

Differential Altitudinal Distribution and Diversity of Plants with Different Photosynthetic Pathways in Arid Southern Saudi Arabia

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Abstract: Distribution and diversity of plants with the C₃, C₄, and CAM modes of photosynthesis were studied on an altitudinal gradient in the arid region southwest of Saudi Arabia. The gradient extended from Red Sea coastal line via Tehama Hills and up Tallan Mountain. The study was conducted during the dry season in order to eliminate factors relating to soil water availability. Plant diversity increased with increased altitude. Plants with the C₄ pathway were more abundant at low altitudes, whereas plants with the C₃ pathway were more abundant at high altitudes. Succulent CAM plants occupied a range of altitudes. Since factors pertaining to soil water availability were eliminated by undertaking the study during the dry season, it appeared that temperature is the major factor influencing altitudinal distribution of plants with different photosynthetic pathways. Results are discussed in terms of heat sensitivity of the CO₂ carboxylating enzyme of C₃ plants, high temperature optima for CO₂ uptake of C₄ plants, and high water use efficiency of CAM plants.

Key words: Altitudinal Distribution, C₃, C₄, Crassulacean acid Metabolism (CAM), Diversity, Photosynthetic pathways

INTRODUCTION

Photosynthetic assimilation of atmospheric CO₂ takes place in plants by three different modes, namely; C₃ mode with plants producing phosphoglyceric acid as their first stable product, C₄ mode with plants producing 4-carbon compounds as their first stable products, and CAM with plants fixing CO₂ predominantly during the dark period. Plants with diverse photosynthetic pathways possess distinct structural, physiological, and biochemical features that leads to different ecological relationships (Edwards and Walker, 1983; Sage, 1999; Silvera *et al.*, 2010). Plants exhibiting the C₄ syndrome possess Kranz anatomy, a CO₂ concentrating mechanism, and high water use efficiency (Kanai and Edwards, 1999). Therefore, C₄ plants can reach high rates of CO₂ fixation under conditions of heat and water stress that cause low intercellular CO₂ levels due to stomatal closure. These C₄ plants also possess higher temperature optima for CO₂ fixation than C₃ plants, require higher irradiance for photosynthetic saturation, and hence their maximum rate of CO₂ uptake is considerably higher than that of C₃ plants (Long, 1999). The C₄ syndrome, therefore, represents an advantage for plants inhabiting regions of high evaporative demand (Long, 1999). Moreover, plants with the CAM pathway avoid gas exchange when environmental conditions favor transpirational water loss by exhibiting daytime stomatal closure and nocturnal CO₂ uptake (Winter and Smith, 1996; Borland *et al.*, 2000; Sayed, 2001a; Sayed 2001b; Lüttge, 2002; Lüttge, 2004; Lüttge, 2008; Drennan, 2009). Thus CAM plants have highly improved water use efficiency that is generally 6-fold higher than that of C₃ plants and 3-fold higher than that of C₄ plants (Lüttge, 2004; Silvera *et al.*, 2010). The CAM pathway is an important metabolic adaptation that allows plants to occupy extremely arid habitats with scarce and intermittent seasonal water availability (Winter and Smith, 1996; Cushman, 2001).

High temperature, high irradiance, scarce water, erratic rainfall, and sand storms are climatic features of the arid regions of southern Saudi Arabia (Fisher and Membery, 1998). Geomorphology of the region reveals various land forms including Red Sea coastal line, Tehama Hills, and high mountains (Ghazanfar, 1998). The wet season is a short three months period (June – August) and the long dry season extends over nine months (Fisher and Membery, 1998). Investigations of altitudinal distribution of plants with different photosynthetic pathways have focused on high slopes of tropical regions (Tieszen *et al.*, 1979; Wooler *et al.*, 2001; Van de Water *et al.*, 2002; Li *et al.*, 2009; Sikolia *et al.*, 2009), and very few have described this distribution in arid

