

**ACCUMULATION OF PROLINE WITH RESPECT TO THE WATER  
RELATIONS OF DESERT AND ALPINE PLANTS UNDER  
NATURAL ENVIRONMENTS**

**BY**

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**ABSTRACT**

*This study included seven desert and five alpine plant species belonging to different life forms; annual, biennial and perennial plants. The ability to accumulate proline was preferential by both specific species and life form. Desert plants exhibited wider daily variation in proline content than alpine plants. Both desert and alpine plants showed negative correlation between proline and water content, while attained positive correlation of proline and water saturation deficit. The species with high specific survival time and high relative drought index were found to accumulate more proline than others. The comparison between desert and alpine plants draws attention to the possible functional aspects of proline accumulation to both drought and temperature stresses.*

## INTRODUCTION

The relationship between proline content and any kind of stress which may increase the plant water deficit such as water, salt, and temperature has been recently reviewed in some depth (Stewart and Lee, 1974; Chu *et al.*, 1978; Stewart and Hanson, 1980; Stewart and Larher, 1980 and Treichel *et al.*, 1984).

Several possible roles have been suggested for the proline accumulation during stress; e.g., osmoregulation and improved water retention under drought, freezing and salinity conditions (Savitskaya, 1967; Stewart and Lee 1974; Treichel, 1975; Jones and Storey, 1978; Withers and King, 1979), stabilization of proteins and removal of ammonia (Henckel *et al.*, 1964; Schobert and Tschesche, 1978), prevention of heat denaturation of enzymes (Paleg *et al.*, 1981), and conservation of nitrogen, carbon and energy for post-stress metabolism (Barnett and Naylor, 1966; Thompson *et al.*, 1966). A further evidence was given by Hubac (1967) who found that proline increases drought tolerance.

In order to elucidate the mechanisms underlying proline accumulation, it is very helpful to correlate plant water relations and proline content. The question then arises as do the plants of different ecological groups and life forms share common eco-physiological features? To answer this question, some plants of two ecologically distinct habitats, namely: the desert and the dry alpine habitats have been investigated. Both the desert and the dry alpine habitats share one common

edaphic factor viz soil water stress. In both habitates soil moisture and temperature are suggested to play a role on the water relations of the native plants (Hegazy, 1987). It is known that large portions of alpine areas have abundance of water, but exposed sites such as the study area are subject to frequent soil moisture stress (Salisbury *et al.*, 1968). In the desert, water and heat stress prevail (Kramer, 1983), whilst, water and cold stress are dominant events in dry alpine areas (Oberbauer and Billings, 1981).

This investigation aims to find out how variable proline accumulation in relation to plant water status is in some desert and alpine plants.

#### MATERIAL AND METHODS

The investigated species were seven desert plants growing naturally in Wadi Hagoul in the eastern desert of Egypt (latitude 29° 15' N, longitude 32° 26' E) and five alpine plants growing naturally on mount allan in Kananaskis, Alberta, Canada (latitude 50° 58' N, longitude 115° 13' W). The alpine plants were growing on the southwest side of the mountain at an elevation of 2250 m above sea level. The nomenclature followed Töckholm (1974) and Moss (1983).

#### The desert plants studied were:

Two annuals; Trigonella stellata Forssk. (Fabaceae) and Schismus barbatus (Hojer *ejusd.* L). Thell (Poaceae). Plants were flowering/fruited at the time of measurement. One

biennial plant; Centaurea aegyptiaca L. (Asteraceae). Plants were flowering at the time of measurement. Four perennials; two of them were flowering/fruitletting, namely: Diplotaxis harra (Forssk). Boiss. (Brassicaceae), and Crotalaria aegyptiaca Benth. (Fabaceae). The other two perennials were growing vegetatively, namely: Cleome droserifolia (Forssk). Del. (Cleomaceae), and Zygophyllum decumbens Del. (Zygophyllaceae).

