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Fatty acid composition of chlorenchyma membrane fractions from three desert succulents grown at moderate and high temperatures

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To help understand the tolerances of desert succulents to extremely high temperatures (above 60°C), the effect of growth temperature on fatty acid composition of various membrane fractions from three species was investigated. When maintained at day/night air temperatures of 30°C/20°C, their chlorenchyma fatty acid compositions were similar to one another and to those of mesophytic leaves, except that desert succulents had appreciably less linolenic acid (18:3) and more oleic acid (18:1) and hence greater fatty acid saturation. The differences were observed in the chloroplast, mitochondrial and microsomal fractions and were more apparent in the nonpolar lipids than the total lipids. For all membrane fractions of *Ferocactus acanthodes*, a shift to 50°C/40°C resulted in a decrease in 18:3 and an increase in 18:1 and hence an increase in fatty acid saturation level. For *Agave deserti* and *Carnegiea gigantea*, however, increasing the day/night air temperatures did not result in increased fatty acid saturation, although their high-temperature tolerances increase about as much as that of *F. acanthodes* as the air temperature is increased. Thus, acquisition of high-temperature tolerance need not be accompanied by marked changes in fatty acid saturation or composition.

Introduction

Desert succulents in their natural habitats often experience tissue temperatures appreciably above ambient air temperature [1–3]. These plants acclimate to high temperatures, i.e., the high temperatures tolerated increase as the ambient temperatures increase. This leads to tolerances of temperatures over 60°C, most likely the greatest high-temperature tolerance among the higher vascular plants [4–6]. Changes in membrane fatty acid composition may be involved, because when *Ariplex lentiformis* [7], *Nerium oleander* [8], *Spinacia oleracea* [9] and *Vicia faba* [10] are acclimated to high temperatures, their leaf membrane fractions contain higher proportions of saturated fatty acids. For *N. oleander* this acclimation to high temperature is associated with a decrease in fluidity (at a given temperature) of the thylakoid polar lipids [8,11]. Furthermore, lipids extracted from mesophytic vascular plants acclimated to low temperatures tend to be enriched in lower-melting unsaturated fatty acids (see Refs. 12–15), though this is not always true (see Refs. 16–18).

The importance of fatty acid saturation in the acclimation process of succulents from hot deserts has apparently not been studied, nor has the fatty acid composition of these plants been reported. If changes in fatty acid saturation are important in high-temperature acclimation in general, then determining the fatty acid composition for extremely heat-tolerant desert succulents may prove useful. In this study, three species of succulents native to

the hot deserts of North America were grown at day/night air temperatures of 30°C/20°C and their fatty acid compositions were compared with those when grown at 50°C/40°C and with those reported for mesophytic leaves.

Materials and Methods

Plant material

Agave deserti Engelm. and *Ferocactus acanthodes* (Lem.) Britt. and Rose were collected from Agave Hill at the Philip L. Boyd Deep Canyon Desert Research Center, 8 km south of Palm Desert, CA, at an elevation of 850 m. *Carnegiea gigantea* (Engelm.) Britt. and Rose was collected from Arizona, 70 km northwest of Phoenix, at an elevation of 500 m. Plants were placed in an M-31 Environmental Growth Chamber with day/night air temperatures of 30°C/20°C or 50°/40°C. A 12-h day at an average photosynthetically active radiation of 400 μmol · $m^{-2} \cdot s^{-1}$ was provided. Plants were watered weekly with 1/40 strength Hoagland solution No. 1 supplemented with micronutrients [19]. Samples of mature tissue were taken after at least 10 days at a particular temperature regime, which allows time for temperature acclimation to occur [5,6,20]. In particular, the half-times for the shift in high-temperature tolerances were 3 days for *A. deserti* [5] and *C. gigantea* [6] and 2 days for *F. acanthodes*.

