

Altitudinal changes in photosynthetic pathways of floristic elements in southern Sinai, Egypt

O.H. SAYED and M.K. MOHAMED

Department of Botany, Faculty of Science, University of Minia, Minia 61519, Egypt

Abstract

High altitude profoundly influenced plant diversity and distribution on mountains of southern Sinai (Egypt). Plants exhibiting the C₃-mode of photosynthesis were widely distributed along the altitudinal transect. Plants exhibiting the C₄-mode were restricted below an altitude of about 1400 m above sea level. The transition from C₃-dominated areas to C₄-dominated areas occurred between 1200 and 1400 m a.s.l.

Additional key words: C₃; C₄; ecophysiology.

Introduction

Sinai is part of the Saharo-Arabian desert with a climate influenced by the Mediterranean in the north and high altitude in the south. Mountains of southern Sinai (Egypt) are characterised by outcrops of smooth-faced granite rocks, and landforms (slopes, terraces, and ridges). This area is floristically rich with 419 species of which 28 are endemic (Danin 1983, 1986, El-Ghareeb and Shabana 1990, Mostafa and Klopatek 1995, Boulos 1997). In this area, photosynthetic pathways and distribution of plant species have been studied (Winter and Troughton 1978,

Winter 1981, Ziegler *et al.* 1981, Vogel *et al.* 1986, Batanouny *et al.* 1988). However, although several studies describing plant distribution along altitudinal gradients in different parts of the world exist in the literature (Tieszen *et al.* 1979, Earnshaw *et al.* 1987), no attention has been given to the effects of high altitude on the flora of southern Sinai. This is why we describe altitudinal changes in photosynthetic pathways of the flora of Mount Musa (Saint Catherine area, southern Sinai, Egypt).

Materials and methods

The study site of Mount Musa, 2285 m a.s.l., is one of the highest mountains in Egypt. Records of temperature, humidity, precipitation, and evaporation for 20 years (1974-1994) supplied by the Authority of Meteorology were used to calculate variability coefficient of rainfall, annual thermal amplitude (Willert *et al.* 1992), and aridity (Sayed 1998). Work was carried out early in the dry season (mid-June) and included only perennial species prevailing at that time of year. Air (50 cm above ground) and soil (5-cm depth) temperatures were measured using a digital thermometer, and humidity was measured using a digital hygrometer (*Maplin Electronics*,

Manchester, U.K.). Soil water potential was determined using a psychrometer (*Wescor*, Logan, Utah, U.S.A.). Carbon isotope discrimination ratio ($\delta^{13}\text{C}$ values) in the ranges -24 to -31 ‰ and -10 to -15 ‰ were considered indicative of C₃- and C₄-modes of photosynthesis, respectively (Griffiths 1993). Quadrats (1 m²) were set at designated altitudes, plant species were identified (Zohary 1966, 1972, Täckholm 1974, Feinbrun-Dothan 1978, 1986, Boulos 1995, El-Hadidi and Fayed 1995, Boulos 1999), and diversity and evenness were calculated (Magurram 1988). Measurements were routinely repeated and standard error was calculated.

Results

For January and June, air temperature was -5 and 35 °C, relative humidity 58 and 29 %, evaporation 5.7 and

17.5 mm, respectively, and a mean annual rainfall of 45 cm y⁻¹ occurred partly as snow during the period Novem-

Received 20 April 2000, accepted 3 July 2000.
Fax: +20 86 363011, e-mail: rumenia@rusys.eg.net

ber-March. Calculations based on these records revealed that the study site had a variability coefficient of

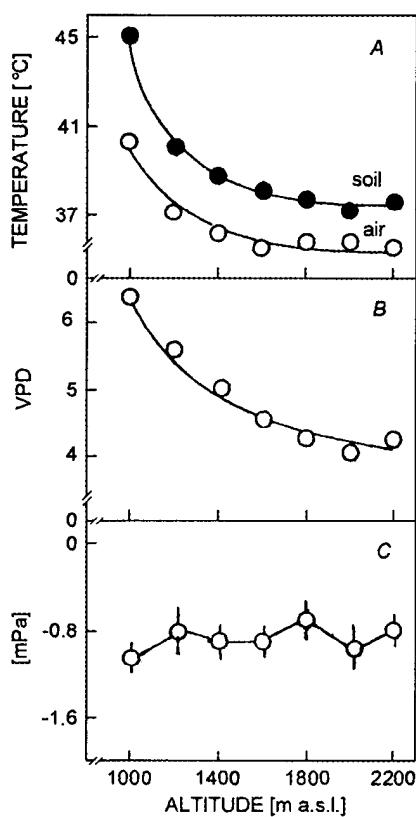


Fig. 1. Altitudinal changes in soil and air temperatures (A), vapour pressure deficit (B), and soil water potential (C) at the study site.