#### **The alpine plants studied were:**

Five perennial species were growing vegetatively, namely: Silene acaulis L. var exscapa (All). DC. (Caryophyllaceae), Saxifraga bronchialis L. ssp. austromontana (Wig). Piper. (Saxifragaceae), Potentilla uniflora Ledeb. (Rosaceae), Solidago multiradiata Ait. ssp. Scopulorum Gray. (Asteraceae), and Oxytropis splendens Dougl. (Fabaceae).

#### **Methods:**

The proline content was determined in fresh plant material according to the method adopted by Bates et al., (1973). leafy plant shoots were detached and rapidly weighed on a torsion balance placed in a tent. Then, the plant material was placed in a stoppered test tube containing 10 ml of 3% aqueous sulfosalicylic acid. In the following day, the material was further processed in the lab. The material was homogenized in porcelain mortar and filtered through whatman number 2 filter paper. Two ml of filtrate was reacted with 2 ml acid-ninhydrin and 2 ml of glacial acetic acid in a test tube for one hour at 100°C, and the reaction terminated in an ice

bath. The reaction mixture was extracted with 4 ml toluene mixed vigorously for 20 sec. The chromophore containing toluene was aspirated from the aqueous phase, warmed to room temperature and the absorbance read at 520 nm using toluene for a blank. The proline concentration was determined from a standard curve and calculated on a fresh weight basis.

The water content was estimated in detached shoots as the percentage of fresh weight of shoots by the following formula;

$$\text{Water content} = [ (\text{fresh weight} - \text{oven dry weight}) / \text{fresh weight} ] \times 100.$$

The oven dry weight was determined after drying for 48 hour at 80°C.

For water saturation deficit determination, a leafy shoot was detached and rapidly weighed for its fresh weight determination, then placed in large test tube which was filled with distilled water. The tube was corked and kept in the tent. In the following day, the material was rapidly blotted with filter paper and its saturated weight determined. Then was dried at 80°C for 48 hour. The water saturation deficit (W.S.D) was calculated by the following equation;

$$\text{W.S.D.} = [ (\text{saturated weight} - \text{fresh weight}) / (\text{saturated weight} - \text{oven dry weight}) ] \times 100.$$

The diurnal changes of proline, water content, and water saturation deficit were determined at regular intervals starting at 01,00h and ending at 21,00h. For each interval five

replicates were taken. The samples were comparable in all measurements (cf. Slavik 1974). The climatic factors including air temperature and wind velocity were measured simultaneously with other experiments at height of one meter above soil surface.

The specific survival time as defined the maximum time of drought survival "ausdauer" of detached shoots was estimated as follows;

$$\text{Ausdauer} = (\text{available water content at complete stomatal closure}) / (\text{cuticular transpiration}).$$

The available water content was calculated in its turn by subtracting the water content at the drought killing point from the water content in the state of complete stomatal closure. Values were determined from the drying out curves of detached shoots based on a technique used by Hegazy (1987) following Pisek and Winkler (1953).

The relative drought index (RDI) was estimated as following;

$$\text{RDI} = (\text{actual water saturation deficit} / \text{critical water saturation deficit}) \times 100.$$

The critical water saturation deficit was estimated as the water saturation deficit at drought killing point (Cf. Larcher, 1980, and Levitt, 1980).

For alpine plants, the measurements were taken in June 1986, when the plants were growing vegetatively after about

one month of snow thawing. There was no rainfall at least one week before the experimental day. While, for desert plants the investigation was undertaken in March 1988, that is in spring when most plants flourish in years with a rainy season.

## RESULTS

### Environmental Conditions:

Daily measurements of air temperature and wind velocity were taken. In the desert study area, the diurnal air temperatures were warm (Fig. 1). The highest temperature of 25.3°C were measured at 11.00 h, whilst, the lowest were 11.5°C at 06.00 h. In the alpine study area, the diurnal temperature changed greatly from day to night (Fig. 1). The progression of temperature changed from -4.3°C at 06.00 h, reaching a maximum of +11.7°C at 16.00 h, and dropped back to -1.0°C by the 21.00 h.

