Phytochemistry, Vol. 33, No. 5, pp. 1009–1014, 1993
Printed in Great Britain.

0031 9422/93 $6.00 + 0.00

POLAR LIPID AND FATTY ACID COMPOSITION OF SOME BRYOPHYTES

VALERY M. DEMBITSKY,* TOMAS REZANKA,† IRINA A. BYCHEK and OLGA M. AFONINA‡

Natural Products Laboratory, Department of Organic Chemistry, The Hebrew University, Jerusalem 91904, Israel; †Institute of Microbiology, Videnska 1083, Prague 14220, Czech Republic; ‡Laboratory of Bryology and Lichenology, Botanical Institute, Russian Academy of Sciences, Saint-Petersburg 197376, Russia

(*Received in revised form* 4 *January* 1993)

Key Word Index—*Marchantia polymorpha*; Marchantiaceae; *Atrichum angustatum*; Polytrichaceae; *Brachythecium* sp.; Brachytheciaceae; phospholipids; neutral lipids; glycolipids; diacylglycerotrimethylhomoserine; fatty acids.

Abstract—Two moss species and one liverwort were examined for their fatty acids by capillary GC-MS in neutral, glyco- and phospholipid fractions. The neutral and phospholipid fractions from *Marchantia polymorpha* yielded 22.65% and 8.47% acetylenic acids, respectively, among which some unusual, rarely occurring acetylenic acids were found, i.e. 8a,11,14-20:3, 6a,9,12,15-18:4 and 5a,8,11,14-20:4. The quantities of total, neutral, phospho- and glycolipids were also estimated. Quantitative determination of a polar lipid not containing phosphorus with an R_f value very close to that of diacylglycerotrimethylhomoserine was performed.

INTRODUCTION

A considerable body of information is available on the total fatty acid composition of Bryophytes, but there are only a few detailed analyses of their lipid composition. The most abundant fatty acids of Bryophytes are also common to most other organisms. Typical for many bryophytes, however, is a high content of acetylenic [1–7], arachidonic and eicosapentaenoic acids [1, 8–12], compounds which are not found very abundantly in the rest of the plant kingdom.

Our previous studies on lipids from mosses growing in the Volga river basin [7] have shown that bryophytes are organisms with a very interesting lipid chemistry. The present paper reports on analysis of polar lipids and fatty acids from three more Bryophytes sampled in the Volga river basin.

RESULTS AND DISCUSSION

The lipid composition of the liverwort and the two mosses is shown in Table 1. Total lipids vary from 23.2 in *Brachythecium* sp. to 68 mg g^{-1} dry wt in *Atrichum angustatum*. Glycolipids make up more than half of the total lipids in *A. angustatum* whilst the quantities of phospholipids are half those of glycolipids in all species.

Among polar lipid classes only seven phospholipids were found; they were PG, PE, LPE, PS, PI, PC, X and one non-phosphorus containing lipid with an R_f corresponding to DGTS. All the examined species yielded this polar lipid when subjected to two-dimensional TLC on silica gel. The results of the phospholipid fraction analysis are given in Table 2. PC varied from 18.3% in *Marchantia polymorpha* to 36% in *Brachythecium* sp. and was the major phospholipid. It was of a special interest to find DGTS in all Bryophyte samples, DGTS varying from 13.8% in *Brachythecium* sp. to 20.8% in *A. angustatum*. DGTS has been reported in some microalgae [13–21], marine green algae [22, 23], phytoflagellates [24], ferns [25] and Protozoa [26]. Sato and Furuya [27, 28] have also described the distribution of this compound in selected species of vascular and green plants.

GC-MS analysis of the neutral lipid fraction from the Bryophytes showed the domination of acetylenic fatty acids in the liverwort *M. polymorpha* (Table 3). The three acetylenic acids were identified amongst the monoenes, 6a-18:1, 9a-18:1, and 12a-18:1, and three amongst the dienes, 6a,9-18:2, 9a,12-18:2 and 9,12a-18:2. Acetylenic acids in the polyenoic acid fraction comprised 11.09%. The moss species yielded much smaller percentages. High

Table 1. Lipid composition of some Bryophytes

Species	TL	NL	GL	PL
Atrichum angustatum	68.0	18.58	56.59	24.83
Brachythecium sp.	23.2	37.72	40.72	27.56
Marchantia polymorpha	63.6	40.66	44.19	14.85

Abbreviations: TL, total lipids; mg g^{-1} dry wt; NL, neutral lipids; GL, glycolipids; PL, phospholipids. NL, GL and PL are given as percentages of TLs.

*Author to whom correspondence should be addressed.

