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Photosynthetic Pathways and the Ecological Distribution of the Chenopodiaceae in Israel

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Summary. Fifty-four species of the Chenopodiaceae in Israel were examined for their anatomical features, $\delta^{13}C$ values, habitat and phytogeographical distribution. 17 species have $\delta^{13}C$ values between $-20^0/_{00}$ and $-30^0/_{00}$ and non-Kranz anatomy (NK) and are therefore considered as C_3 plants. 37 species have $\delta^{13}C$ values between $-10^0/_{00}$ and $-18^0/_{00}$ and Kranz or C_4-Suaeda type anatomy and are therefore considered as C_4 plants. Some C_4 plants have leaf structure which seems to be intermediate between the Kranz and the C_4-Suaeda type of leaf anatomy.

The segregation of the species into photosynthetic groups shows tribal and phytogeographical grouping. Most of the C_3 Chenopods are either mesoruderal plants or coastal halophytes, with a distribution area which covers the Euro-Siberian as well as the Mediterranean phytogeographical regions. The C_4 Chenopods are mainly desert or steppe xerohalophytes with a distribution area which includes the Saharo-Arabian and/or Irano-Turanian phytogeographical regions.

Introduction

One of the characteristics of plants with the C_4 photosynthetic pathway is the spatial co-ordination between the anatomical and biochemical features. In most of the C_4 plants this involves segregation of enzymes between two types of cells – the leaf mesophyll and the bundle sheath cells (Black 1973; Laetsch 1974). However, the proximity of the Kranz cells to the vascular bundles is not an ultimate requirement for the C_4 photosynthesis. For example, *Suaeda monoica,* a C_4 halophyte of the Chenopodiaceae, has a different anatomical leaf structure. In this species the leaves had differentiated into three types of photosynthesizing cell layers varying in anatomy and enzyme distribution and the vessels are surrounded by the water tissue (Shomer-Ilan et al. 1975, 1979).

The questions in issue were, thus, as follows:

1. Is *Suaeda monoica* a unique plant, or does it represent a type among the C_4 plants? As other species of the Chenopodiaceae have a similar anatomy (Volkens 1887; Brown 1975), it seemed interesting to screen for plants with a similar correlation between anatomy and photosynthetic pathway.

2. Is there any correlation between the origin and ecology of the different species of the Chenopodiaceae and their photosynthetic pathway? The Chenopodiaceae form a dominant group in the flora and vegetation of saline and desert habitats in Israel. Thus, it seemed interesting to search for such correlations.[1)]

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Materials and Methods

Anatomy

Plants were collected in their native habitats. Leaves and stems were sectioned and their anatomy examined and described.

$\delta^{13}C$ values

The carbon isotope ratios were determined after combustion of the organic matter at 900° C under a stream of pure oxygen, using an auxillary CuO furnace at 700° C in order to ensure complete combustion. The isotope measurements were performed on an Atlas MAT 86, double-inlet, double collector isotope-ratio mass-spectrometer. Herbarium samples were run in duplicates and the overall reproducibility is estimated at $\pm 0.25\%$–0.3%.

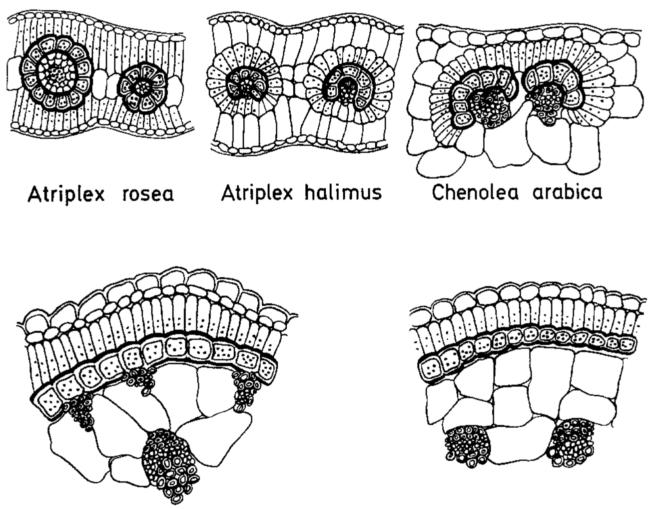

Fig. 1. Intermediate structures between K and ST leaf type among various C_4 species of the Chenopodiaceae

[1] After submission of this manuscript to Oecologia, the authors were informed by the editors, that a paper "C_4 plants of high biomass in arid regions of Asia – occurence of C_4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR" by K. Winter had been sumitted at the same time

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Table 1. Chenopods in Israel