Generally, in alpine study area, lower wind speeds were experienced during night than during the day. The overall wind pattern of the alpine area goes side by side with the temperature pattern (Fig. 1). The greatest speed reached 55.7 Km/h at 16.00 h. For desert study area, the wind pattern was somewhat sporadic with little day-night differences. The highest speed attained was 20.7 Km/h at the 01.00 h, while the lowest speed was 11.2 Km/h at the 06.00 h.

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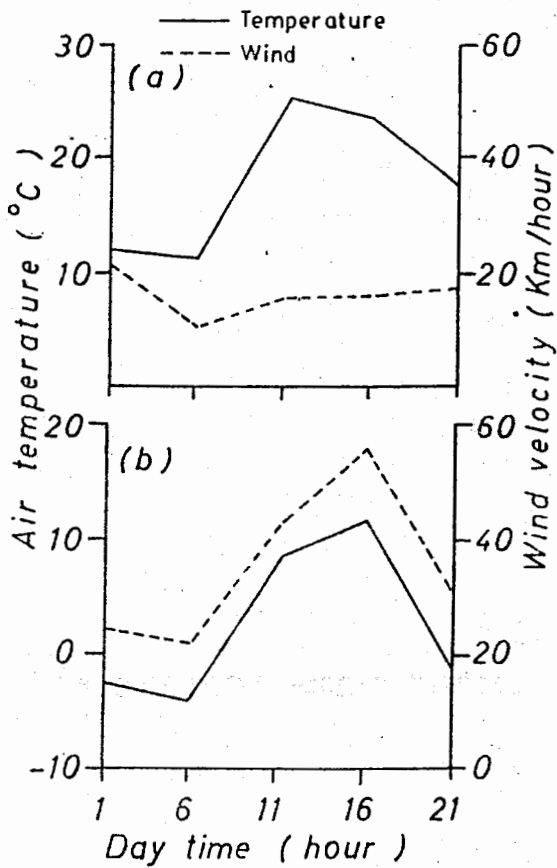


Fig. 1

Diurnal variation of air temperature and wind velocity in the two study areas during the day of measurements.

(a) Wadi Hagul area in the eastern desert of Egypt.

(b) Mount Allan alpine area in Kanaskis Alberta, Canada.

**Proline:**

The diurnal course of proline content of the investigated desert and alpine species is shown in Fig. 2. In desert plants, the lowest proline content was measured at the 06.00 h, then it showed a gradual rise till the 16.00 h. At night, the proline content showed a steady decrease towards the following morning. The daily course of proline content in alpine plants was the same as in desert plants, with the exception that the highest proline content was obtained at different times of the day depending on the species. For example, S. bronchialis showed the highest proline content at the 11.00 h, while S. acaulis at the 16.00 h. The remaining three alpine species attained the highest proline content at the 21.00 h.

The desert plants exhibited wider daily variation in proline content than alpine plants. The difference between the average highest and the average lowest proline content reached 43.2 u.mol/g fresh weight in the desert plant Z. decumbens, while was as low as 1 u.mol/g fresh weight in D. harra. In alpine plants, the difference between the highest and the lowest values of proline was 5.2 u.mol/g fresh weight in O. splendens and 2.2 u.mol/g fresh weight in P. uniflora. Generally, desert plants accumulate more proline than alpine plants.

**Water content:**

The water content of the shoots of both desert and alpine plants had a maximum around the 06.00 h, (Fig. 3), indicating

