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 Aw. 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 Umbelliferae, 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 above the caudex. The length of pseudoscape formed was determined from naturally occurring plants in concrete holding rings and in the field.

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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.
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 gauge copper/constantan thermocouple connected to a Bt-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 Horst and Ehringer (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; 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 > 0.1).

Pseudoscape height was also independent of plant size (r^2 = 0.05, n = 56, P > 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 > 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 > 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 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.