rainfall of 12, an annual thermal amplitude of 15 K, and an aridity of $8.6 \text{ mm } ^\circ\text{C}^{-1}$.

Soil and air temperatures and vapour pressure deficit decreased with increased altitude (Fig. 1A,B). Soil water potential remained almost unchanged, but was slightly higher at 1200 and 1800 m a.s.l. (Fig. 1C). A total of 33 perennials belonging to 15 families were recorded (Table 1). Five species (*Anabasis articulata*, *Atriplex halimus*, *Calligonum polygonoides*, *Heliotropium strigosum*, and *Salsola tetrandra*) had Kranz anatomy and $\delta^{13}\text{C}$ values characteristic of C_4 plants, whereas others had $\delta^{13}\text{C}$ values characteristic of C_3 plants. Diversity and evenness increased with increasing altitude, with diversity being slightly higher at 1200 and 1800 m a.s.l. (Fig. 2A,B). The number of C_3 species increased, whereas that of C_4 species decreased with increased altitude (Fig. 2C).

Discussion

Although most of Sinai is of Saharo-Arabian phytogeographical characteristics (McGinnies *et al.* 1968),

While C_3 species were widely distributed along the altitudinal transect, C_4 species were restricted below 1400 m a.s.l. (Table 2). Diversity correlated well with vapour pressure deficit and altitude (Fig. 3).

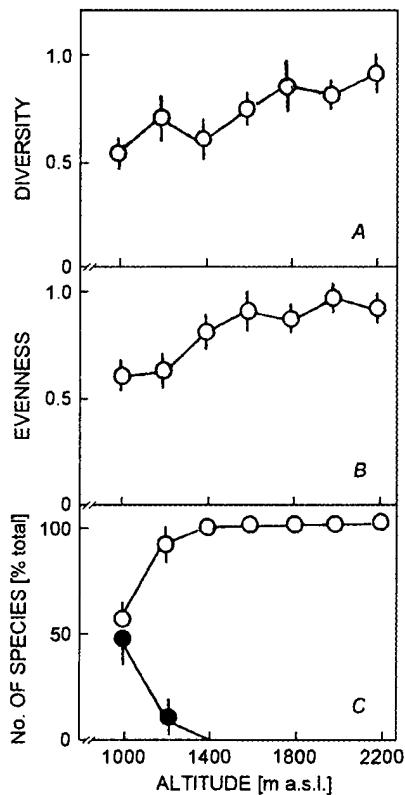


Fig. 2. Altitudinal changes in plant diversity (A), evenness (B), and number (C) of C_3 and C_4 species.

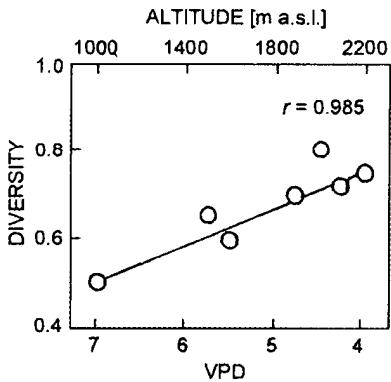


Fig. 3. Correlation between diversity, vapour pressure deficit, and altitude.

high mountains of Saint Catherine area are dominated by Irano-Turraean and endemic plant species (Mostafa and

Table 1. Recorded species (CFP = CO_2 fixation pathway, $\delta^{13}\text{C}$ = carbon isotope discrimination, H = herb, KA = Kranz anatomy, LF = Life form, S = shrub).