or semiarid regions (Sayed and Mohamed, 2000). These investigations have generally related altitudinal distribution of photosynthetic pathways to variations of either temperature or water availability. Although water availability affects plant distribution, temperature seems to be more influential in determining altitudinal competitive interactions between C₃, C₄, and CAM plants (Lee-Thorp and Beaumont, 1995; Epstein *et al.*, 1997; Fredlund and Tieszen, 1997; Lüttge, 2004). Hence, a debate exists as to the relative importance of temperature and water availability in determining altitudinal plant distribution (Li *et al.*, 2007). Work presented in this paper aimed at addressing this debate by describing the distribution of C₃, C₄, and CAM plants along an altitudinal gradient in arid southwest of Saudi Arabia. Work was carried out deep into the dry season in order to eliminate effects of water availability on plant distribution. Work also aimed at providing a comparative ecophysiological perspective of altitudinal distribution of these three types of CO₂ fixation pathways and implications for plants inhabiting arid regions.

MATERIALS AND METHODS

Plant species along the studied altitudinal gradient were surveyed by setting five quadrates (25 m² each) at different altitudes of 10, 50, 100, 400, 800, 1200, and 1600 meters above sea level (m.a.s.l.). These altitudes were chosen in order to cover the wide diversity of landforms along the altitudinal gradient including sand dunes, desert plain, wadi, desert pavement, and mountain. The 150 km-long gradient in Jazan Province southwest of Saudi Arabia was in the range N17°.00' E42°.33' to N17°.25' E43°.09'. The time for data acquisition in mid-March well into the dry season was chosen to eliminate possible effects of soil moisture on plant distribution since at that time the last effective rainfall would have occurred six months earlier. Air and soil temperatures were recorded using a field weather meter (Kestrel 2000, Boothwyn, Philadelphia, USA) and an infrared field thermometer (Fluke, Everett, WA, USA), and air relative humidity was measured using a digital hygrometer (Maplin Electronics, Manchester, UK). Chlorenchyma of stem succulent species was separated along the stem length and its cell sap titratable acidity was determined (Osmond *et al.*, 1991). Titratable acidity measurements were routinely repeated and the mean of five measurements and standard deviation were calculated. Abundance of species exhibiting the C₃, C₄, and CAM modes of photosynthesis was calculated as the percentage of species in each group relative to the total number of species of the three groups (Magurran, 1988). Diversity (D) was determined using the diversity index:

$$D = (S - 1) / \ln N$$

where, S is the number of recorded species, and N is the total number of individuals summed over all species (Magurran, 1988).

Nomenclature of recorded plant species followed that of Collenette (1999). Recognition of species as C₃ or C₄ was based on the absence or presence of Kranz anatomy. Recognition of species as CAM plants depended on the difference between dusk and dawn chlorenchyma titratable acidity (ΔT). Carbon isotope discrimination ($\delta^{13}C$) available in the literature was also used to recognize C₃, C₄, and CAM species. Values of $\delta^{13}C$ in the ranges of -24 to -31‰, -10 to -15‰, and -12 to -22‰ were considered indicative of C₃, C₄, and CAM, respectively (Griffiths, 1993).

Results:

Plant species recorded along the altitudinal gradient included 15 herb species, 14 shrub species, 6 grass species, 2 tree species, and one sedge (Table 1). These species included 13 C₃-, 10 C₄-, and 14-CAM species of which 11 were stem succulent species and 3 were leaf succulent species (Table 1, Table 2). Air and soil temperatures decreased with increased altitude whereas air relative humidity increased with increased altitude (Table 2). Although species diversity increased with increased altitude, the number of C₄ species decreased with increased altitude whereas that of C₃ species increased with increased altitude (Table 2). The number of species with the CAM pathway generally decreased with increased altitude (Table 2). However, with the exception of the low altitudes of 10 and 50 m.a.s.l., these CAM species appeared to be distributed over a range of altitudes along the gradient and exhibited greater abundance compared to C₃ and C₄ species particularly at the intermediate altitudinal altitudes of 200, 400, and 800 m.a.s.l. (Table 2).