Membrane fractionation

Chlorenchyma tissue (0.5–1 g) was removed using a razor blade and then ground with a mortar and pestle in 20 ml of 50 mM Hepes (pH 7.8), 400 mM sorbitol, 10 mM KCl, 3 mM $MgCl_2$, 4 mM EGTA, 0.2% (w/v) bovine serum albumin (defatted) and 2.0% (w/v) polyvinylpyrrolidone (PVP-40T; Sigma, St. Louis, MO). Coarse debris was removed by filtering through cheesecloth to obtain a tissue homogenate, which was used for lipid extraction or was further processed by centrifuging at $2000 \times g$ for 5 min to obtain material for specific membrane fractions (all centrifugations were performed using a Sorvall RC-2 with an SS-34 rotor, except for $100\,000 \times g$, where a Beckman L5-50 ultracentrifuge with an SW-27 rotor was used). The resulting pellet was resuspended in 10 mM Hepes (pH 7.2), 400 mM sorbitol, 10 mM KCl, 2 mM $MgCl_2$, 1 mM EGTA and 0.2% (w/v) bovine serum albumin (defatted), centrifuged to $1500 \times g$ and then stopped, and the supernatant was decanted and recentrifuged for 5 min at $3000 \times g$ to obtain the chloroplast pellet [21]. The supernatant from the original $2000 \times g$ centrifugation was centrifuged at $12\,000 \times g$ for 20 min, the resulting pellet resuspended in the second medium, centrifuged at $2000 \times g$ for 5 min, the supernatant decanted and then centrifuged at $12\,000 \times g$ for 20 min to obtain the mitochondrial pellet [22]. To obtain the microsomal fraction [23,24], the supernatant from the initial $12\,000 \times g$ centrifugation was centrifuged at $100\,000 \times g$ for 30 min, the pellet resuspended in the second medium plus 5.6% (w/w) dextran (472 000 M_r; Sigma) and poly(ethylene glycol) (3350 approximate M_r; Sigma), and then centrifuged at $500 \times g$ for 5 min. The supernatant was decanted and then diluted with 5 volumes of the second medium before centrifuging at $100\,000 \times g$ for 30 min to obtain the microsomal pellet. All isolation procedures were carried out at 0°C.

Lipid extraction

Total lipids were extracted from the various fractions using a method modified from Bligh and Dyer [25]. The membrane-fraction pellets were suspended in 5 ml of 0.9% (w/v) NaCl and then 10 ml of isopropanol containing 0.005% (w/v) butylated hydroxytoluene were added to them and to the tissue homogenates (all organic solvents were re-distilled, analytical grade). After agitation, 5 ml of chloroform containing 0.005% (w/v) butylated hydroxytoluene were added and the lipids were extracted into the chloroform phase, which was then drawn off. After re-extracting the alcoholic phase with another 5 ml of chloroform, the pooled chloroform extracts were mixed with 5 ml of water. After phase separation, residual water in the chloroform phase was removed with anhydrous sodium sulfate, and the chloroform phase was evaporated under nitrogen to concentrate the lipids. Polar lipids were isolated by thin-layer chromatography of the lipid extracts on pre-coated Silica-Gel 60 TLC plates (EM Laboratories; Elmsford, NY) using 80 : 20 : 1 (by vol.) of petroleum ether/diethyl ether/glacial acetic acid [26]; polar lipids remained at or near the origin, as

verified by comparison with chromatography of authentic lipids.

Fatty acid analysis

The total and the polar lipid preparations were refluxed overnight in 10% (v/v) benzene plus 1% H_2SO_4 (v/v) in methanol to form fatty acid methyl esters [27]. The methylated fatty acids were extracted and then purified on a silicic acid column [28]. Fatty acids were analyzed by gas-liquid chromatography through a 6 ft × 1/8 in column packed with 10% SP-2330 on 100/120 Supelcoport (Supelco; Bellefonte, PA) in a Hewlett-Packard 5830 Gas Chromatograph attached to a Hewlett-Packard 18850A GC Terminal. The chromatograms were run from 170°C to 210°C at 1 Cdeg/min. The fatty acid methyl esters were identified by comparing their retention times with those of authentic fatty acid methyl esters.

Results

Fatty acid composition at day/night temperatures of 30°C/20°C

The fatty acid compositions of various chlorenchyma fractions were similar for extracts from the chlorenchyma of *A. deserti* (Table I), *C. gigantea* (Table II) and *F. acanthodes* (Table III) grown at day/night air temperatures of 30°C/20°C. For the tissue homogenate and all membrane fractions, the major fatty acids were the three unsaturated 18-carbon acids (18 : 1, oleic; 18 : 2, linoleic; and 18 : 3, linolenic), and the saturated 16-carbon acid (16 : 0, palmitic). In virtually all fractions myristic acid (14 : 0) comprised less than 5% and stearic acid (18 : 0) less than 10% of the total fatty acids. Thus, for any particular species and for its four chlorenchyma fractions, the fatty acid composition of the total lipids was not significantly different