Family/Species	LF	KA	$\delta^{13}\text{C}$	CFP
Asclepiadaceae				
<i>Calotropis procera</i> (Ait.) Ait.f.	S	—	-27.9	C_3
Asteraceae				
<i>Achillea fragrantissima</i> (Forssk.) Sch. Bip.	H	—	—	C_3
<i>Artemisia judaica</i> L.	S	—	-28.8	C_3
<i>Atractylis flava</i> Desf. <i>Carduus</i> (Forssk.) C. Chr.	H	—	-26.8	C_3
<i>Echinops spinosus</i> L.	H	—	-26.8	C_3
<i>Launaea nudicaulis</i> (L.) Hook. f.	H	—	-30.0	C_3
<i>Launaea spinosa</i> (Forssk.) Sch. Bip. ex Kuntze	H	—	-28.5	C_3
<i>Pulicaria crispa</i> (Forssk.) Oliv.	S	—	—	C_3
<i>Pulicaria incisa</i> (Lam.) D.C.	S	—	—	C_3
Boraginaceae				
<i>Heliotropium strigosum</i> Willd.	S	—	-13.0	C_4
Brassicaceae				
<i>Farsetia aegyptiaca</i> Turra	S	—	-24.6	C_3
<i>Zilla spinosa</i> (L.) Prantl.	S	—	-27.3	C_3
Capparaceae				
<i>Capparis spinosa</i> L.	S	—	-25.5	C_3
Caryophyllaceae				
<i>Gymnocarpos fruticosus</i> (Vahl.) Pers.	S	—	-28.1	C_3
Chenopodiaceae				
<i>Anabasis articulata</i> (Forssk.) Moq. In A.D.C.	S	+	-11.7	C_4
<i>Atriplex halimus</i> L.	S	+	-14.8	C_4
<i>Salsola tetrandra</i> Forssk.	S	+	-13.2	C_4
Cleomaceae				
<i>Cleome droserifolia</i> (Forssk.) Del.	H	—	-26.8	C_3
Cucurbitaceae				
<i>Citrullus colocynthis</i> (L.) Schrad.	H	—	-24.4	C_3
Lamiaceae				
<i>Lavendula coronopifolia</i> Poir. In Lam.	S	—	—	C_3
<i>Phlomis aurea</i> Decne.	S	—	—	C_3
<i>Salvia aegyptiaca</i> L.	S	—	—	C_3
<i>Teucrium polium</i> L.	S	—	—	C_3
Polygonaceae				
<i>Calligonum polygonoides</i> L. <i>comosum</i> (L'Her.) Soslov	S	—	-11.9	C_4
<i>Polygonum equisetiforme</i> Sm.	H	—	-28.7	C_3
Rubiaceae				
<i>Galium sinaicum</i> (Del. ex Decne.) Boiss.	H	—	—	C_3
Solanaceae				
<i>Hyoscyamus muticus</i> L.	S	—	—	C_3
<i>Lycium arabicum</i> Schweinf.	S	—	-26.1	C_3
Tamaricaceae				
<i>Tamarix nilotica</i> (Ehrenberg.) Bge.	S	—	-26.6	C_3
Zygophyllaceae				
<i>Fagonia cretica</i> L.	S	—	-28.5	C_3
<i>Fagonia mollis</i> Del.	H	—	-26.3	C_3
<i>Peganum harmala</i> Sm.	S	—	-25.8	C_3
<i>Zygophyllum coccineum</i> Muschl.	S	—	-29.4	C_3

Klopatek 1995, Boulos 1997). Meteorological records indicated that although this area is the highest and coldest in Sinai, it had variability coefficient of rainfall, annual thermal amplitude, and aridity typical of arid zones. Although in such habitats rainfall is the major force influencing plant diversity and distribution (Lawlor 1993,

Sayed 1998), high altitude at the study site may have profound effects. Soil and air temperatures, and vapour pressure deficit decreased with increased altitude (Fig. 1A,B). The high mountains of Saint Catherine area have more annual rainfall than the rest of Sinai (Mostafa and Klopatek 1995), an observation that was reflected in the

increased diversity with increased altitude (Fig. 2A,B). Moreover, at the study site plants grew in little pockets of soil on slopes, and in larger plots of soil with higher water holding capacity on terraces (Danin and Plitmann 1987, Mostafa and Klopatek 1995). This high soil water holding capacity perhaps accounts for high diversity observed on terraces located at 1200 and 1800 m a.s.l. (Fig. 2A). However, soil water potential did not vary

significantly with increased altitude (Fig. 1C) since work was carried out during the dry season (mid-June) when the last effective rainfall occurred three months earlier (mid-March). This timing for the experiment was chosen to ensure the presence of only perennial species (Table 1), and to see if the distribution of plants exhibiting the C₃ or C₄ photosynthesis was influenced by factors other than soil moisture.