Table 1: Recorded species (CFP = carbon fixation pathway, $\delta^{13}\text{C}$ = carbon isotope discrimination, ΔT = dawn – Dusk Titratable Acidity ($\mu\text{equiv. g}^{-1}$ Fresh Wt.), LF = life form, G = grass, H = herb, S = shrub, T = Tree) (References: B = Batanouny *et al.*, 1988; S&M = Sage and Monson, 1999; S1 = Sayed, 2000; S2 = Sayed, 2001a).

Altitude (m.a.s.l.)	Land Form	Family/Species	LF	KA	$\delta^{13}\text{C}/\text{Ref.}$	ΔT	CFP	
10 N17°.00' E42°.33'	Sand Dunes	Cyperaceae						
		<i>Cyperus conglomerates</i> Rottb.	H	+	-/S&M	--	C4	
		Fabaceae						
		<i>Indigofera argentia</i> Burm. f.	H	-	--	--	C3	
50 N17°.09' E42°.39'	Desert Plain	Poaceae						
		<i>Panicum turgidum</i> Forssk.	G	+	-12.7/B	--	C4	
		Boraginaceae						
		<i>Heliotropium petrocarpum</i> (DC.)Hochst.&Steud.	H	+	-/S&M	--	C4	
100 N17°.18' E42°.47'	Wadi	Fabaceae						
		<i>Indigofera argentea</i> Burm.f.	H	-	--	--	C3	
		Poaceae						
		<i>Aristida metabilis</i> Trin. & Rupr.	G	+	-/S&M	--	C4	
		<i>Panicum turgidum</i> Forssk.	G	+	-12.7/B	--	C4	
		Acanthaceae						
		<i>Blepharis ciliaris</i> Forssk.	H	-	-/S&M	--	C4	
		Asclepiadaceae						
		<i>Caralluma acutangula</i> (Decne.) N.E.Br.	S	-	--	150±3	CAM	
		<i>Caralluma subulata</i> (Forssk.) Decne.	S	-	--	153±2	CAM	
		<i>Duvalia velutina</i> Lavranos	S	-	--	138±5	CAM	
		Euphorbiaceae						
		<i>Euphorbia triaculeata</i> Forssk.	S	-	--	182±2	CAM	
		Fabaceae						
<i>Indigofera spinosa</i> Forssk.	H	-	--	--	C3			
Poaceae								
<i>Aristida metabilis</i> Trin.& Rupr.	G	+	-/S&M	--	C4			
<i>Cenchrus ciliaris</i> L.	G	+	-11.0/B	--	C4			
<i>Lasiurus hirsutus</i> (Forssk) Boiss.	G	+	-11.7/B	--	C4			
200 N17°.20' E42°.48'	Desert Plain	Aloaceae						
		<i>Aloe vera</i> (L.) Burm. f.	S	-	-/S2	--	CAM	
		Asclepiadaceae						
		<i>Caralluma acutangula</i> (Decne.) N.E.Br.	S	-	-/S2	150±3	CAM	
		<i>Caralluma edulis</i>	S	-	--	129±5	CAM	
		<i>Duvalia velutina</i> Lavranos	S	-	--	138±5	CAM	
		<i>Sarcostemma forsskoliana</i>	S	-	--	--	CAM	
		Euphorbiaceae						
		<i>Euphorbia triaculeata</i> Forssk.	S	-	--	182±2	CAM	
		Fabaceae						
		<i>Acacia ehrenbergiana</i> Hayne	T	-	--	--	C3	
<i>Acacia tortilis</i> (Forssk.) Hayne	T	-	--	--	C3			
Vitaceae								
<i>Cissus quadrangularis</i> L.	S	-	-/S2	--	CAM			
400 N17°.25' E42°.51'	Desert Pave-ment	Asclepiadaceae						
		<i>Caralluma acutangula</i> (Decne.) N.E.Br.	S	-	-/S2	150±3	CAM	
		<i>Caralluma penicillata</i> (Deflers) N.E.Br.	S	-	--	--	CAM	
		Fabaceae						
		<i>Indigofera spinosa</i> Forssk.	H	-	--	--	C3	
		Poaceae						
		<i>Aristida adscenionis</i> L.	G	+	-12.7/B	--	C4	
Vitaceae								
<i>Cissus quadrangularis</i> L.	S	-	-/S2	--	CAM			
800 N17°.21' E43°.06'	Tallan Moun-tain	Asclepiadaceae						
		<i>Caralluma penicillata</i> (Deflers) N.E.Br.	S	-	--	--	CAM	
		Commelinaceae						
		<i>Commelina benghalensis</i> L.	H	-	--	--	C3	
		Boraginaceae						
		<i>Heliotropium strigosum</i> Willd.	H	-	-13.0/B	--	C4	
		Euphorbiaceae						
		<i>Euphorbia inarticulate</i> Schweinf.	S	-	--	--	CAM	
		<i>Euphorbia granulate</i> Forssk.	S	-	--	--	CAM	
		Fabaceae						
		<i>Indigofera spinosa</i> Forssk.	H	-	--	--	C3	
		Nyctaginaceae						
		<i>Commicarpus plumbagineus</i> L.	H	-	--	--	C3	
Poaceae								
<i>Eargrostis papposa</i> (Roem. & Schult.) Steud.	G	+	-/S&M	--	C4			
Vitaceae								
<i>Cissus quadrangularis</i> L.	S	-	-/S2	--	CAM			