TABLE I

FATTY ACID COMPOSITION OF *AGAVE DESERTI* CHLORENCHYMA

Total lipids and polar lipids were extracted from the tissue homogenate and various membrane fractions of plants maintained for a minimum of 10 days at day/night air temperatures of 30°C/20°C (upper numbers) or 50°C/40°C (lower numbers). Results are expressed as percent mole fraction (mole fraction × 100) of the six major fatty acids listed and are the means ± S.D. for at least four measurements. 14 : 0 = myristic acid; 16 : 0 = palmitic acid; 18 : 0 = stearic acid; 18 : 1 = oleic acid; 18 : 2 = linoleic acid; 18 : 3 = linolenic acid. The double-bond index is defined as the average number of double bonds per fatty acid molecule.

Fatty acid	Tissue homogenate		Chloroplast fraction		Mitochondrial fraction		Microsomal fraction	
	Total lipids	Polar lipids	Total lipids	Polar lipids	Total lipids	Polar lipids	Total lipids	Polar lipids
14 : 0	6.9 ±4.1	1.1 ±0.5	3.5 ±2.9	1.1 ±0.7	0.4 ±0.4	0.6 ±0.4	1.3 ±2.8	0.4 ±0.1
	5.4 ±4.5	0.9 ±0.7	2.6 ±2.1	0.6 ±0.1	1.5 ±1.5	0.4 ±0.1	0.8 ±0.8	0.0 ±0.0
16 : 0	32.1 ±2.6	32.5 ±2.2	27.6 ±7.5	29.1 ±6.4	26.2 ±6.6	32.5 ±3.7	31.2 ±6.8	31.7 ±3.9
	25.0 ±2.6	24.6 ±2.4	25.5 ±3.4	26.8 ±2.7	29.3 ±2.9	29.6 ±3.2	29.3 ±6.7	30.0 ±5.4
18 : 0	8.7 ±1.9	8.2 ±1.7	5.2 ±2.5	5.7 ±3.1	8.6 ±0.9	4.9 ±1.5	10.5 ±5.2	6.2 ±0.8
	5.0 ±1.0	4.0 ±0.9	4.0 ±0.9	3.2 ±0.4	3.8 ±0.7	3.1 ±0.5	5.2 ±1.3	5.0 ±1.4
18 : 1	14.0 ±1.5	15.6 ±1.7	12.4 ±2.6	15.4 ±3.4	16.9 ±2.6	17.9 ±1.9	20.9 ±2.8	20.2 ±1.4
	18.4 ±3.6	19.6 ±2.4	17.1 ±1.8	17.4 ±2.2	20.8 ±4.2	21.3 ±4.1	23.2 ±6.1	24.0 ±5.5
18 : 2	19.2 ±1.3	19.5 ±2.7	20.2 ±7.1	17.6 ±3.0	25.0 ±3.2	21.8 ±3.5	23.0 ±3.8	25.4 ±2.5
	28.0 ±4.0	29.7 ±6.3	29.2 ±6.3	30.1 ±7.6	28.4 ±5.6	28.9 ±5.8	27.7 ±6.3	27.6 ±6.6
18 : 3	19.1 ±1.6	23.0 ±2.9	31.1 ±6.3	31.2 ±5.7	23.0 ±5.5	22.4 ±6.0	13.1 ±3.2	16.0 ±1.5
	18.2 ±6.5	21.2 ±6.7	21.5 ±8.8	21.9 ±8.8	16.1 ±6.1	16.8 ±6.4	13.8 ±4.3	13.4 ±3.1
Double-bond index	1.10 ± 0.06	1.24 ± 0.07	1.46 ± 0.14	1.44 ± 0.16	1.36 ± 0.21	1.29 ± 0.14	1.06 ± 0.17	1.19 ± 0.20
	1.29 ± 0.20	1.43 ± 0.09	1.40 ± 0.18	1.43 ± 0.14	1.26 ± 0.11	1.30 ± 0.13	1.20 ± 0.16	1.19 ± 0.12

TABLE II

FATTY ACID COMPOSITION OF *CARNEGIEA GIGANTEA* CHLORENCHYMA

Conditions are as for Table I.