Table 2. Altitudinal distribution [m a.s.l.] of plant species recorded at the study site.

Species	CFP	Altitude						
		1000	1200	1400	1600	1800	2000	2200
<i>Anabasis articulata</i>	C ₄	+						
<i>Atriplex halimus</i>	C ₄	+						
<i>Calligonum polygonoides</i>	C ₄	+	+					
<i>Heliotropium strigosum</i>	C ₄	+	+					
<i>Salsola tetrandra</i>	C ₄	+						
<i>Zygophyllum coccineum</i>	C ₃	+	+					
<i>Artemisia judaica</i>	C ₃	+	+					
<i>Callotropis procera</i>	C ₃	+	+					
<i>Citrullus colocynthis</i>	C ₃	+	+					
<i>Cleome droserifolia</i>	C ₃	+	+	+				
<i>Hyoscyamus muticus</i>	C ₃	+	+	+				
<i>Lavendula coronopifolia</i>	C ₃	+	+					
<i>Lycium arabicum</i>	C ₃	+	+					
<i>Phlomis aurea</i>	C ₃	+	+					
<i>Peganum harmala</i>	C ₃	+	+	+				
<i>Teucrium polium</i>	C ₃	+	+	+	+			
<i>Zilla spinosa</i>	C ₃	+	+	+	+			
<i>Capparis spinosa</i>	C ₃		+	+	+			
<i>Fagonia cretica</i>	C ₃		+	+	+			
<i>Launaea spinosa</i>	C ₃		+	+	+			
<i>Pulicaria crispa</i>	C ₃		+	+	+	+		
<i>Achillea fragrantissima</i>	C ₃		+	+	+	+	+	
<i>Fagonia mollis</i>	C ₃		+	+	+	+	+	
<i>Atractylis flava</i>	C ₃			+	+	+	+	
<i>Pulicaria undulata</i>	C ₃			+	+	+	+	
<i>Echinops spinosus</i>	C ₃				+	+	+	
<i>Farsetia aegyptiaca</i>	C ₃				+	+	+	
<i>Gymnocarpos fruticosus</i>	C ₃				+	+	+	
<i>Launaea nudicaulis</i>	C ₃				+	+	+	
<i>Salvia aegyptiaca</i>	C ₃				+	+	+	
<i>Galium sinaicum</i>	C ₃					+	+	
<i>Polygonum equisetiforme</i>	C ₃					+	+	
% C ₃		54.55	91.67	100	100	100	100	100
% C ₄		45.45	8.33	0	0	0	0	0

The recognition that C₄ photosynthesis as a CO₂ concentrating mechanism was fundamentally different to C₃ photosynthesis (Edwards and Walker 1983) stimulated work on comparative ecophysiology of C₃ and C₄ plants (Winter 1981, Hattersley 1983, Jones 1985, Batanouny *et al.* 1988, Sayed 1994, Nieva *et al.* 1999, Tang and Zhang 1999). Plants exhibiting the C₄-mode of photosynthesis possess higher temperature optima for CO₂ fixation and improved water use efficiency (Jones 1985, Hattersley 1992, Nelson and Langdale 1992, Leegood *et al.* 1997, Long 1999). These features were reflected in

a survey of plants along a temperature gradient (Jones 1985) and along a gradient involving a double stress of drought and salinity (Sayed 1994). In the present study, plant diversity showed a good correlation with air temperature and humidity along the investigated altitudinal transect (Fig. 3). Moreover, while C₃ and C₄ species were equally numerous at 1000 m a.s.l., C₃ species were more numerous with increased altitude, and C₄ species were restricted below an altitude of about 1400 m a.s.l. (Fig. 3C). This difference in altitudinal distribution of C₃ and C₄ species perhaps pertained to air temperature and humidity

rather than soil moisture since soil water potential was almost unchanged with increased altitude. Similar results were reported along an altitudinal transect in Kenya in which C_4 species were not present when mean annual minimum temperature was below 8 °C (Tieszen *et al.* 1979). In Hawaii the transition from complete C_4 to C_3 dominance occurs at 1000-2000 m a.s.l. (Rundel 1980), and in New Guinea this transition was also observed at about 2500 m a.s.l. (Earnshaw *et al.* 1990). Moreover, there is also evidence for latitudinal interaction with the