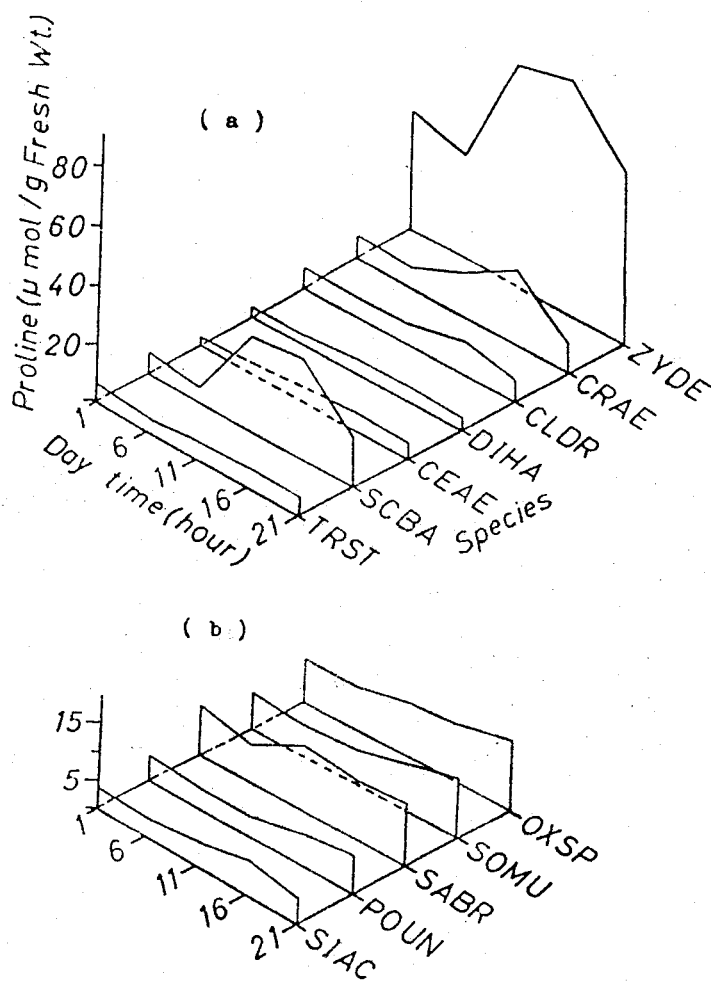


Fig. 2

Diurnal course of proline content in:-

- (a) seven species of desert plants. TRST=Trigonella stellata, SCBA=Schismus barbatus, CEAE=Centaurea aegyptiaca, DIHA=Diploaxis harra, CLDR=Cleome droserifolia, CRAE=Crotalaria aegyptiaca, and ZYDE=Zygopetalon deserti.
- (b) five species of alpine plants. SIAC=Silene acaulis, POUN=Potentilla uniflora, SABR=Saxifraga bronchialis, SOMU=Solidago multiradiata, and OXSP=Oxytropis splendens.

that the water uptake was higher than the water loss. The lowest water content of desert plants was obtained at the 16.00 h, while for alpine plants was at the 21.00 h, then increased towards the following morning.

The linear regression of proline content versus water content showed a "negative" correlation in all desert and alpine species investigated (Table 1). This implies that large values of proline accumulation were associated with small values of water content. This was true for both desert and alpine plants.

#### **Water saturation deficit:**

The daily course of water saturation deficit goes hand in hand with the daily course of proline accumulation (Fig. 4). With the increase of water saturation deficit, the amount of proline accumulation was enhanced in both desert and alpine plants.

The linear regression of proline versus water saturation deficit showed a "positive" correlation in all species (Table 1). This indicates that large values of proline content were associated with large values of water saturation deficit.

#### **Specific survival time (SST) and relative drought index (RDI):**

The SST and the RDI indicate how long after stomatal closure the detached shoots of the species investigated can remain undamaged without a supply of water. In desert plants,

Table 1: The linear regression between proline content and water content (A), and between proline content and water saturation deficit (B) of the different species investigated.