Fatty acid	Tissue homogenate		Chloroplast fraction		Mitochondrial fraction		Microsomal fraction	
	Total lipids	Polar lipids	Total lipids	Polar lipids	Total lipids	Polar lipids	Total lipids	Polar lipids
14:0	0.4 ±0.5	0.5 ±0.5	0.6 ±0.5	0.4 ±0.2	0.2 ±0.1	0.5 ±0.4	0.2 ±0.2	0.4 ±0.2
	1.5 ±0.5	0.4 ±0.1	0.7 ±0.6	0.5 ±0.1	0.4 ±0.1	0.2 ±0.1	0.0 ±0.0	0.0 ±0.0
16:0	25.3 ±4.3	17.7 ±2.5	21.2 ±4.6	19.1 ±2.2	18.3 ±3.3	20.3 ±1.1	19.8 ±4.3	19.3 ±1.7
	21.7 ±1.9	16.3 ±4.0	18.5 ±3.5	20.2 ±2.4	15.4 ±5.3	20.7 ±1.3	15.5 ±2.0	17.6 ±5.2
18:0	6.0 ±1.4	5.6 ±0.6	6.9 ±3.0	5.6 ±1.3	6.6 ±2.3	4.9 ±0.5	5.1 ±0.8	7.1 ±1.6
	6.6 ±1.3	5.6 ±0.9	6.2 ±1.2	4.8 ±0.4	6.2 ±1.3	5.3 ±0.7	7.3 ±1.8	6.4 ±1.8
18:1	28.9 ±2.4	34.7 ±6.1	24.7 ±4.2	24.8 ±3.3	36.5 ±2.6	35.2 ±1.4	36.9 ±3.5	38.0 ±2.6
	31.3 ±1.6	32.8 ±1.2	29.2 ±3.2	28.3 ±4.0	36.0 ±1.6	34.2 ±1.6	40.1 ±2.7	39.6 ±3.7
18:2	10.5 ±1.7	9.2 ±1.4	8.0 ±1.0	7.9 ±0.7	9.9 ±1.5	10.1 ±1.2	11.9 ±2.1	9.0 ±3.3
	9.1 ±1.2	10.1 ±1.1	9.5 ±1.4	10.1 ±1.3	9.9 ±1.4	10.0 ±1.1	9.4 ±1.3	9.8 ±1.0
18:3	29.0 ±5.2	32.4 ±4.6	38.6 ±4.2	42.2 ±5.8	28.4 ±3.0	29.0 ±1.2	26.1 ±3.7	26.3 ±3.9
	29.8 ±2.4	34.8 ±2.6	36.0 ±4.2	36.1 ±5.5	32.2 ±2.2	29.5 ±2.0	27.6 ±3.1	26.6 ±1.4
Double-bond index	1.37±0.15	1.50±0.06	1.57±0.10	1.67±0.13	1.42±0.06	1.42±0.03	1.39±0.07	1.35±0.07
	1.39±0.08	1.57±0.09	1.56±0.12	1.57±0.14	1.52±0.09	1.43±0.06	1.42±0.10	1.39±0.05

TABLE III

FATTY ACID COMPOSITION OF *FEROCACTUS ACANTHODES* CHLORENCHYMA

Conditions are as for Table I.