distribution of C_4 species involving a transition from C_3 -dominated areas to C_4 -dominated areas that is influenced by temperature (Sage *et al.* 1999). In the arid regions of central Asia, C_4 species were absent where growth season temperature was less than 8 °C (Pyankov and Mokronosov 1993). It can, therefore, be concluded that low temperatures prevailing at high altitudes of Mount Musa (southern Sinai) restricted the occurrence of C_4 species and hence shifted the balance of competition in favour of C_3 species.

References

Batanouny, K.H., Stichler, W., Ziegler, H.: Photosynthetic pathways, distribution, and ecological characteristics of grass species in Egypt. - *Oecologia* **75**: 539-548, 1988.

Boulos, L.: Flora of Egypt - Checklist. - Al-Hadara Publishing, Cairo 1995.

Boulos, L.: Endemic flora of the Middle East and North Africa. - In: Barakat, H.N., Hegazy, A.K. (ed.): Reviews in Ecology, Desert Conservation, and Development. Pp. 229-260. Metropol, Cairo 1997.

Boulos, L.: Flora of Egypt. - Al-Hadara Publishing, Cairo 1999.

Danin, A.: Desert Vegetation of Israel and Sinai. - Cana Publishing, Jerusalem 1983.

Danin, A.: Flora and Vegetation of Sinai. - Proc. roy. Soc. Edinburgh **89**: 159-168, 1986.

Danin, A., Plitmann, U.: Revision of plant geographical territories of Israel and Sinai. - *Plant Syst. Evol.* **159**: 43-51, 1987.

Earnshaw, M.J., Winter, K., Ziegler, H., Stichler, W., Crutwell, N.E.G., Kerenga, K., Gribb, P.J., Wood, J., Croft, J.R., Carver, K.A., Gunn, T.C.: Altitudinal changes in the incidence of crassulacean acid metabolism in vascular epiphytes and related life forms in Papua New Guinea. - *Oecologia* **73**: 566-572, 1987.

Earnshaw, M.J., Carver, K.A., Gunn, T.C., Kerenga, K., Harvey, V., Griffiths, H., Broadmeadow, M.S.J.: Photosynthetic pathways, chilling tolerance, and cell sap osmotic potential values of grasses along an altitudinal gradient in Papua New Guinea. - *Oecologia* **84**: 280-288, 1990.

Edwards, G., Walker, D.A.: C_3 , C_4 : Mechanisms, and Cellular and Environmental Regulation of Photosynthesis. - Blackwell Scientific Publications, Oxford 1983.

El-Ghareeb, R., Shabana, M.A.: Distribution of plant species along physiognomic gradients in two wadi beds of southern Sinai. - *J. Arid Environ.* **19**: 169-173, 1990.

El-Hadidi, M.N., Fayed, A.: Materials for excursion flora of Egypt. - *Tackholmia* **15**: 1-23, 1995.

Feinbrun-Dothan, N.: Flora Palaestina 2. - Israel Academy of Sciences and Humanities, Jerusalem 1978.

Feinbrun-Dothan, N.: Flora Palaestina 4. - Israel Academy of Sciences and Humanities, Jerusalem 1986.

Griffiths, H.: Carbon isotope discrimination. - In: Hall, D.O., Scurlock, J.M.O., Bolhár-Nordenkampf, H.R., Leegood, R.C., Long, S.P. (ed.): Photosynthesis and Production in a Changing Environment. Pp. 181-192. Chapman & Hall, London - Glasgow - New York - Melbourne - Madras 1993.

Hattersley, P.W.: The distribution of C_3 and C_4 grasses in Australia in relation to climate. - *Oecologia* **57**: 113-128, 1983.

Hattersley, P.W.: C_4 photosynthetic pathway variation in grasses (*Poaceae*): Its significance for arid and semi-arid lands. - In: Chapman, G.P. (ed.): Desertified Grassland: Their Biology and Managements. Pp. 181-212. Academic Press, London 1992.

Jones, C.A.: C_4 Grasses and Cereals. - John Wiley & Sons, New York 1985.

Lawlor, D.W.: Photosynthesis: Metabolism, Control and Physiology. - Longman Scientific and Technical, Harlow 1993.