Species	Y = a + bX	r	
<b>Desert Plants</b>			
<u>Trigonella stellata</u>	A: Y= 28.661-0.316 X	-0.974	**
	B: Y= 4.446-0.154 X	0.697	ns
<u>Schismus barbatus</u>	A: Y=257.986-3.536 X	-0.946	*
	B: Y=-23.745+3.619 X	0.879	*
<u>Centaurea aegyptiaca</u>	A: Y= 30.152-0.327 X	-0.883	*
	B: Y=- 3.799+0.792 X	0.931	*
<u>Diplotaxis harra</u>	A: Y= 11.174-0.103 X	-0.703	ns
	B: Y= 0.793+0.135 X	0.920	*
<u>Cleome droserifolia</u>	A: Y= 24.482-0.290 X	-0.879	*
	B: Y= 3.799+0.172 X	0.944	*
<u>Crotalaria aegyptiaca</u>	A: Y=125.071-1.644 X	-0.686	ns
	B: Y=-23.279+1.635 X	0.907	*
<u>Zygophyllum decumbens</u>	A: Y=444.904-4.487 X	-0.626	ns
	B: Y=- 5.829+3.070 X	0.963	**
<b>Alpine Plants</b>			
<u>Silene acaulis</u>	A: Y= 36.590-0.402 X	-0.938	*
	B: Y=- 0.204+0.422 X	0.841	ns
<u>Potentilla uniflora</u>	A: Y= 33.292-0.417 X	-0.881	*
	B: Y= 0.073+0.355 X	0.680	ns
<u>Saxifraga bronchialis</u>	A: Y=125.162-1.454 X	-0.670	ns
	B: Y= 3.202+0.393 X	0.322	ns
<u>Solidago multiradiata</u>	A: Y= 67.462-0.860 X	-0.992	**
	B: Y=- 1.353+0.572 X	0.797	ns
<u>Oxytropis splendens</u>	A: Y= 33.084-0.368 X	-0.976	**
	B: Y=- 7.586+0.801 X	0.932	*

ns = non significant

\* = significant at 5% level

\*\* = significant at 1% level.

Table 2: Specific survival time (SST) and relative drought index (RDI) of detached transpiring shoots of the investigated desert and alpine species. Standard deviations follow the average values (n=5).

Species	SST (hour)	RDI(%)
<b>Desert plants</b>		
<u>Trigonella stellata</u>	14.5 ± 2.2	31.5 ± 2.5
<u>Schismus barbatus</u>	15.3 ± 2.8	46.1 ± 3.8
<u>Centaurea aegyptiaca</u>	15.1 ± 1.6	45.8 ± 2.4
<u>Diplotaxis harra</u>	18.2 ± 3.1	53.6 ± 5.1
<u>Cleome droserifolia</u>	28.6 ± 3.5	82.3 ± 4.5
<u>Crotalaria aegyptiaca</u>	---	---
<u>Zygophyllum decumbens</u>	35.8 ± 3.9	86.5 ± 4.2
<b>Alpine plants</b>		
<u>Silene acaulis</u>	26.3 ± 2.8	71.5 ± 5.8
<u>Potentilla uniflora</u>	21.2 ± 2.5	63.4 ± 4.2
<u>Saxifraga bronchialis</u>	32.9 ± 3.2	82.1 ± 3.6
<u>Solidago multiradiata</u>	18.7 ± 1.9	48.2 ± 3.1
<u>Oxytropis splendens</u>	18.5 ± 1.4	44.2 ± 2.3

the SST ranged from 14.5 to 35.8 h, while for alpine plants the SST fluctuated within the range of 18.5 to 23 h, (Table 2). The RDI for desert plants ranged from 31.5 to 86.5%, whilst, for alpine plants it ranged from 44.2 to 82.1% (Table 2). This indicates that desert plants had wider range of SST and RDI than alpine plants. For both desert and alpine plants, the species having high SST characterized by high RDI, and the opposite was hold true.

It is noteworthy that species with relatively high proline content characterized by high SST and RDI. This was hold true for both desert and alpine plants.

## DISCUSSION

The diurnal course of the proline in the investigated desert and alpine species showed that the proline pool was dynamic. In desert plants, the diurnal changes of proline content fluctuated from about two times up to ten times, while in alpine plants only about two times. The rates of proline accumulation were adjusted to changes in plant water relations and the environmental conditions. A basic character of all species investigated was that proline content increased during the day and declined at night.

In conditions of decreased water content and increased water saturation deficit, high levels of proline were accumulated. All desert and alpine plants investigated exhibited similar relationships in proline accumulation versus either water content (negative correlation) or water



saturation deficit (positive correlation). This may play a role in the adaptation of the plants to the desert and the dry alpine environments with strong winds. Therefore, the consequence of water saturation deficit poses one of the most complex ecophysiological problems in which experimental isolation of the plant from its natural environment is of doubtful value (Kozlowski, 1968-1983). This agrees with Pahlich and Grieb (1983) who pointed out that the increased water saturation deficit seems to be a major factor producing metabolic perturbation which finally result in proline accumulation.

