate. Throughout the experiment the plants in the "hothouses" maintained a higher rate of caudex elongation than their nearest neighbours. This result supports the hypothesis that the rate of elongation is proportional to microsite temperature.

The consequences of developing a pseudoscape were investigated by comparing leaf temperatures and water relations of control plants to plants which had rocks placed around and under the pseudoscape so that these plants were effectively prostrate. Comparative diurnal measurements were collected for leaf temperature, leaf water potential, transpiration, vapour concentration deficit (ΔW), and leaf conductance (Figs. 5 and 6). The first measurements were done at 0800 before the treatment was applied. The plants were indistinguishable at that time (Figs. 5, 6). After the ground surface was raised to the leaf height around the experimental plants large differences in physiological activity became apparent. Leaf temperatures of the experimental plants were closer to soil temperatures and therefore much warmer than those of the control plants. Leaf water potentials were lower in the experimental plants (Fig. 5). Vapour concentration deficits followed leaf temperatures closely, with experimental plants experiencing very large deficits at noon while the control plants experienced relatively constant ΔW throughout most of the day (Fig. 6). Leaf conductance to water vapour was lower in the experimental plants. This result might not be expected if *C. longipes* responded to high leaf temperature by increasing transpiration. Experimental plants actually had lower transpiration rates than controls for part of the day. This pattern was explained by the stomatal sensitivity of *C. longipes* leaves to decreased humidity (Fig. 7B). A negative relationship existed between leaf conductance to water vapour and ΔW. This is a common pattern observed in other species that have a direct stomatal response to humidity (Farquhar 1978, Schulze and Hall 1982). The negative relationship of leaf conductance to ΔW was strong enough that transpiration remained independent of ΔW (Fig. 7A).

The results of this experiment indicated that caudex elongation affected more than just leaf temperature. Additionally, leaf to air vapour pressure deficits were decreased and leaf conductances to water vapour increased. These changes may have important consequences for carbon gain and the ratio of assimilation to water vapour.

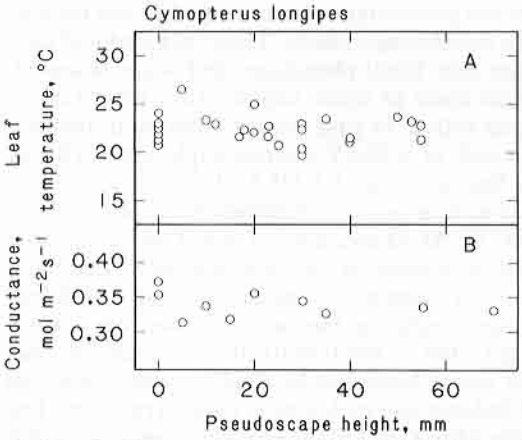

Fig. 3A. Leaf temperature in relation to pseudoscape height. Leaf temperature was independent of pseudoscape height ($n = 27$, $r^2 = 0.037$)

B Leaf conductance in relation to pseudoscape height. Leaf conductance was independent of pseudoscape height ($n = 10$, $r^2 = 0.08$)

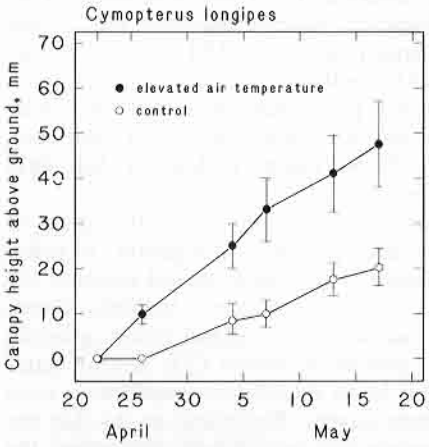

Fig. 4. Pseudoscape elongation of 8 *C. longipes* naturally growing plants enclosed in plastic mini-hothouses (closed dots) and of their nearest unmanipulated neighbors (open dots). The points are means with standard error bars. Canopy height was measured as the distance from the base of the rosette to the ground surface

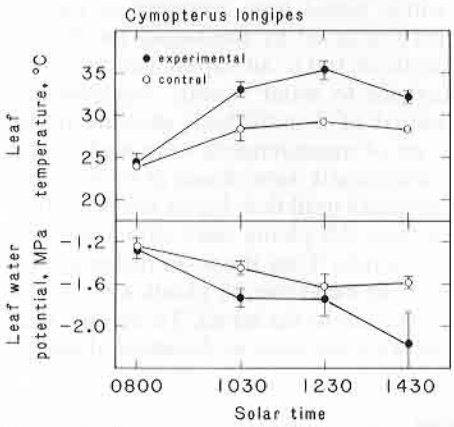

Fig. 5. Leaf temperatures and leaf water potentials of 8 *C. longipes* plants growing naturally. After 0800 4 plants were considered experimental and had rocks placed under the pseudoscape so that these plants were effectively prostrate. Points represent means with standard error bars