Leegood, R.C., Caemmerer, S. von, Osmond, C.B.: Metabolite transport and photosynthetic regulation in C_4 and CAM plants. - In: Dennis, D.T., Turpin, D.H., Lefebvre, D.D., Layzell, D.B. (ed.): Plant Metabolism. Pp. 341-369. Longman, Essex 1997.

Long, S.P.: Ecology of C_4 photosynthesis: Environmental responses. - In: Sage, R.F., Monson, R.K. (ed.): C_4 Plant Biology. Pp. 215-249. Academic Press, London 1999.

Magurran, A.E.: Ecological Diversity and its Measurement. - Croom Helm, London 1988.

McGinnies, W.G., Goldman, B.J., Paylore, P.: Deserts of the World. - Univ. Arizona Press, Tucson 1968.

Mostafa, A.A., Klopatek, J.M.: Vegetation and landforms of the Saint Catherine area, southern Sinai, Egypt. - *J. Arid Environ.* **30**: 385-392, 1995.

Nelson, T., Langdale, J.A.: Developmental genetics of C_4 photosynthesis. - *Annu. Rev. Plant Physiol. Plant mol. Biol.* **43**: 25-47, 1992.

Nieva, F.J.J., Castellanos, E.M., Figueroa, M.E., Gil, F.: Gas exchange and chlorophyll fluorescence of C_3 and C_4 saltmarsh species. - *Photosynthetica* **36**: 397-406, 1999.

Pyankov, V.L., Mokronosov, A.T.: General trends in changes of the earth's vegetation related to global warming. - *Russ. J. Plant Physiol.* **40**: 443-458, 1993.

Rundel, P.W.: The ecological distribution of C_4 and C_3 grasses in the Hawaiian islands. - *Oecologia* **45**: 354-359, 1980.

Sage, R.F., Wedin, D.A., Li, M.: The biogeography of C_4 photosynthesis: Patterns and controlling factors. - In: Sage, R.F., Monson, R.K. (ed.): C_4 Plant Biology. Pp. 313-373. Academic Press, London 1999.

Sayed, O.H.: Edaphic gradients and species attributes influencing plant distribution in littoral salt marshes of Qatar. - *Qatar Univ. Sci. J.* **14**: 257-262, 1994.

Sayed, O.H.: Phenomorphology and ecophysiology of desert succulents in eastern Arabia. - *J. Arid Environ.* **40**: 177-189, 1998.

Täckholm, V.: Student Flora of Egypt. - Cairo University Press, Cairo 1974.

Tang, H.P., Zhang, X.S.: A new approach to distinguishing photosynthetic types of plants. A case study in Northeast China Transect (NECT) platform. - *Photosynthetica* **37**: 97-106, 1999.

Tieszen, L.L., Senyimba, M.M., Imbamba, S.K., Troughton, J.H.: The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. - *Oecologia* **37**: 337-350, 1979.

Vogel, J.C., Fuls, A., Danin, A.: Geographical and environmental distribution of C₃ and C₄ grasses in the Sinai, Negev and Judean deserts. - *Oecologia* **70**: 258-265, 1986.

Willert, D.J. von, Eller, B.M., Werger, M.J.A., Brinckmann, E., Ihlenfeldt, H.: Life Strategies of Succulents in Deserts. - Cambridge University Press, Cambridge 1992.

Winter, K.: C₄ plants of high biomass in arid regions of Asia - occurrence of C₄ photosynthesis in *Chenopodiaceae* and *Polygonaceae* from the Middle East and USSR. - *Oecologia* **48**: 100-106, 1981.

Winter, K., Troughton, J.H.: Photosynthetic pathways in plants of coastal and inland habitats in Israel and the Sinai. - *Flora* **167**: 1-34, 1978.

Ziegler, H., Batanouny, K.H., Sankhla, N., Vyas, O.P., Stichler, W.: The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt, and Iraq. - *Oecologia* **48**: 93-99, 1981.

Ziegler, H., Batanouny, K.H., Sankhla, N., Vyas, O.P., Stichler, W.: The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt, and Iraq. - *Oecologia* **48**: 93-99, 1981.

Zohary, M.: Flora Palaestina. - Israel Academy of Sciences and Humanities, Jerusalem 1966, 1972.