

C₄ SPECIES IN THE HIGHLANDS OF IRAN & AFGHANISTAN

EVA BORCHERS*, W. FREY** & H. H. HILGER**

ABSTRACT. 238 species, most of them predominating in characteristic vegetation units of the Iranian highland, have been investigated with regard to Kranz anatomy (C₄ photosynthesis). Most of the C₄ species live in saline habitats, whereas the xeromorphic open scrub and dwarf-shrublands, as well as the high mountain grass slopes, are inhabited by C₃ species. Only in the Chenopodiaceae do C₄ species belong to the indigenous Irano-Turanian floristic element. The lack of C₄ species at altitudes above 1700 m is ascribed to low average minimum temperatures during the cold season.

ZUSAMMENFASSUNG. 238 für die Vegetation des Iranischen Hochlandes charakteristische Pflanzenarten wurden auf den Besitz von Kranzzellen (C₄-Photosynthese) hin untersucht. Während die Xeromorphen offenen Gebüschformationen und Xeromorphen offenen Zwerggesträuche sowie die Grasfluren der Gebirge von C₃-Arten aufgebaut werden, leben die C₄-Arten bevorzugt auf versalzten Standorten. Das Fehlen der C₄-Arten in Höhen über 1700 m wird auf die zu niedrigen Durchschnittstemperaturen während der kalten Jahreszeit zurückgeführt.

INTRODUCTION

C₄ plants, characterized by the occurrence of the four-carbon malic and aspartic acids as initial products of CO₂ fixation during photosynthesis, are mainly known from tropical, non-asiatic regions with seasonal aridity. Their ecological behaviour indicates that they are particularly well adapted to dry habitats and high light intensity. Many investigations have been carried out in other parts of the world (e.g. in southwest USA (Welkie & Caldwell, 1970; Teeri & Stowe, 1976), South America, South Africa and India (Sankhla et al., 1975), and the Saharan desert (Winter et al., 1976)) but to date only Winter & Troughton (1978) have studied C₄ plants from the Near East, their study concentrating on Sinai and Negev.

The Iranian highland and its fringelands, with the exception of the southern coastal area of the Caspian Sea (Hyrcanian district and woodland), belong to the dry belt of the Ancient World. This area is decidedly arid and so quite comparable with other areas showing a high occurrence of C₄ plants. Much of the vegetation is Irano-Turanian steppe and desert plant communities. Xeromorphic dwarf-shrublands and thorn-cushion formations cover large areas, while in contrast extensive plains and swamps of halophytic vegetation dominate the undrained salt-lakes and kewirs (salt-clay deserts). In the high surrounding mountains above 3000 m alpine grasslands also occur, and cover large areas in the Elburz and Hindu Kush ranges.

This paper deals with a study of C₄ plants of the Iranian highland, paying particular attention to their ecological and systematic distribution.

MATERIAL AND METHODS

Characteristic species (markers) from dominant Iranian highland vegetation units such as xeromorphic scrub, xeromorphic dwarf-shrublands, thorn-cushion

*Wielandstr. 8, D-8051 Erding, BRD

**Botanisches Institut (I) der Justus-Liebig-Universität Giessen, Senckenbergstr. 17-21, D-6300 Giessen, BRD

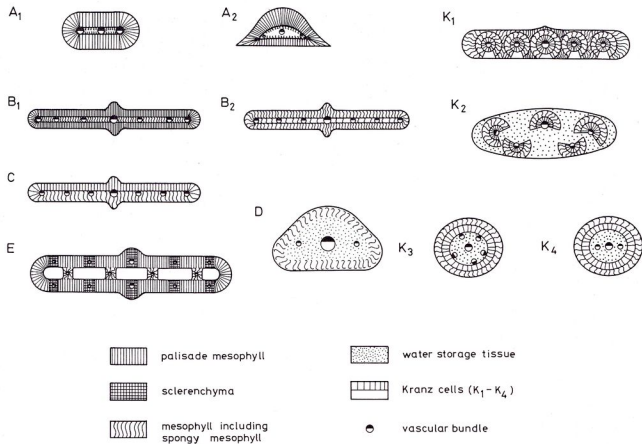


FIG. 1. General (A-E) and Chenopodiaceous (K_1-K_4) leaf anatomy. Explanation in text, p. 101.

formations, grasslands, and halophytic communities were taken for study. A few samples were also investigated from the fringelands and of azonal vegetation such as mangrove swamp. Particular attention was paid to members of families already known to contain many C₄ species. Following Downton (1975) and Welkie & Caldwell (1970) we used Kranz cell anatomy (Haberlandt, 1896) and starch-grain concentration in bundle-sheath chloroplasts as the diagnostics to identify C₄ plants. Clearly only physiological studies can give an absolutely certain determination of C₄ species, but in all cases yet reported plants with distinct Kranz cell anatomy show the C₄ pathway (Ray & Black, 1979), so it seems safe to regard this character as an indicator of C₄ species.

The specimens used in the investigation were collected by Frey et al. in 1965 and 1974–8; leaf material was obtained from herbarium sheets in the TAVO herbarium (SFB 19 Tübinger Atlas des Vorderen Orients, Fach Botanik), all of which are labelled as having been used in the study.

Dried leaves were boiled in distilled water and either hand-sectioned or embedded in paraffin-wax and cut by microtome. Lignin was stained by the phloroglucin/HCl method and starch by treatment with Lugol's solution.