Fatty acid	Tissue homogenate		Chloroplast fraction		Mitochondrial fraction		Microsomal fraction	
	Total lipids	Polar lipids	Total lipids	Polar lipids	Total lipids	Polar lipids	Total lipids	Polar lipids
14:0	2.1 ±0.9	0.6 ±0.2	3.4 ±1.1	1.5 ±0.9	0.6 ±0.2	0.4 ±0.1	0.0 ±0.0	0.0 ±0.0
	2.6 ±1.5	1.3 ±0.5	1.5 ±1.5	0.9 ±0.5	0.6 ±0.5	0.7 ±0.6	0.0 ±0.0	0.0 ±0.0
16:0	28.1 ±4.1	22.1 ±5.3	27.4 ±3.6	26.3 ±2.8	26.1 ±1.2	27.1 ±1.9	25.4 ±3.7	22.9 ±6.4
	29.1 ±2.7	25.2 ±3.4	26.6 ±2.8	27.0 ±2.7	26.5 ±1.6	28.7 ±2.0	26.6 ±4.6	27.9 ±4.9
18:0	4.2 ±0.8	4.8 ±2.0	3.6 ±1.0	3.1 ±0.9	4.8 ±0.6	3.9 ±0.8	5.9 ±0.7	5.1 ±1.3
	10.3 ±6.2	5.4 ±1.3	5.0 ±0.9	4.7 ±1.2	6.0 ±1.4	5.2 ±0.6	9.0 ±3.3	7.6 ±1.0
18:1	19.1 ±2.6	21.2 ±4.3	18.8 ±3.3	19.2 ±3.5	25.0±1.6	23.7 ±4.2	31.6 ±3.0	31.7 ±4.0
	26.5 ±4.9	29.5 ±3.6	25.3 ±2.3	27.0 ±3.3	31.5 ±3.7	28.1 ±4.5	34.7 ±2.5	34.9 ±2.1
18:2	18.7 ±4.0	20.3 ±4.6	17.7 ±3.1	17.3 ±3.0	19.4 ±6.0	22.5 ±8.2	21.0 ±7.5	24.5 ±8.2
	17.6 ±4.4	20.5 ±2.2	20.8 ±1.4	20.5 ±1.9	20.6 ±4.5	21.2 ±3.5	18.1 ±2.0	19.8 ±5.1
18:3	27.7 ±5.0	31.1 ±4.1	29.0 ±4.2	32.6 ±4.0	24.1 ±6.2	22.3 ±7.4	16.1 ±4.7	15.8 ±5.0
	13.8 ±3.1	18.2 ±3.6	20.8 ±5.0	19.9 ±5.6	14.8 ±5.3	16.1 ±5.9	11.6 ±5.2	9.8 ±2.6
Double-bond index	1.40±0.13	1.55±0.08	1.41±0.11	1.52±0.09	1.36±0.07	1.36±0.12	1.22±0.10	1.28±0.09
	1.03±0.10	1.25±0.08	1.29±0.14	1.28±0.18	1.17±0.17	1.19±0.11	1.06±0.14	1.04±0.07

from that of the polar lipids ($\alpha < 0.05$ determined by the *t*-test was used to establish differences). Some of the minor differences between species include more fatty acid saturation for *A. deserti*, because of its lower 18 : 3 content, and less 18 : 2 and more 18 : 1 for *C. gigantea*. Also, the chloroplast fractions of *A. deserti* and *C. gigantea* were enriched in 18 : 3 relative to their other fractions.

Effect of increasing growth temperature on fatty acid composition

For *F. acanthodes* increasing the day/night growth temperature from 30°C/20°C to 50°C/40°C caused 18 : 3 to decrease in all fractions and 18 : 1 to increase for both the total and the polar lipids (Table III; $\alpha < 0.05$). Hence, acclimation to the higher temperature resulted in fewer double bonds (increased saturation) in its fatty acids. On the other hand, the fatty acid composition of *C. gigantea* (Table II) did not change appreciably as the growth temperature was raised. For *A. deserti* (Table I), the saturation level of the tissue homogenate polar lipids actually decreased with increasing growth temperature, reflecting a decrease in 16 : 0 and 18 : 0 and an increase in 18 : 1 and 18 : 2, while the overall saturation level of the other three fractions was unaffected even though the individual fatty acid percentages changed.

Discussion

When maintained at day/night air temperatures of 30°C/20°C, the chlorenchyma fatty acid compositions of all three desert succulents studied were quite similar to one another (Tables I–III). The fatty acid compositions were also similar to those of mesophytic leaves (Table IV), except for the lower 18 : 3 and higher 18 : 1 content and hence greater saturation in the succulents, particularly in the chloroplast fraction. Because greater fatty acid saturation leads to decreased membrane fluidity [36–38], the membrane fluidity of these desert succulents at high temperatures may not exceed that suitable for the functioning of membrane-bound enzymes [38,39], which can aid survival in hot environments.

For *F. acanthodes* a shift in day/night temperatures from 30°C/20°C to 50°C/40°C was accompanied by greater saturation of its chlorenchyma fatty acids, as 18 : 3 decreased and 18 : 1 increased (Table III). Similar increases in fatty acid saturation at elevated temperatures occur for other plants [7–10] and can help maintain membrane fluidity within an optimal range [38]. The high temperature tolerance of *F. acanthodes* increases by about 8 Cdeg to approx. 66°C when day/night temperatures are changed from 30°C/20°C to 50°C/40°C [5,20], which could be related to the fatty acid changes in the membranes. However, the chlorenchyma fatty acid compositions of *A. deserti* (Table I) and *C. gigantea* (Table II) did not become more saturated when the growth temperatures were raised, even though the high-temperature tolerance increases by 5 Cdeg to 61°C for *A. deserti* and by 7 Cdeg to 63°C for *C. gigantea* as day/night temperatures are raised from 30°C/20°C to 50°C/40°C [6,20].