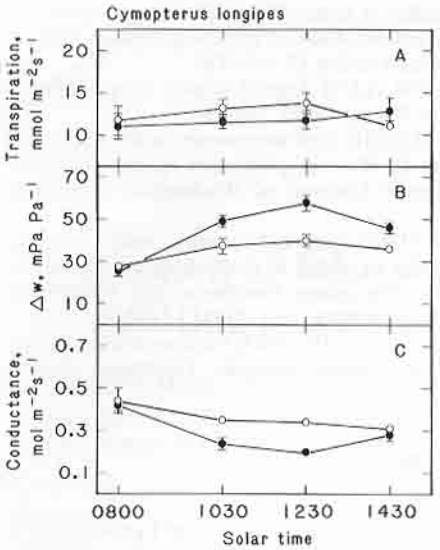

Fig. 6A. Transpiration rate of the plants described in Fig. 5. Control plants (open dots), experimental (closed dots)
B Leaf to air vapour concentration deficit of control plants (open dots) and experimental plants (closed dots)
C Leaf conductance to water vapour of control plants (open dots) and experimental plants (closed dots)

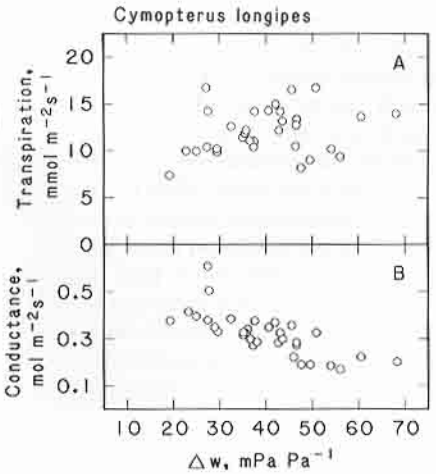

Fig. 7A. Relationship of transpiration to leaf to air vapour concentration deficits. Data is from both the control and experimental plants described in Fig. 5 and 6. Transpiration was independent of ΔW ($n=32$, $r^2=0.03$ $P>0.1$)
B Relationship of leaf conductance to water vapour. Leaf conductance was negatively correlated with ΔW, ($Y=0.575-0.006*X$ $n=32$, $r^2=0.57$ $P<0.01$)

To evaluate this, the temperature dependence of photosynthesis was measured in the field. Under ambient atmospheric conditions and high irradiance net photosynthesis showed only a slight dependence on leaf temperature between 17–34° C (Fig. 8). Photosynthetic rate changed less than 10% over this temperature range; leaf conductance remained essentially constant as well. Photosynthetic rate was diffusion limited. Increasing internal carbon dioxide concentrations from 240 µl l^{-1} to 1,100 µl l^{-1} not only increased the photosynthetic rate, but indicated that the photosynthetic apparatus was temperature stable up to temperatures of at least 38° C, which is far above the values typically observed under natural conditions. These data suggest that pseudoscape growth was not functioning to elevate leaves from a potentially lethal temperature in the microclimate profile, but instead the pseudoscape growth, although probably controled by temperature, was more likely a response to water limitations and the increased ΔW associated with increased temperature that the leaves would otherwise experience at the ground surface.

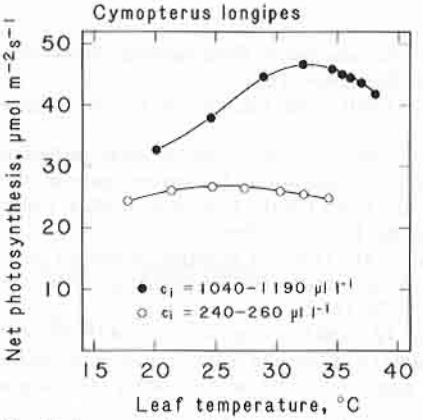

Fig. 8. An example of the temperature response of photosynthesis of *C. longipes* growing naturally. Leaves of intact plants were exposed to an irradiance of 1.55 mmol photons m^{-2} s^{-1} and a ΔW of 26 mPa Pa^{-1} except at the lowest temperatures, where ΔW was maintained as large as possible (17–22 mPa Pa^{-1}). Temperature responses were measured under normal CO_2 conditions (350 µl l^{-1} ambient, open dots) and CO_2 saturated conditions (1,400 µl l^{-1} ambient, closed dots)

Photosynthesis is proportional to leaf conductance (Körner et al. 1979; Werk et al. 1983) and thus *C. longipes* plants exposed to higher ΔW will have reduced photosynthetic rates. Our results indicate that the reduced leaf conductances offset increased ΔW so that transpiration remains more or less constant with increases in ΔW. Therefore, given the observed photosynthetic rates, A/E ratios should decline with increasing ΔW. Lower photosynthetic rates and lower A/E ratios will likely result in reduced growth and reproduction.

Caudex elongation in *C. longipes* is a unusual phenomenon which seems to extend the time during which its leaves are exposed to favorable humidity conditions. Early in the spring while the weather is cool its leaves remain on the soil surface. As hotter temperatures are encountered the leaves are gradually lifted into cooler microclimates not by increasing internodal distances but instead through changes in caudex elongation which are proportional to temperature. Other herbaceous plants can achieve a similar change in microclimatic conditions through different mechanisms by growing as rosettes in the winter and spring and then extending internodal distances as the weather warms up. The data collected in this study suggest that these movements and changes in growth form affect more than just leaf temperature. The effect on the ΔW may be much more important. The reduced ΔW resulted in a larger A/E ratio. Since water uptake requires an investment to roots, an increase in A/E may translate into greater net carbon gain, especially in the semi arid habitats in which *C. longipes* naturally occurs.

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