GENERAL LEAF ANATOMY

For the purposes of the investigation leaves were classified into the types shown in Fig. 1. Many plants studied showed xeromorphic and/or succulent features as adaptations to extreme arid habitats; the mesomorphic dorsiventrally flattened leaf with a clear distinction of palisade and spongy mesophyll (type C of Fig. 1) was of infrequent occurrence. Type A1 of Fig. 1 is an equifacial centric leaf and A2 an equifacial triangular one: the latter is the typical leaf of thorn-cushions. Type B represents a flattened equifacial leaf, either with well-developed (B1) or reduced palisade chlorenchyma (B2). Succulent leaves (D) contain a water-storage tissue. Type E represents the typical leaf of monocotyledons.

The C₄-Chenopodiaceae exhibit a special leaf architecture in generally succulent leaves (Carolin et al., 1975). The peripheral chlorenchyma is separated into distinct Kranz cells and palisade mesophyll. In most cases peripheral vascular bundles accompany the main central bundle. In the Atriplicoid type (K1) Kranz cells and mesophyll are radially arranged around the vascular tissue, leaving a gap on the abaxial surface below each bundle. The Kochioid type (K2) differs from the Atriplicoid in two ways: the Kranz cells form an arc around the xylem of the peripheral bundles and there is a central water-storage tissue present. The Salsoloid type (K3) resembles the Kochioid, but Kranz cells and mesophyll form complete hypodermal layers to which some peripheral bundles are attached. In the Suaedoid type (K4) the peripheral bundles are separated from the Kranz cells by surrounding aqueous tissue.

RESULTS

Table 1 gives all species recorded with Kranz cell arrangement and Table 2 A–F the non-Kranz species subdivided by life form. Table 3 is devoted to the grasses, while Table 4 shows the ratio of Kranz to non-Kranz species in those families where both types occur.

TABLE 1

SPECIES WITH KRANZ CELL ARRANGEMENT

In all tables authors for plant species follow Rechinger (1963—)

A, annual	PG, phytogeographic area
CA, Central-Asiatic	PR, pluriregional
DS, dwarf-shrub	PT, palaeotropical
E, episodal desert forb community	R, ruderal
F, forb	Rb, riverbanks
FC, forb community	S, scrub
H, halophytic	Sd, semidesert shrublands
h, halophile influenced	TK, type of Chenopod. Kranz anatomy (see text, p. 101)
Hind., Hindu Kush	TS, tree or shrub
IT, Irano-Turanian	X, xeromorphic dwarf-shrublands
Khor., Khorasan	
ME, Mediterranean	

	Locality	Alt. (m)	PG	Veg. units	Growth form	TK
Amaranthaceae						
<i>Aerva persica</i>	Bander-Abbas/Iran	100	PT	X	DS	
<i>Amaranthus graecizans</i>	Maharlu Lake/Iran	1460	PR	R	A	
<i>A. retroflexus</i>	Maharlu Lake/Iran	1460	PR	R	A	
Chenopodiaceae						
<i>Aellenia subaphylla</i>	S Aminabad/Iran	2070	IT	h,X	F	3
<i>A. sp. (77-1093)</i>	Shahabbas/Iran	800		H	F	3
<i>Anabasis setifera</i>	Qeshm/Iran	50	SA	h,X	DS	3
<i>Arthrophytum wakhanicum</i>	Sharan, Hind./Afgh.	2800	CA	X	F	3
<i>Atriplex halimus</i>	Maharlu Lake/Iran	1460	ME,SA	H	DS	1
<i>A. leucoclada</i>						
var. <i>turcomanica</i>	Maharlu Lake/Iran	1460	IT,SA	R,h	F	1
<i>A. sp. (75-107)</i>	Maharlu Lake/Iran	1460		R	F	1
<i>A. sp. (78-2)</i>	Tuz Gölü/Turkey	905		H	A	1
<i>Bassia sp. (75-1046)</i>	Abadeh/Iran	1700		X	A	2
<i>Girgensohnia sp. (75-1052)</i>	SE Abadeh/Iran	1800		X	F	3
<i>Halarchon vesiculosum</i>	Dasht-i-Margo/Afgh.	900	CA	h,E	A	3
<i>Halimocnemis sp. (75-806)</i>	S Aminabad/Iran	2070		h,X	A	3
<i>Halocharis pillosa</i>	—	—		H	A	3
<i>H. sp. (75-179)</i>	Maharlu Lake/Iran	1460		h,X	A	3
<i>Haloxylon aphyllum</i>	Dasht-e-Shah, Khor./Iran	1600	IT	h	DS	3
<i>Kochia prostrata</i>	SE Abadeh/Iran	1800	PT	h,X	F	2
<i>K. scoparia</i>	SE Abadeh/Iran	1700	IT	h,X	A	1
<i>K. sp. (77-909)</i>	Hassanabad/Iran	500			F	2
<i>K. sp. (77-1059)</i>	Qeshm/Iran	50		R	A	2
<i>Noaea mucronata</i>	Maharlu Lake/Iran	1460	IT	R,h	F	3
<i>Petrosimonia brachiata</i>	Tuz Gölü/Turkey	905	IT,SA	R	A	3
<i>Salsola cf. aucheri</i>	Dasht-e-Shah, Khor./Iran	1700	IT	H	F	3
<i>S. cf. aurantica</i>	W Ashkhaneh/Iran	850	IT	X	F	3
<i>S. baryosma</i>	Maharlu Lake/Iran	1460	SU	H	DS	3
<i>S. collina</i>	Sharan, Hind./Afgh.	2800		h,X	A	3
<i>S. cf. glauca</i>	Khorasan/Iran	1800	IT	H	F	3
<i>S. cf. laricifolia</i>	SE Abadeh/Iran	1700	IT	h,X	F	3
<i>S. sp. (75-810)</i>	S Aminabad/Iran	2070		h,X	A	3

TABLE 1 (contd)