Species	Phytogeographical distribution								Chorotype**	$\delta^{13}C$ (‰)	Structural Anatomical Type	Photo-synthetic Type
	Sud	SA	IT	ES			M					
				E.	W.Sb.	E.Sb.	NW	G				
Xerophytes & Xerohalophytes												
Aellenia hierochuntica (Bornm.) Aellen			+						W.IT	−11.1		C_4
Aellenia lancifolia (Boiss.) Ulbrich			+						W.IT	−11.8		C_4*
Anabasis articuláta (Forssk.) Moq.		+	+						SA(W.IT)	−12.4	SST	C_4*
Anabasis setifera Moq.	+	+	+						E.SA(W.IT)	−12.8	SST	C_4*
Atriplex hálimus L.	+	+		(+)				+	SA.M	−14.3	K	C_4
Atriplex leucoclada Boiss.		+	+						S.A.IT	−15.6	K	C_4
Atriplex gláuca L.		+	+						SA	−12.9	K	C_4
Bassia muricáta (L.) Aschers.		+	+						SA	−14.7	ST	C_4
Chenoléa arábica Boiss.		+	(+)						E.SA	−12.5	K	C_4*
Halogéton alopecurioídes (Del.) Moq.		+	(+)						SA	−11.8	ST	C_4*
Haloxylon persicum Bge.		+	+						W.IT-E.SA	−12.6	SST	C_4
Hammada negevénsis Iljin et Zoh.		End							E.SA	−12.3	SST	C_4
Hammada salicornia (Moq.) Illjin	+	+							Sud(E.SA)	−12.3	SST	C_4*
Hammada scoparia (Pomel) Iljin		+	+						SA.W.IT	−13.4	SST	C_4*
Hammada schmittiana (Pomel) Botsch.		+							W.SA	−13.6	SST	C_4
Noaea mucronáta (Forssk.) Asch. et Schw.		+	+						W.IT	−13.3	ST	C_4*
Salsola baryösma (Roem. et Schult.) Dandy	+	+							Sud.SA	−14.2	ST	C_4
Salsola schweinfurthii Solms-Laub.			+						E.SA	−14.1		C_4
Salsola volkénsii Aschers. et Schw.		+	(+)						E.SA	−11.8		C_4
Salsola tetrandra Forssk.		+	+						SA	−13.2	ST	C_4*
Thermophilous Hydrohalophytes and Xerohalophytes												
Bassia erióphora (Schrad.) Aschers.	+	+	+						E.SA-W.IT	−12.8	ST	C_4
Seidlitzia rosmarinus Bge. ex. Boiss.	+	+	+						E.SA	−12.6	ST	C_4*
Suaeda aspháltica (Boiss.) Boiss.		+	(+)						E.SA	−13.9	ST	C_4
Suaeda fruticosa Forssk. ex J.F. Gmel.	+	+							Sud-(E.SA)	−13.9	ST	C_4*
Suaeda monóica Forssk. ex. J.F. Gmel.	+	+							Sud(Trop)	−14.2	ST	C_4*
Suaeda vermiculata Forssk. ex. J.F. Gmel.	+	+							E.SA	−14.2	ST	C_4
Tragánum nudatum Del.	+	+							SA	−11.8	K	C_4
Xero-Ruderals												
Anabasis syriaca Iljin			+						W.IT	−13.0	SST	C_4

Table 1 (continued)