Table 1: Continue

1200	Tallan Moun-tain	Boraginaceae							
N17° 22' E43° 09'		<i>Heliotropium longiflorum</i> Hochst. & Steud.	H	+	--/S&M	--			C4
		Chenopodiaceae							
		<i>Chenopodium schraderianum</i> Schult.	H	-	--	--			C3
		Lamiaceae							
		<i>Ocimum filamentosum</i> Forrsk.	H	-	--	--			C3
		<i>Lavendula pubescence</i> Decne.	H	-	--	--			C3
		Nyctaginaceae							
		<i>Commicarpus plumbagineus</i> L.	H	-	--	--			C3
		Sloanceae							
		<i>Solanum incanum</i> L.	H	-	--	--			C3
		Vitaceae							
		<i>Cissus quadrangularis</i> L.	S	-	--/S2	--			CAM
		<i>Cissus rotundifolia</i> (Forrsk.) Vahl	S	-	--/S2	--			CAM
1600	Tallan Mountain	Asclepiadaceae							
N17° 22' E43° 09'		<i>Caralluma quadrangula</i> (Forrsk.) N.E.Br.	S	-	--	--			CAM
		Boraginaceae							
		<i>Heliotropium longiflorum</i> Hochst. & Steud.	H	-	--/S&M	--			C4
		Euphorbiaceae							
		<i>Euphorbia cactus</i> Ehrenb. Ex. Boiss.	S	-	--	--			CAM
		Fabaceae							
		<i>Indigofera spinosa</i> Forrsk.	H	-	--	--			C3
		Lamiaceae							
		<i>Ocimum forrskolei</i> Benth.	H	-	--	--			C3
		<i>Leucas alba</i> (Forrsk.) Sebald	H	-	--	--			C3
		Nyctaginaceae							
		<i>Commicarpus plumbagineus</i> L.	H	-	--	--			C3
		Tiliaceae: <i>Grewia tembensis</i> Fresen.	H	-	--	--			C3

Table 2: Altitudinal distribution and diversity of species exhibiting C3 (○), C4 (●), and CAM (◇), and variations of climatic factors along the studied gradient (CFP = Carbon fixation pathway, S = Succulence, LS = Leaf succulent, SS = Stem succulent).