	Locality	Alt. (m)	PG	Veg. units	Growth form	TK
S. sp. (76-371)	Bander-Khamir/Iran	100		h,X	DS	3
Suaeda vermiculata	Qeshm/Iran	50	SA	h,S	F	4
S. sp. (75-924)	Maharlu Lake/Iran	1460		H	A	4
S. sp. (76-549)	Bander-Khamir/Iran	100		H	F	4
Cyperaceae						
Cyperus laevigatus	Maharlu Lake/Iran	1460		h,Fc	F	
C. longus var. pallidus	Jurm/Afgh.	1650		Rb	F	
C. rotundus	Kunduz/Afgh.	400		R	F	
Poaceae						
Aeluropus litoralis	Maharlu Lake/Iran	1460	PR	H	F	
Bothriochloa ischaemum	Jokham, Hind./Afgh.	1700	PR	R	F	
Cynodon dactylon	Maharlu Lake/Iran	1460	PR	R	F	
Setaria viridis	Maharlu Lake/Iran	1460	PR	R	A	
Stipagrostis plumosa var. plumosa	Kewir Nat. Res./Iran	950	PR	h,X	A	
Tragus racemosus	Bander-Abbas/Iran	100	PR	Sd	A	
Zygophyllaceae						
Tribulus longipetalus	Kewir Nat. Res./Iran	900	SU	R	A	
T. terrestris	Shiraz/Iran	1600	PR	R,h	A	

TABLE 2

SPECIES WITH NON-KRANZ CELL ARRANGEMENT

H, halophyte; h, halophile influenced; HS, halophytic status; LA, leaf anatomy — see Fig. 1 and p. 101 for explanation of categories.

TREES AND SHRUBS	Locality	Alt.(m)	LA	HS	Veg. unit
Avicenniaceae					
Avicennia marina (tree)	Qeshm/Iran	50	C	H	Mangrove forests
Mimosaceae					
Acacia aucheri (tree)	Bander-Khamir/Iran	100	Al		Extremely xeromorphic woodlands
Rhamnaceae					
Ziziphus spina-christi (tree)	N Bander-Abbas/Iran	900	Bl		Xer. dwarf-shrublands
Chenopodiaceae					
Halocnemum strobilaceum	Bander-Khamir/Iran	10	D	H	Halophytic comm.
Convolvulaceae					
Convolvulus anthocladus	Maharlu Lake/Iran	1800	A2		Semidesert shrublands
Lamiaceae					
Perovskia abrotanoides	Bodjnurd/Iran	1000	NK		Xer. dwarf-shrublands
Tamaricaceae					
Myricaria germanica	Jokham Valley, Hind./Afgh.	1800	A1		Alluvial scrub
Tamarix macrocarpa	Maharlu Lake/Iran	1500	A2	H	Halophytic comm.
T. ramosissima	Jokham Valley, Hind./Afgh.	1800	A1		Alluvial scrub
T. tetrandra	Maharlu Lake/Iran	1480	A2	h	Halophytic comm.

TABLE 2 (contd)

	Locality	Alt.(m)	LA	HS	Veg. unit
Thymelaeaceae					
<i>Daphne mucronata</i>	Ardekan, Fars/Iran	2000	B1		Xer. dwarf-shrublands with shrubs
Zygophyllaceae					
<i>Zygophyllum atriplicoides</i>	Ashkhaneh, Khor./Iran	850	B1		Open xeromorphic scrub
<i>Z. eurypterum</i> subsp. <i>eurypterum</i>	Sarisang, Hind./Afgh.	2100	B1		Semidesert shrublands
THORN-CUSHIONS					
Caryophyllaceae					
<i>Acanthophyllum scapiflorum</i>	Ghazni/Afgh.	2000	A2		Xer. dwarf-shrublands with thorn-cushions
<i>A. sp.</i> (77-132)	Damavand, Elburz/Iran	2000	A2		" " " "
<i>A. sp.</i> (77-1019)	Varangrud, Elburz/Iran	3600	A2		Alpine forb formation
<i>A. sp.</i> (75-921)	Rud-i-Shah/Iran	2500	A2		
Fabaceae					
<i>Astragalus lasioseni</i>	Parshui, Hind./Afgh.	3800	A2		Xer. dwarf-shrublands with thorn-cushions
Plumbaginaceae					
<i>Acantholimon sp.</i> (75-279)	Kuh-i-Sabzpushan/Iran	2000	A2		Xer. dwarf-shrublands with thorn-cushions
<i>A. sp.</i> (75-946)	Maharlou Lake/Iran	1800	A2		" " " "
<i>A. sp.</i> (77-807)	Varangrud, Elburz/Iran	3000	A2		Forb formation with thorn-cushions
<i>A. sp.</i> (77-1061)	Kondor, Elburz/Iran	2200	A2		Xer. dwarf-shrublands with thorn-cushions
DWARF-SHRUBS					
Asteraceae					
<i>Artemisia lamprocarpos</i>	Hazarat, Hind./Afgh.	1800	A1		Xer. dwarf-shrublands
<i>A. macrocephala</i>	Iskazer, Hind./Afgh.	2600	A1		" " " "
<i>A. turczaninowiana</i>	Parshui, Hind./Afgh.	4000	A1		" " " "
<i>Hertia intermedia</i>	Ghazni/Afgh.	2600	NK		" " " "
<i>Lactuca orientalis</i>	Bodjnurd/Iran	1850	NK		" " " "
Boraginaceae					
<i>Echiochilon kotschy</i> subsp. <i>tuberculosum</i>	Bander-Khamir/Iran	200	D		Semidesert shrublands
<i>Heliotropium bacciferum</i>	Bander-Abbas/Iran	100	B1		" " " "
<i>Onosma dasytrichum</i>	Borazjan, Fars/Iran	1000	B1		Xer. dwarf-shrublands
<i>Trichodesma incanum</i>	Hazarat, Hind./Afgh.	1750	B1		" " " "
Brassicaceae					
<i>Aethionema elongatum</i>	Ardekan/Iran	1800	NK		Xer. dwarf-shrublands
<i>Diceratella canescens</i>	N Bander-Abbas/Iran	850	B2		" " " "
<i>Farsetia heliophila</i>	Qeshm/Iran	100	A		Open xer. scrub
<i>Fortuynia garcinii</i>	Bander-Khamir/Iran	100	B2		" " " "
<i>Matthiola flavida</i>	Maharlou Lake/Iran	1800	B1		Xer. dwarf-shrublands
<i>M. ovatifolia</i>	SE Aminabad/Iran	2000	B1		" " " "
<i>Morieria spinosa</i>	SE Abadeh/Iran	2100	A		" " " "