Although fatty acid saturation levels may lead to appropriate membrane fluidity at both 30°C/20°C and 50°C/40°C for *A. deserti* and *C. gigantea* and thus account for their lack of major fatty acid changes versus the observed changes for *F. acanthodes* and certain other plants [7–10], changes critical to membrane fluidity could still occur at a scale too small to be easily detected. For instance, alteration in the membrane fluidity of *Tetrahymena pyriformis* with ambient temperature occurs before any major changes in fatty acid saturation [40]. Instead, fluidity adjustments are associated with changes in a small fraction of the fatty acid molecules present in certain lipids [41]. Similar results have been observed for the microsomal and chloroplast membranes of *Dunaliella salina* [42,43]. Also, high-temperature acclimation in spinach leaves occurs more quickly than do increases in fatty acid saturation, and the saturation changes occur without further increases in high-temperature tolerance [9].

The relative unsaturation of chloroplast membranes (Tables I–IV) and the extreme sensitivity of the photosynthetic process to high temperatures [44] have led to considerable emphasis on the role of chloroplast membranes in mechanistic studies of high temperature acclimation in plants [8–10]. For chloroplasts of *N. oleander*, heat stability of the association between the light-harvesting complex and the photosystem II core complex is im-

TABLE IV

FATTY ACID COMPOSITION OF MESOPHYTIC LEAVES OF ANGIOSPERMS

The data are expressed as percent or the five or six major fatty acids listed and are for plants grown at moderate temperatures (±S.D. indicated when multiple species are averaged).

Fatty acid	Whole leaf fraction		Chloroplast fraction		Mitochondrial fraction [d]		Microsomal fraction [d]	
	Total lipids [a]	Polar lipids [b]	Total lipids [c]	Polar lipids [d]	Total lipids	Polar lipids	Total lipids	Polar lipids
14:0	1.6± 0.9	–	0.5±1.1	–	–	–	–	–
16:0	14.4± 1.8	23.1	11.0±3.6	20.0	19.8	22.2	20.0	23.6
18:0	2.4± 1.3	0.7	2.0±1.6	3.1	4.0	3.8	4.8	4.9
18:1	7.4± 4.7	9.6	4.3±3.5	4.5	6.0	7.0	6.2	8.9
18:2	16.0± 7.4	31.1	7.0±2.8	15.3	31.1	40.8	27.9	34.4
18:3	58.1±10.2	35.5	75.4±8.1	57.2	38.3	26.2	41.1	28.2
Double-bond index	2.14	1.78	2.41	2.07	1.85	1.67	1.85	1.63

[a] Averaged from thirteen species [16].
[b] One species [29].
[c] Averaged from six species [30–34].
[d] One species [35].

proved when the plants are grown at higher temperatures [45]. Changes are not restricted to chloroplast membranes. For *F. acanthodes*, changes in the fatty acid composition of mitochondrial and microsomal fractions also occurred upon increasing the growth temperature (Table III). These changes are presumably not caused by contamination with chloroplast fragments, because they were also observed in the polar lipids, which are at high levels in mitochondria and microsomes [46]. Moreover, changes associated with temperature acclimation are found in microsomal membranes of *T. pyriformis* [40,41] and *D. salina* [42].

In conclusion, the fatty acids of chlorenchyma membranes of desert succulents, whose levels have not been previously reported, are appreciably more saturated than those of mesophytic leaves, even when the succulents are maintained at day/night temperatures of 30°C/20°C. The presumed reduced fluidity at any given temperature for desert succulent membranes as a consequence of their greater fatty acid saturation could prove beneficial in hot environments. Increasing day/night temperatures to 50°C/40°C, which increases the high-temperature tolerance of desert succulents [5,6,20], did not result in increased fatty acid saturation for all three species. Thus, high-temperature acclimation in desert succulents may not be directly correlated with major changes in fatty acid composition or the saturation level of the membrane lipids.

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