Under desert environments, Treichel *et al.*, (1984) found that proline accumulation increased during the dry season. Also, the proline content was kept at lower level in water stressed plants than in watered plants (Rajagopal *et al.*, 1977). For the present investigation, although being less tolerant to drought, the desert annual *T. stellata* and the biennial *C. aegyptiaca* had low proline content when compared to the drought tolerant perennials, the annual grass *S. barbatus* accumulated high amounts of proline. This can be attributed to the phenological status at time of measurements, where *S. barbatus* was in fruiting stage.

For alpine plants, proline accumulation continued even at night when temperatures dropped below 0°C. This appears to be a more direct response to the decrease in temperature. As pointed out by Benko (1968) and Chu *et al.*, (1978), the accumulation of proline in response to low temperature has been connected with the plant resistance to cold and frost injury. This agrees with of Withers and King (1979) who

conclude that proline may act as a non-toxic solute; protecting the cell against the denaturing effects of hyperosmolality induced by dehydration during freezing. Meanwhile, Aspinall and Paleg (1981) suggest that proline accumulation is induced by both low temperatures and water deficit. However, no complete explanation can be offered at the present time.

Since only detached shoots were used in this study, the values of SST and RDI cannot represent the overall drought resistance of the individual plants. If whole individuals were used, the SST and the RDI may have reached several times the values obtained. For example, the detached shoots of the alpine cushion plant *S. acaulis* showed SST of 26.3 h, in this study, while Rauh (1939) found that the whole plant can survive several weeks when cutted from its main root. This is due to the contribution of the stored water within the plant body. The results showed that species with high SST and RDI accumulated high amounts of proline. This may indicate that the increase in proline content is necessary for the survival of moisture deficient tissues. This agree with the findings of Britikov *et al.* (1964), Stewart *et al.* (1966), Cavalieri and Huang (1979). However, Tymms and Gaff (1979) pointed out that, the ability of resurrection plants to survive air-drying is not attributable to accumulation of free proline *Per se*.

In conclusion, free proline accumulation in desert and alpine plants can be attributed to a general principle of reaction upon increasing stress. The stresses due to temperature and water deficit appear to play a major determining role which directly affects proline accumulation,

which in turn ensures the plant's survival of environmental stress. The generality of proline accumulation as a response to water deficit and low temperature, in plant species apparently adapted to different habitats needs further investigations.

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تراكم البرولين بالنسبة للعلاقات المائحية  
في النباتات المحراوية ونباتات الألبين  
تحت الظروف البيئية الطبيعية

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جامعة المنوفية

أجريت هذه الدراسة على سبعة نباتات صحراوية ( حولية ومعمرة ) وخمسة من نباتات أعالي الجبال ( نباتات الألبين ) . ولقد أوضحت الدراسة أن قدرة النباتات المختلفة على تكوين البرولين تختلف حسب الجنس وحسب شكل حياة النبات . تبين أيضا أن المسار لايومى لتراكم البرولين فى النباتات المحراوية . فوق كثيرا نظيره فى نباتات الألبين . كما اوضحت النتائج وجود علاقة طردية سالبة بين المحتوى المائفى للنباتات وكمية البرولين المتراكمة بينما توجد علاقة طردية بـسـين كمية البرولين والنقص فى التشبع المائى للنباتات المختلفة .

ويمكن القول أن الأجناس التى تتميز بطول فترة الاحتفاظ بالحيوية مع زيادة معامل الجفاف لها القدرة على تراكم كميات من البرولين تفوق الأجناس النباتية الأخرى . وقد أوضحت المقارنة بسـين النباتات المحراوية ونباتات الألبين أهمية تراكم البرولين اخل النباتات استجابة لعاملـسـى الجفاف والحرارة .