TABLE 2 (contd)

	Locality	Alt.(m)	LA	HS	Veg. unit
DWARF-SHRUBS (contd)					
Capparidaceae					
<i>Capparis spinosa</i> var. <i>spinosa</i>	Shiraz/Iran	1700	B1		Xer. dwarf-shrublands
<i>C. spinosa</i> var. <i>mucronifolia</i>	Qeshm/Iran	50	B1		" " "
Chenopodiaceae					
<i>Halocnemum strobilaceum</i>	Tuz Gölü/Turkey	850	D	H	Halophytic comm.
<i>Kochia</i> sp. (75-931)	Maharlû Lake/Iran	1460	D	H	" "
Convolvulaceae					
<i>Convolvulus dorycnium</i> subsp. <i>oxysepalus</i>	Maharlû Lake/Iran	1800	A2		Xer. dwarf-shrublands
<i>C. leiocalycinus</i>	Maharlû Lake/Iran	1800	A		" " "
<i>C. leptocladius</i>	Bander-Khamir/Iran	200	A		Semidesert shrublands
<i>Cressa cretica</i>	Maharlû Lake/Iran	1460	A1	H	Halophytic comm.
Euphorbiaceae					
<i>Euphorbia</i> sp. (75-568)	Bander-Khamir/Iran	100	B		Xer. dwarf-shrublands
<i>E. sp.</i> (75-809)	S Aminabad/Iran	2070	B		" " "
<i>E. sp.</i> (75-1020)	SE Sisakht/Iran	2750	B2	h	Xer. dwarf-shrublands with forbs
Fabaceae					
<i>Astragalus infestus</i>	Mukur/Afgh.	1100	B1		Xer. dwarf-shrublands
<i>A. macropterus</i>	Pajuka, Hind./Afgh.	3200	B1		" " "
<i>Trigonella griffithii</i>	Rabat, Hind./Afgh.	2300	C		Xer. dwarf-shrublands with forbs
Frankeniaceae					
<i>Frankenia hirsuta</i>	E Isfahan/Iran	1600	A1	AH	Halophytic comm.
<i>F. persica</i>	Maharlû Lake/Iran	1460	A1	H	" "
Lamiaceae					
<i>Teucrium polium</i>	W Bodjurd/Iran	1000	B		Xer. dwarf-shrublands
<i>Ziziphora clinopodioides</i>	Jokham, Hind./Afgh.	2700	B		Forb comm. with dwarf-shrubs
Polygonaceae					
<i>Polygonum myrtillifolium</i>	Jokham, Hind./Afgh.	3600	B1		Forb comm.
<i>Pteroporum olivieri</i>	Sharok, Elburz/Iran	1800	B1		Evergreen needle-leaved woodlands
Rutaceae					
<i>Haplophyllum perforatum</i>	Hazarat, Hind./Afgh.	2100	B1		Xer. dwarf-shrublands
Thymelaeaceae					
<i>Dendrostellera lessertii</i>	N Isfahan/Iran	1600	B1		Xer. dwarf-shrublands
HERBACEOUS PLANTS					
Apiaceae					
<i>Eryngium</i> cf. <i>bibersteinianum</i>	Babolsar/Iran	10	C	h	Coastal dunes
<i>Prangos pabularia</i>	Salang, Hind./Afgh.	2650	A		Xer. dwarf-shrublands and perennial forb comm.
Asteraceae					
<i>Achillea millefolium</i>	Kandavan, Elburz/Iran	3000	A1	H	Forb comm.
<i>Erigeron orientalis</i>	Parshui, Hind./Afgh.	3600	C		" "

TABLE 2 (contd)