Species	Phytogeographical distribution								Chorotype**	$\delta^{13}C$ ($^0/_{00}$)	Structural Anatomical Type	Photo-synthetic Type
	Sud	SA	IT	ES			M					
				E.	W.Sb.	E.Sb.	NW	G				
Atriplex rosea L.			+	+					ES-IT	−13.6	K	C_4
Kochia scoparia (L.) Schrad.	+	+	+						Sud-W.IT	−13.4	K	C_4
Salsola inérmis Forssk.		+	+						E.SA	−12.3	ST	C_4
Aellenia autrani (Post) Zoh.			+						W.IT	−11.1		C_4
Coastal Hydrohalophytes												
Halimione portulacoides (L.) Aellen			+	+	+			+	ES-M-W.IT	−28.6	NK	C_3
Halocnémum strobilaceum (Pall) M.B.	+	+	+	+	+			+	M-IT-SA	−25.6	NK	C_3
Halopeplis amplexicáulis (Vahl) Ung. Sternb.		+						+	M-SA	−22.5	NK	C_3
Arthrocnemum fruticosum (L.) Moq.	+	+						+	M-SA	−27.7	NK	C_3
Arthrocnemum macrostachyum (Moric.) Moris et Delponte	+	+	+	(+)				+	M-SA	−26.8	NK	C_3
Arthrocnemum perénne (Mill.) Moss	+				+			+	M-S-ES	−27.5	NK	C_3
Salicornia europaea L.		+	+	+				+	M-ES	−24.7	NK	C_3
Salsola sóda L.			+	+	+			+	ES-NM-W.IT	−11.9	ST	C_4
Suaeda aegyptiaca (Hasselq.) Zoh.	+	+	+						E.SA	−13.0	ST	C_4
Suaeda spléndens (Pourr.) Gren. et Godr.								+	NW	−13.4	ST	C_4
Coastal Aerohalophytes												
Suaeda véra Forssk, ex J.F. Gmel					(+)		+		M	−27.2	NK	C_3
Salsola kali L.	+	+	+	+	+	+		+	ES-M-IT	−12.6	ST	C_4*
Ruderals												
Atriplex hastata L			+	+				+	ES-M-IT	−25.2	NK	C_3
Atriplex semibaccata R.Br.									Aust. intr.	−13.1	K	C_4
Beta vulgaris L.	+	+	+	+				+	ES-M-W.IT	−26.2	NK	C_3
Chenopodium álbum L.	+		+	+				+	Trop. Am.	−26.6	NK	C_3
Chenopodium ambrosioides L.		+	+	+	+			+	ES-M-IT	−28.3	NK	C_3
Chenopodium murále L.	+	+	+	+	+	+		+	Bor-Trop	−24.3	NK	C_3
Chenopodium opulifolium Schrad.	+	+	+	+	+			+	Bor-Trop	−24.8	NK	C_3
Chenopodium polyspérmum L.			+	+	+	+	+		ES-M-IT	−26.8	NK	C_3
Chenopodium rúbrum L.			+	+	+	+	+		ES-M-IT	−26.2	NK	C_3
Chenopodium vulvária L.		+	+	+	+			+	ES=M-IT	−28.3	NK	C_3

Photosynthetic pathways in relation to ecological distribution of the Chenopodiaceae (for explanation of the structural anatomical types see Section Results and Discussion)

* Plants that showed no diurnal malate fluctuation

** Phytogeographical distribution and Chorotype – after Grinberg-Fertig, I. (1966)

ES = Euro-Siberian; IT = Irano Turanian; M = Mediterranian; Sud = Sudanian; SA = Saharo Arabian; W.Sb = West Siberian; E.Sb = East Siberian; E = Europe; NW = North West; G = General

The data are expressed in the δ notation:

$$\delta^{13}C = \frac{(\text{R sample} - \text{R standard})}{(\text{R standard})} \times 1000$$

where R is the $^{13}C/^{12}C$ ratio. The data is reported against the Chicago PDB standard.

Results and Discussion

Fifty four species of the Chenopodiaceae in Israel were examined for their anatomical features, $\delta^{13}C$ values, habitat analysis and phytogeographical distribution.

Four types of anatomical features were observed in the leaves and stems of the various chenopods examined.

1. Plants with "normal" or "non-Kranz" leaf anatomy (NK), i.e. plants that have leaves with one type of photosynthesizing cells.
2. Plants with "Kranz type" leaf anatomy (K), i.e. plants that have leaves with two types of photosynthesizing cells (Fig. 1).
3. Plants with "C_4-Suaeda type" leaf anatomy (ST) i.e. plants that have leaves with three types of photosynthesizing cells (Fig. 1).
4. Plants with succulent assimilating internodes (SST). The chlorenchymatous cortex of the stems of such species is similar in structure to that of the leaves of the "C_4-Suaeda type".

$\delta^{13}C$ analysis of the examined Chenopods (Table 1) shows clearly that two groups can be observed: one group (17 species) consists of the highly ^{13}C discriminating species with $\delta^{13}C$ values between $-20‰$ and $-30‰$. Such values are typical for plants with C_3 photosynthetic pathway (Black 1973).

Another group (37 species) includes the less ^{13}C discriminating species with $\delta^{13}C$ values between $-10‰$ and $-18‰$. Such values are typical for plants with C_4 metabolism, i.e. C_4 or CAM plants. C_4 plants can be distinguished by a leaf anatomy with at least 2 distinct types of cells, whereas CAM plants can be distinguished by their diurnal malate fluctuation (Black 1973). Examination of the leaf anatomy of the low ^{13}C discriminating group of plants showed (Table 1) that 8 species have Kranz anatomy (K), 16 species have C_4-Suaeda type anatomy (ST) and 8 species have stems with C_4-Suaeda type anatomy (SST). The structure of some rare plants was not checked. Furthermore, many of these plants do not show the typical diurnal malate fluctuation of CAM plants (Shomer-Ilan et al. 1975; Winter et al. 1976). Thus, it is assumed that they may be classified as true C_4 plants. Similar results were reported by Winter (in press).