Species	CFP	S	Altitude (m.a.sl.)							
			10	50	100	200	400	800	1200	1600
<i>Cyperus conglomeratus</i>	C4	-	●							
<i>Panicum turgidum</i>	C4	-	●	●						
<i>Heliotropium petrocarpum</i>	C4	-		●						
<i>Aristida metabolis</i>	C4	-		●	●					
<i>Blepharis ciliaris</i>	C4	-			●					
<i>Cenchrus ciliaris</i>	C4	-			●					
<i>Lasiurus hirsutus</i>	C4	-			●					
<i>Aristida adscensionis</i>	C4	-					●			
<i>Eragrostis papposa</i>	C4	-						●		
<i>Heliotropium strigosum</i>	C4	-						●		
<i>Heliotropium longiflorum</i>	C4	-							●	●
<i>Indigofera argentea</i>	C3	-	○	○						
<i>Indigofera spinosa</i>	C3	-			○		○	○		○
<i>Acacia ehrenbergiana</i>	C3	-				○				
<i>Acacia tortilis</i>	C3	-				○				
<i>Commelina benghalensis</i>	C3	-						○		
<i>Commicarpus plumbagineus</i>	C3	-						○	○	○
<i>Chenopodium schraderianum</i>	C3	-							○	
<i>Ocimum filamentosum</i>	C3	-							○	
<i>Ocimum forrskolei</i>	C3	-								○
<i>Lavendula pubescence</i>	C3	-							○	
<i>Solanum incanum</i>	C3	-							○	
<i>Leucas alba</i>	C3	-								○
<i>Grewia tembensis</i>	C3	-								○
<i>Aloe vera</i>	CAM	LS				◇				
<i>Caralluma acutangula</i>	CAM	SS			◇	◇	◇			
<i>Caralluma edulis</i>	CAM	SS				◇				
<i>Caralluma penicillata</i>	CAM	SS					◇	◇		
<i>Caralluma quadrangula</i>	CAM	SS								◇
<i>Cralluma subulata</i>	CAM	SS			◇					
<i>Cissus quadrangularis</i>	CAM	LS				◇	◇	◇		
<i>Cissus rotundifolia</i>	CAM	LS							◇	
<i>Duvalia velutina</i>	CAM	SS			◇	◇				
<i>Euphorbia cactus</i>	CAM	SS								◇

Table 2: Continue

<i>Euphorbia granulate</i>	CAM	SS							◇
<i>Euphorbia inarticulate</i>	CAM	SS							◇
<i>Euphorbia triaculeata</i>	CAM	SS			◇	◇			
<i>Sarcostemma forrskoliana</i>	CAM	SS							◇
Abundance (% of species)	C4		66.7	75.0	44.4	0.00	20.0	22.2	12.5
	C3		33.3	25.0	11.2	22.2	20.0	33.3	62.5
	CAM		0.00	0.00	44.4	77.8	60.0	44.4	25.0
Air Temperature (°C)			45.0	45.0	45.0	45.0	36.0	35.0	35.0
Soil Temperature (°C)			48.0	47.0	45.0	45.0	40.0	33.0	30.0
Relative Humidity (%)			35.0	35.0	35.0	35.0	35.0	37.0	40.0
Diversity of Species			4.20	5.92	6.90	7.00	7.00	7.40	18.5

Discussion:

The studied altitudinal gradient included areas of the Red Sea coastal line, arid areas in the transitional zone of Tihama Hills, and elevated slopes of Tallan Mountain. This gradient, therefore, presented a wide variety of landforms including sand dunes, desert plain, wadi, desert pavement, and mountain. On this gradient phanerophytes were represented by members of the genus *Acacia*, namely; *A. ehrenbergiana* and *A. tortilis* (Table 1). The gradient was also rich in perennial herbs, grasses, and succulent species (Table 1). Plant diversity increased with increased altitude in a pattern that reflected the observed altitudinal decline of air temperature (Table 2). Results showed that C₄ plants exhibited a declining abundance while C₃ plants showed an increasing abundance with increased altitude (Table 2). The observed increased abundance of C₃ plants with increased altitude correlated with decreased air temperature. Since factors pertaining to soil water availability were eliminated by undertaking the present study well into the long dry season, air temperature was perhaps the major factor influencing plant diversity and distribution along the studied altitudinal gradient. Distinct differences between C₃ and C₄ modes of photosynthesis have stimulated comparative ecophysiological studies of these two pathways (Ziegler *et al.*, 1981; Batanouny *et al.*, 1988, Sayed, 1994; Nieva *et al.*, 1999; Tang and Zhang, 1999; Sayed and Mohamed, 2000). Plants with the C₄ mode of photosynthesis possess high temperature optima for CO₂ uptake and high water use efficiency (Leegood *et al.*, 1997; Long, 1999; Sage *et al.*, 1999). Our results indicated that plant diversity correlated well with decreased air temperature along the studied altitudinal gradient (Table 2). The observed differences in spatial distribution of C₃ and C₄ species along the altitudinal gradient pertained to air temperature rather than water availability since the study was undertaken during the dry season. Previous studies of plant distribution along altitudinal gradients in the tropics have shown that C₄ species were absent where minimum air temperature was below 8°C (Tieszen *et al.*, 1979; Earnshaw *et al.*, 1990). In arid regions C₄ species were also absent where growth season temperatures were below 8°C (Pyankov and Mokronosov, 1993; Sayed and Mohamed, 2000). It is, therefore, thought that altitudinal variation of air temperature profoundly affects competitive interactions between C₃ and C₄ plants. This conclusion gains support from similar previously published results (Lee-Thorp and Beaumont, 1995; Epstein *et al.*, 1997; Fredlund and Tieszen, 1997; Wang *et al.*, 2003; Shi *et al.*, 2006; Li *et al.*, 2007; Li *et al.*, 2009). Moreover, high abundance of C₄ plants at low altitudes pertains to the sensitivity of phosphoenol pyruvate carboxylase to low temperature which makes it difficult for C₄ plants to compete at high altitudes (Chen *et al.*, 2009). On the other hand, heat sensitivity of the C₃ pathway is well documented (Georgieva, 1999; Law and Crafts-Brandner, 1999; Georgieva and Brugnoli, 2002). The photosynthetic rate and carbohydrate reserves of C₃ plants decline under heat stress with carboxylation reactions being the initial site of damage (Feller *et al.*, 1998; Huang *et al.*, 1998; Law and Crafts-Brandner, 1999; Huang and Gao, 2000). Heat sensitivity of C₃ plants is thought to be due to heat sensitivity of the enzymes ribulose bis-phosphate carboxylase/oxygenase (rubisco) and rubisco activase (Sharkey *et al.*, 2001; Demireuska-Kepova and Feller, 2004) with the activation of rubisco by rubisco activase being the most heat sensitive step (Portis, 1995; He *et al.*, 1997; Salvucci and Ogren, 1996; Neuwald *et al.*, 1999; Crafts-Brandner and Salvucci, 2000; Ristic *et al.*, 2009). Heat sensitivity of the C₃ pathway is also thought to involve reduction of rubisco activity due to heat-induced conformational changes. This heat-induced impairment of rubisco activity explains the sensitivity of the C₃ pathway to high temperature (He *et al.*, 1997; Ristic *et al.*, 2009) and provides a sufficient explanation for the observed low abundance of C₃ plant at low altitudes. It can also be concluded that low temperatures prevailing at high altitudes limit the occurrence of C₄ species and hence shift the competitive balance in favour of C₃ species.

Furthermore, despite the absence of succulent CAM species at coastal line areas, they exhibited a wide distribution on the studied gradient (Table 1, Table 2). Since stomatal opening during the dark period for CAM nocturnal CO₂ uptake minimizes transpirational water loss, the most important benefit of CAM photosynthesis seems to be increased plant water use efficiency (Lüttge, 2004; Dodd *et al.*, 2002; Lüttge, 2008). Plants with

the CAM pathway are reported to have water use efficiency that is generally 6-fold higher than that of C_3 plants and 3-fold higher than that of C_4 plants (Nelson *et al.*, 2005; Silvera *et al.*, 2010). Considering the nine-month-long dry season of arid regions southwest of Saudi Arabia, the remarkably high water use efficiency associated with the CAM pathway represents an ecological advantage that enables succulent CAM species to attain the observed wide distribution along the studied altitudinal gradient.

Conclusions:

It can be concluded that low temperatures prevailing at high altitudes make it difficult for C_4 plants to survive and hence shift the ecological balance in favour of C_3 plants. Moreover, on altitudinal gradients of arid regions temperature is perhaps more important in controlling the altitudinal distribution of C_3 and C_4 plants. It can also be concluded that high water use efficiency associated with the CAM pathway is an ecological advantage that enables CAM species be widely wide distributed along srif regions altitudinal gradient.

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