	Locality	Alt.(m)	LA	HS	Veg. unit
HERBACEOUS PLANTS (contd)					
Brassicaceae					
<i>Alyssum bracteatum</i>	W Isfahan/Iran	1600	B2		Ephemeral forb comm.
<i>Erysimum oleifolium</i>	Neyriz/Iran	1400	B2		Xer. dwarf-shrublands
<i>E. persepoltanum</i>	Ardekan/Iran	1900	B		" " "
<i>Hesperis</i> cf. <i>curdica</i>	Maharlu Lake/Iran	1800	B2		" " "
<i>Lepidium latifolium</i>	Hazarat, Hind./Afgh.	1900	B		" " "
Caryophyllaceae					
<i>Dianthus orientalis</i>	Dalir, Elburz/Iran	2400	A		Ruderal comm.
Chenopodiaceae					
<i>Atriplex</i> sp. (78-1)			A1	H	Halophytic comm.
Convolvulaceae					
<i>Convolvulus arvensis</i>	Maharlu Lake/Iran	1460	B		Ruderal comm.
<i>C. fatmensis</i>	Bander-Khamir/Iran	100	B		" "
<i>C. pseudocantabrica</i>	Mukur/Afgh.	1200	A		" "
Cyperaceae					
<i>Cladium mariscus</i>	Maharlu Lake/Iran	1460	E		Tall sedge swamp
<i>Fimbristylis dichotoma</i>	Spe Valley, Hind./Afgh.	2400	E		Low sedge swamp
<i>Kobresia stenocarpa</i>	Parshui, Hind./Afgh.	3700	NK		" "
<i>Scirpus triquetus</i>	Maharlu Lake/Iran	1460	NK		Reed swamp
<i>S. sp.</i> (78-9)	Tuz Gölü/Turkey	905	NK	h	Halophytic comm.
Euphorbiaceae					
<i>Euphorbia boissieriana</i>			B1		Mixed dwarf-scrub and herbaceous formation
<i>E. sp.</i> (76-714)	Sirjan/Iran	1700	B2	h	Xer. dwarf-shrublands
<i>E. sp.</i> (75-20)	N Isfahan/Iran	1600	B2	h	Xer. dwarf-shrublands with shrubs
<i>E. sp.</i> (75-759)	N Sisakht/Iran	2300	B1		Xer. dwarf-shrublands
<i>E. sp.</i> (75-398)	Ardekan/Iran	2000	B1		" "
<i>E. sp.</i> (75-1022)	Sisakht/Iran	2750	A		Xer. dwarf-shrublands with forbs
<i>E. sp.</i> (75-1021)	Sisakht/Iran	2800	B		" " " " " "
Juncaceae					
<i>Juncus rigidus</i>	Tuz Gölü/Turkey	905	D	h	Halophytic comm.
<i>J. subulatus</i>	Maharlu Lake/Iran	1460	D		Tall sedge swamp
Lamiaceae					
<i>Marrubium</i> cf. <i>cuneatum</i>	Bodjnurd/Iran	1000	NK		Coastal dunes
<i>Phlomis cashmeriana</i>	Salang, Hind./Afgh.	2500	C		Subalpine forb formation
<i>Stachys parviflora</i>	Ybak/Afgh.	1300	B		Forb formation
Plumbaginaceae					
<i>Limonium</i> sp. (78-6)	Tuz Gölü/Turkey	905	B1	h	Halophytic comm.
Potamogetonaceae					
<i>Potamogeton perfoliatus</i>	Tuz Gölü/Turkey	905	D	H	Halophytic comm.
Primulaceae					
<i>Samolus valerandi</i>	Yasuj/Iran	1800	C		Flushes
Scrophulariaceae					
<i>Scrophularia scabiosifolia</i>	Parshui, Hind./Afgh.	3700	B1		Forb formation

TABLE 2 (contd)

	Locality	Alt.(m)	LA	HS	Veg. unit
Typhaceae					
<i>Typha angustifolia</i>	Maharlu Lake/Iran	1460	E		Reed swamp
Zygophyllaceae					
<i>Peganum harmala</i>	Iskazer, Hind./Afgh.	2600	NK		Ruderal comm.
<i>Zygophyllum fabago</i>					
subsp. <i>dolichocarpum</i>	SE Amirabad/Iran	1700	B1		Ruderal comm.
<i>Z. fabago</i> subsp. <i>fabago</i>	Gadok, Elburz/Iran	1700	B1		Xer. dwarf-shrublands
ANNUALS					
Asteraceae					
<i>Filago pyramidata</i>	Tuz Gölü/Turkey	900	A1	H	Halophytic comm.
<i>Senecio coronopifolius</i>	Pajuka, Hind./Afgh.	2850	B2		Xer. dwarf-shrublands with forbs
<i>S. vernalis</i>	Babolsar/Iran	10	B	h	Coastal dunes
Boraginaceae					
<i>Arnebia decumbens</i>					
subsp. <i>decumbens</i>	Bander-Abbas/Iran	200	B2		Open xeromorphic scrub
<i>Heterocaryum scovitsianum</i>	Maharlu Lake/Iran	1800	B1		Xer. dwarf-shrublands
Brassicaceae					
<i>Alyssum desertorum</i>	Maharlu Lake/Iran	1600	B		Xer. dwarf-shrublands
<i>A. linifolium</i>	Maharlu Lake/Iran	1500	A		" " "
<i>Anastatica hierochuntica</i>	Bander-Abbas/Iran	50	B2	h	Forb comm. with shrubs
<i>Camelina rumelica</i>	Maharlu Lake/Iran	1800	C		Open xeromorphic scrub
<i>Chorispora tenella</i>	S Sirjan/Iran	1800	B	H	Scrub
<i>Clypeola aspera</i>	Maharlu Lake/Iran	1500	B2		Xer. dwarf-shrublands
<i>Isatis raphanifolia</i>	Maharlu Lake/Iran	1500	B2		" " "
<i>Sterigmotemon</i> sp. (VO 2104)	Isfahan/Iran	1600	B2		" " "
Capparidaceae					
<i>Cleome ariana</i>	Jokham, Hind./Afgh.	2400	B		Ruderal comm.
Caryophyllaceae					
<i>Spergularia marina</i>	Maharlu Lake/Iran	1460	D	H	Halophytic comm.
Chenopodiaceae					
<i>Ceratocarpus</i> cf. <i>arenarius</i>	SE Abadeh/Iran	2000	D		Xer. dwarf-shrublands
<i>Chenopodium album</i>	Maharlu Lake/Iran	1500	B1	h	Ruderal comm.
<i>C. botrys</i>	Jokham, Hind./Afgh.	2300	B1		" "
<i>C. glaucum</i>	Paghman/Afgh.	2100	B1		" "
<i>C. foliosum</i>	Jokham, Hind./Afgh.	2700	B1		" "
<i>C. murale</i>	Qeshm/Iran	50	B2		" "
<i>Haloepelis pygmaea</i>	Maharlu Lake/Iran	1460	D	H	Halophytic comm.
<i>Kochia</i> sp. (76-595)	Qeshm/Iran	50	NK		Ruderal comm.
<i>Londesia</i> cf. <i>eriantha</i>	N Busher/Iran	500	B2	H	Halophytic comm.
<i>Salicornia europaea</i>	Maharlu Lake/Iran	1460	D	H	" " "
Euphorbiaceae					
<i>Euphorbia</i> sp. (76-581)	Qeshm/Iran	50	B1		Ruderal comm.
<i>E. sp.</i> (76-969)	N Shiraz/Iran	1100	B2		Xer. dwarf-shrublands
<i>E. sp.</i> (76-352)	Bander-Abbas/Iran	100	B2		Semidesert shrublands
<i>E. sp.</i> (76-525)	Bander-Khamir/Iran	100	B	h	Ruderal comm.
<i>E. sp.</i> (75-126)	Maharlu Lake/Iran	1500	NK		" "
<i>E. sp.</i> (76-28)	Abbassabad/Iran	1000	A		" "
<i>E. sp.</i> (75-208)	Maharlu Lake/Iran	1800	B2		Xer. dwarf-shrublands