Classification of the examined plants into phytogeographical or ecological groups renders additional interesting information (Table 1). Many of the Chenopods exhibit a wide distribution area over the Holarctic plant kingdom. Some of them have a wide distribution in primary habitats, whereas others inhabit mostly secondary-ruderal habitats. Most of the ruderal as well as the hydrohalophytic chenopods in the Mediterranean area of Israel are apparently C_3 plants with non-Kranz anatomy and with $\delta^{13}C$ values in the range between $-22‰$ and $-29‰$. The xerohalophytes seem to be mainly C_4 plants with $\delta^{13}C$ values between $-11‰$ and $-18‰$ and with a variety of anatomical leaf structures (K, ST, SST).

Plants with a leaf anatomy that looks like intermediate structures between K and ST leaf type can be seen among the various species (Fig. 1). In the type represented by *Atriplex rosea* we find the typical "Kranz" anatomy of C_4 plants (Laetsch 1974). The bundle sheath cells of this species surround the vessels. In *Atriplex halimus* the bundle sheath is open. In the *Chenolea arabica* type only one side of the bundle is enveloped. In the type represented by *Salsola kali* the "Kranz cells" form one layer below the outer chlorenchyma, but vascular bundles are still attached to it. In *Suaeda monoica* pseudo-"Kranz cells" are completely detached from the vascular bundles.

The construction of a phylogenetic trend out of the above data is intriguing. Ulbrich (1934) based his classification of the Chenopodiaceae on the structure of the embryo as well as on the structure of the perisperm. Accordingly *Atriplex, Bassia* and *Chenolea* are placed in the Cyclolobeae, the less developed group. Salsola and Suaeda, with the spiral embryo, are placed in the Spirolobeae, the most developed section. On the other hand, Bisalputra (1962) suggested a classification which is based on the phylogenetic trands of the vascular system. Accordingly *Salsola, Suaeda* and *Bassia* should be placed in the most primitive group, whereas *Atriplex* is among the most advanced one. The five types of leaf cells organization which are described in the present article may be arranged in any of the suggested phylogenetic orders, and therefore, it is hard to decide a direction of a phylogenetic trend. However, this data might contribute to such evaluation when taken together with physiological features. If the proximity of "Kranz cells" to the vessels may lead to increased efficiency in transport of sugars from the leaf, then such a feature should be regarded as a more developed one. Accordingly, *Atriplex*, with the typical "Kranz" anatomy, should be placed in the most advanced group, as was suggested by Bisalputra (1962). *Suaeda* accordingly should be placed in the most primitive group.

The Chorotype of the investigated plants yields some additional hints as to their origin. Most of the C_3 plants are either ruderal plants or coastal halophytes with a distribution area which covers the Euro-Siberian as well as the Mediterranean phytogeographical regions (Table 1). The C_4 species with the exception of the coastal plants *Suaeda splendens, Salsola kali* and *Salsola soda*, are mainly desert or steppe plants, with distribution areas which include the Saharo-Arabian and/or the Irano-Turanian phytogeographical regions. C_4 Thermohydrohalophytes are mainly from tropical origin.

The segregation of the species into photosynthetic groups shows also tribal groupings within the chenopods. Species of the Beteae (*Beta*), Chenopodieae (*Chenopodium*), Salicorneae (e.g. *Salicornia, Arthrocnemum*), and some of the Atripliceae (e.g. *Halimione*) are C_3 plants and clearly Euro-Siberian or Mediterranean elements. On the other hand species of the Camphorosmeae (e.g. *Bassia, Chenolea*) and Salsoleae (e.g. *Salsola, Aellenia* etc.) are C_4 plants and of steppe or desert origin. The Atripliceae and Suaedeae include C_4 as well as C_3 species.

Conclusions

Some seventy per cent of the Chenopodiaceae in Israel are C_4 plants and the majority of them have C_4-*Suaeda* type anatomy (ST-SST). Intermediate structure between K and ST can be seen among the various species.

The origin and habitat of the species was found to correlate with their photosynthetic pathways.

It seems that the flora of Israel got its Chenopods from the following sources: The coastal hydrohalophytes and meso-ruderal Chenopods reached Israel either from Europe in the North or from the Mediterranean coasts in the West; they are mainly C_3 plants. The xerophytic and xerohalophytic desert and saline Chenopods seem to originate from a warm and dry climate. They probably immigrated to Israel from the Irano-Turanian deserts in the North-East, East or from the Arabian and Sudanian deserts in the South. They are mainly C_4 plants.

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