TABLE 2 (contd)

	<i>Locality</i>	<i>Alt.(m)</i>	<i>LA</i>	<i>HS</i>	<i>Veg. unit</i>
ANNUALS (contd)					
Fabaceae					
<i>Medicago minima</i>	Babolsar/Iran	10	B1	h	Coastal dunes
Frankeniaceae					
<i>Frankenia pulverulenta</i>	Qeshm/Iran	50	NK	h	Ephemeral forb comm.
Gentianaceae					
<i>Blackstonia perfoliata</i>	Tuz Gölü/Turkey	905	D	H	Halophytic comm.
Plumbaginaceae					
<i>Psylliostachys leptostachys</i>	Maharlu Lake/Iran	1460	NK	H	Halophytic comm.
<i>P. spicata</i>	N Borazjan/Iran	1300	B2	H	
Polygonaceae					
<i>Polygonum aviculare</i>	Maharlu Lake/Iran	1500	B1		Ruderal comm.
Solanaceae					
<i>Datura stramonium</i>	Kunduz/Afgh.	400	B2		Ruderal comm.
Thymelaeaceae					
<i>Thymelaea mesopotamica</i>	Maharlu Lake/Iran	1600	B1		Ruderal comm.
<i>T. passerina</i>	Yasuj/Iran	1800	B		Flushes
AQUATIC PLANTS					
Lemnaceae					
<i>Lemna trisulca</i>	Maharlu Lake/Iran	1460			Free-floating freshwater comm.
Potamogetonaceae					
<i>Potamogeton pusillus</i>	Maharlu Lake/Iran	1460			Free-floating freshwater comm.
Zannichelliaceae					
<i>Zannichellia palustris</i>	Maharlu Lake/Iran	1460			Free-floating freshwater comm.

TABLE 3

GRASS SPECIES WITH NON-KRANZ CELL ARRANGEMENT

L, longevity; A, annual; P, perennial

*after Freitag (1975)

**after Tutin et al. (1980)

	Locality	Alt.(m)	L
Meliceae			
<i>Melica ciliata</i>	Rudbarak, Elburz/Iran	1800	P
subsp. <i>jacquemontii</i>	Varangrud, Elburz/Iran	3800	P
subsp. <i>inaequiglumis</i>	Varangrud, Elburz/Iran	3000	P
subsp. <i>persica</i>	Sisakht, Zagros/Iran	2300	P
Stipeae			
<i>Piptatherum laterale</i> *	Jokham, Hind./Afgh.	3900	P
<i>P. platyanthum</i> *	Jokham, Hind./Afgh.	3300	P
<i>P. purpurascens</i> *	Parshui, Hind./Afgh.	3700	P
<i>Stipa arabica</i> **	Pajuka, Hind./Afgh.	2850	P
<i>S. caucasica</i>	Jokham, Hind./Afgh.	3300	P
<i>S. kirghisorum</i>	Parshui, Hind./Afgh.	4000	P
Agrostideae			
<i>Alopecurus arundinaceus</i>	Varangrud, Elburz/Iran	2200	P
<i>A. aucheri</i>	Varangrud, Elburz/Iran	3000	P
<i>A. pratensis</i>	NW Ardekan, Zagros/Iran	2300	P
<i>A. textilis</i>	Alam-Kuh, Elburz/Iran	3700	P
<i>Calamagrostis pseudophragmites</i>	Varangrud, Elburz/Iran	2500	P
<i>Dayeuxia parsana</i>	Varangrud, Elburz/Iran	2600	P
<i>Phleum boissieri</i>	Kelardasht, Elburz/Iran	2800	A
<i>P. paniculatum</i>			
var. <i>ciliatum</i>	Rudbarak, Elburz/Iran	2100	A
<i>P. paniculatum</i>			
var. <i>paniculatum</i>	Rudbarak, Elburz/Iran	1800	A
Aveneae			
<i>Arrhenatherum elatius</i>	Rudbarak, Elburz/Iran	1800	P
<i>A. kotschyi</i>	Varangrud, Elburz/Iran	2400	P
<i>Koeleria pyramidata</i> **	Rudbarak, Elburz/Iran	2800	P
<i>Trisetum rigidum</i>	Varangrud, Elburz/Iran	2200	P
Bromeae			
<i>Boissiera squarrosa</i>	Karadj Valley/Iran	2300	A
<i>Bromus briziformis</i>	Maljil, Elburz/Iran	2400	A
<i>B. danthoniae</i>			
var. <i>danthoniae</i>	Damavand, Elburz/Iran	2000	A
<i>B. gracillimus</i>	Parshui, Hind./Afgh.	4050	A
<i>B. scoparius</i>			
var. <i>scoparius</i>	Varangrud, Elburz/Iran	2200	A
<i>B. tectorum</i>	Varangrud, Elburz/Iran	2200	A
<i>B. tomentellus</i>	Varangrud, Elburz/Iran	2800	A
Festuceae			
<i>Dactylis glomerata</i>			
subsp. <i>hispanica</i>	Varangrud, Elburz/Iran	3000	P
<i>Eremopoa persica</i>	Jokham, Hind./Afgh.	3900	A
<i>Poa sinaica</i>	Babolsar/Iran	10	P
<i>Psilurus incurvus</i>	Maharlu Lake/Iran	1500	A
<i>Sphnanopus divaricatus</i>	Borazjan/Iran	300	A
<i>Vulpia myuros</i>	Maharlu Lake/Iran	1500	A

TABLE 3 (contd)

	Locality	Alt.(m)	L
Seslerieae			
Sesleria phleoides	Rudbarak, Elburz/Iran	2800	P
Triticeae			
Aegilops tauschii	Dalir, Elburz/Iran	1800	A
Agropyron afghanicum	Kuh-e-Dinar, Zagros/Iran	2500	A
A. imbricatum	Varangrud, Elburz/Iran	3000	A
A. libanoticum	Kelardasht, Elburz/Iran	2800	A
A. longe-aristatum	Varangrud, Elburz/Iran	2200	A
A. tauri	Varangrud, Elburz/Iran	2400	A
A. trichophorum	Sisakht, Zagros/Iran	2300	A
Eremopyrum bonaepartis			
subsp. bonaepartis	N Ghazvin/Iran	1200	A
Heterantherium piliferum	Damavand, Elburz/Iran	2000	A
Hordeum violaceum	Varangrud, Elburz/Iran	2200	P
Psathyrostachys caduca	Parshui, Hind./Afgh.	3900	P
P. fragilis	Alam-Kuh, Elburz/Iran	3200	P
Taeniatherum crinitum	SE Ardekan/Iran	2000	A
Monermeae			
Parapholis incurva	Borazjan/Iran	1600	A
Milieae			
Zingeria trichopoda	NW Ardekan/Iran	2300	A
Arundineae			
Phragmites australis	Maharlu Lake/Iran	1470	P

Tribes of *C4* Poaceae (see table 1)

Aeluropodeae:	Aeluropus littoralis
Andropogoneae:	Bothriochloa ischaemum
Chlorideae:	Cynodon dactylon
Aristideae:	Stipagrostis plumosa
Paniceae:	Setaria viridis
Zoiseae:	Tragus racemosus

TABLE 4

RATIO OF KRAZ TO NON-KRAZ TAXA

	Trees K/NK	Shrubs K/NK	Thorn- cushions K/NK	Dwarf- shrubs K/NK	Peren- nials K/NK	Annuals K/NK	Hydro- phytes K/NK	Total K/NK	%K
Amaranthaceae	-/-	-/-	-/-	1/-	2/-	-/-	-/-	3/-	100
Chenopodiaceae	-/-	5/1	-/-	15/2	-/1	12/10	-/-	32/14	70
Cyperaceae	-/-	-/-	-/-	-/-	3/5	-/-	-/-	3/5	37
Poaceae	-/-	-/-	-/-	-/-	3/27	3/24	-/-	6/51	11
Zygophyllaceae	-/-	-/2	-/-	-/-	-/3	2/-	-/-	2/3	28
Total K species	-	5	-	16	8	17	-	46	
Total NK species (all families studied)	3	10	9	37	65	65	3	192	

DISCUSSION

Table 1 shows that the Kranz cell species of the Iranian highland belong to families in which the occurrence of such species is worldwide, and that they are mostly shrubs, dwarf-shrubs and annuals. Shrubs, dwarf-shrubs and thorn-cushions of C₃ type predominate in non-saline or slightly saline habitats (Table 2), while C₄ plants play an important role in the vegetation of saline soils (see Table 1). To some extent, however, our data are misleading since Chenopodiaceae have been over-represented in our investigations in relation to their importance in the flora. Table 4 gives the ratio of Kranz to non-Kranz taxa.

Chenopodiaceae: This family is noted for a high proportion of C₄ species, largely from ruderal and saline habitats; it is the only one in which the C₄ species discovered belong to the indigenous Irano-Turanian floristic element. According to our investigation the ratio of C₄ to C₃ Chenopodiaceae in the Iranian highland is about 7:1.

Amaranthaceae: Only C₄ species were encountered in this family which, however, is of no great importance in the flora of the Iranian Highland.

Poaceae: Kranz anatomy is limited to certain tribes (Tieszen et al., 1979) but in total occurs in 40–50% of world grasses. The C₄ species encountered (Table 1) are not indigenous to the Irano-Turanian flora but are pluriregional, while C₃ grasses, shown in Table 3, are dominant in the mountain grasslands of the Hindu Kush and Elburz. In neighbouring northern India all 24 grass species investigated by Sankhla et al. (1975) are of C₄ type. Winter et al. (1976) showed an increase in C₄ grasses in the passage from the Mediterranean to the more southern arid Saharo-Arabian and Sudanian phytogeographic regions. As observations by Teeri & Stowe (1976) in northern America and Tieszen et al. (1979) in Kenya have indicated, the abundance of C₄ grass species is correlated with a minimum average temperature of about 8°C. Under Iranian highland conditions (Shiraz 5.7°C lowest winter average temperature) C₄ grasses seem to be no longer able to compete with C₃ ones. They can grow only in exceptional cases and as annuals that develop in the warm season. Our investigations show that there is a boundary for C₄ grasses at an altitude of 1700 m. Above this line C₄ grasses do not grow because of too low nocturnal and winter temperatures: the grasslands and tussocks of the mountains consist of C₃ species only.

Cyperaceae: Apart from the genus *Cyperus* itself, all the other Cyperaceae investigated were of C₃ type. Smith & Brown (1973) considered *Fimbristylis caroliniana* to be of Kranz type but the species of this genus investigated here were clearly non-Kranz.

Zygophyllaceae: The pluriregional *Tribulus longipetiolatus* and *T. terrestris* are C₄ species. *Zygophyllum atriplicoides* and *Z. eurypterum*, which are more typical species of the Iranian flora, are of C₃ type.

There are a number of families in which C₄ species might have been expected but were not discovered. In the Asteraceae Smith & Turner (1975) reported many C₄ species from climatic regions of other continents comparable to the Iranian highland. In the Boraginaceae we expect that further investigations will reveal C₄ *Heliotropium* species, as discovered by Sankhla et al. (1975) in India. The Euphorbiaceae is another family where C₄ species are important but were not found in this study.

CONCLUSIONS

To summarize, we can say that the great majority of the characteristic Irano-Turanian plant species are of C_3 photosynthetic type. These are the elements of non-saline xeromorphic scrub, the essential *Artemisia*, *Acantholimon*, *Acanthophyllum*, and tragacanthous *Astragalus* species of the dwarf-shrublands and thorn-cushion formations, and most of the forbs and mountain grasses. Our work supports the opinion stated by Winter & Troughton (1978) that the most simple and effective way of adaptation to a winter-cold/summer-hot environment is the reduction of the transpiring surface to a minimum during the dry season. Most C_3 shrubs and dwarf-shrubs in the area show arido-active behaviour. For the predominating shrubs and dwarf-shrubs the more effective C_4 - CO_2 fixation mechanism seems to play no part. The advantages of the C_4 syndrome, such as water economy and increasing productivity, are important in the dense populations of saline, ruderal, and segetal habitats. Our investigations show clearly that in the Iranian highland C_4 species have their focal point only in these vegetation units. Among the halophytes the C_4 pathway implies a specific and important adaptation: it is likely that high CO_2 fixation rates are well suited to their energy requirements and cause an increase of the osmotic value by synthesis of organic acids.

ACKNOWLEDGEMENTS

We thank W. Otto for kindly reading the English text. The study was supported by the Sonderforschungsbereich 19 'Tübinger Atlas des Vorderen Orients'. We wish to thank Mr I. C. Hedge and other staff of the herbarium, RBG, Edinburgh, and Mr Kramer and Mr Kürschner, Institut für Biologie I in Tübingen, for determining specimens.

REFERENCES

- CAROLIN, R. C., JACOBS, S. W. & VESK, M. (1975). Leaf structure in Chenopodiaceae. *Bot. Jahrb. Syst.* 95: 226–255.
- DOWNTON, W. J. S. (1975). The occurrence of C_4 photosynthesis among plants. *Photosynthetica* 9: 96–105.
- FREITAG, H. (1975). The genus *Piptatherum* (Gramineae) in Southwest Asia. *Notes R.B.G. Edinb.* 33: 341–408.
- HABERLANDT, G. (1896). *Physiologische Pflanzenanatomie*, ed. 2. Leipzig: Engelmann.
- RAY, T. B. & BLACK, C. C. (1979). The C_4 pathway and its regulation. In GIBBS, M. & LATZKO, E., eds., *Encyclopedia of plant physiology new series 6 — photosynthesis II*: 77–101. Berlin, Heidelberg, New York: Springer.
- RECHINGER, K. H. (ed.) (1963–). *Flora Iranica*. Graz: Akademische Druck- und Verlagsanstalt.
- SANKHLA, N., ZIEGLER, H., VYAS, O. P., STICHLER, W. & TRIMBORN, P. (1975). Eco-physiological studies on Indian arid zone plants. V: a screening of some species for the C_4 -pathway. *Oecologia (Berlin)* 21: 123–129.

- SMITH, B. N. & BROWN, W. V. (1973). The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. *Amer. J. Bot.* 60: 505–513.
- & TURNER, B. L. (1975). Distribution of Kranz syndrome among Asteraceae. *Amer. J. Bot.* 62: 541–545.
- TEERI, J. A. & STOWE, L. G. (1976). Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia (Berlin)* 23: 1–11.
- TIESZEN, L. L., SENYIMBA, M. M., IMBAMBA, S. K. & TROUGHTON, J. H. (1979). The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia (Berlin)* 37: 337–350.
- TUTIN, T. G., HEYWOOD, V. H., BURGESS, N. A., VALENTINE, D. H., WALTERS, S. M. & WEBB, D. A. (eds.) (1980). *Flora Europaea*, vol. 5. Cambridge: University Press.
- WELKIE, G. W. & CALDWELL, M. (1970). Leaf anatomy of species in some dicotyledon families as related to the C₃ and C₄ pathways of carbon fixation. *Can. J. Bot.* 48: 2135–2146.
- WINTER, K. & TROUGHTON, J. H. (1978). Photosynthetic pathways in plants of coastal and inland habitats of Israel and the Sinai. *Flora* 167: 1–34.
- , — & CARD, K. A. (1976). $\delta^{13}\text{C}$ values of grass species collected in the Northern Sahara desert. *Oecologia (Berlin)* 25: 115–123.