Table 2. Distribution of phospholipids and polar lipid DGTS in some Bryophytes

Species	PG	PC	PE	PI+LPE	PS	X	DGTS
Atrichum angustatum	20.0±0.6	22.3±0.4	17.3±0.5	9.9±0.3	6.1±0.3	3.6±0.1	20.8±1.4
Brachythecium sp.	20.7±0.7	36.0±0.8	15.0±0.4	7.0±0.3	3.6±0.3	3.9±0.2	13.8±1.2
Marchantia polymorpha	15.5±0.5	18.3±0.4	18.3±0.5	11.3±0.6	11.7±0.5	5.5±0.3	15.3±1.3

Abbreviations: PG, phosphatidylglycerol; PC, phosphatidylcholine; PI, phosphatidylinositol; PE, phosphatidylethanolamine; LPE, lyso-PE; PS, phosphatidylserine; PI+LPE, the sum of PI and LPE; DGTS, diacylglycerotrimethylhomoserine (amount determined by method of ref. [42], P content calculated on PE basis); X, phosphorus-containing unidentified polar lipid.

amounts (4.88 and 8.89%) of 18:2 and 18:3 acetylenic acids were noteworthy in *M. polymorpha*.

The glycolipid fraction had unsaturation at levels above 82% (Table 4). However, the contents of arachidonic and eicosapentaenoic acids were not high at 8% in *M. polymorpha*, 7% in *Brachythecium* sp. and 4% in *A. angustatum*. Acetylenic acids were not detected in this fraction.

The phospholipid fraction (Table 5) was found to contain the greatest variety of iso- and anteiso- acids. The summed content of arachidonic and eicosapentaenoic acids in the phospholipid fraction was somewhat higher than that in the neutral or glycolipid ones and reached 15% in *M. polymorpha*. All the above mentioned unsaturated acids are given as the summed contents of their respective isomers. Hansen and Rossi [12] studied 25 moss species for the presence 20:4 and 20:5 acids. Six species belonging to the families Brachytheciaceae and Hypnaceae contained the highest levels of these polyunsaturated acids (from 23 to 47%). The marine green seaweeds *Cladophora albida* [29], *C. sericea* [30], *C. fragile* [31], *Entoromorpha intestinalis* [32], *E. clathrata* [33] and *Ulva rigida* [30] accumulate from 14 to 45% of 20:4 and 20:5 acids in their total fatty acids. Several mosses such as *Bryum bicolor*, *Hylocomium splendens*, *Mnium cuspidatum*, *M. medium*, *Plagiothecium laetum* and *Pleurozium schreberi* contain 20:4 and 20:5 acids as major fatty acids [9, 34–37].

We did not find acetylenic acids in either the glyco- or phospholipid fractions of the mosses, but found them in the phospholipid fraction (8.47%) in the liverwort (Tables 4 and 5). The fatty acid patterns of some moss species

Table 3. Fatty acid composition of neutral lipid fractions

	M. polymorpha	*Brachythecium* sp.	*A. angustatum*
12:0	0.52	0.71	1.13
13:0	0.08	0.11	0.33
14:0	0.17	0.24	0.33
15:0	0.60	0.82	0.63
16:0	10.03	16.34	18.16
17:0	0.66	0.90	0.96
18:0	3.55	5.75	8.62
19:0	0.25	0.19	0.43
20:0	0.43	0.71	1.34
21:0	0.78	0.27	—
22:0	0.23	2.00	—
23:0	0.49	0.27	0.70
24:0	0.14	0.19	0.70
25:0	0.35	0.47	0.48
26:0	0.60	0.82	0.46
iso-12:0	0.08	0.11	0.33
iso-13:0	0.17	0.24	0.33
iso-14:0	0.31	0.43	0.48
iso-15:0	0.14	0.19	0.33
iso-16:0	0.08	0.11	—
iso-17:0	0.14	0.27	0.21
anteiso-13:0	0.17	0.24	0.15
anteiso-15:0	0.43	0.58	0.48
anteiso-17:0	0.06	0.11	0.10
anteiso-19:0	0.14	0.08	0.27
Pristanic	0.06	0.08	—
Phytanic	—	0.08	0.21

Table 3. *Continued*

Saturated	20.66	32.31	37.16
Iso-	0.92	1.35	1.68
Anteiso-	0.80	1.01	1.00
12:1 (n-5)	0.31	0.43	0.48
13:1 (n-5)	0.52	0.71	1.13
14:1 (n-5)	0.17	0.24	0.15
15:1 (n-9)	0.58	0.79	0.63
15:1 (n-7)	0.17	0.24	—
16:1 (n-9)	1.47	8.07	8.94
16:1 (n-7)	2.40	4.13	3.00
iso-17:1 (n-9)	0.31	0.47	0.43
anteiso-17:1 (n-9)	0.14	0.39	0.53
17:1 (n-9)	0.60	0.82	0.48
17:1 (n-7)	0.37	0.50	0.33
18:1 (n-11)	0.98	1.92	1.39
18:1 (n-9)	6.22	20.13	19.12
18:1 (n-7)	0.95	1.02	0.76
6a-18:1*§	1.85	—	—
9a-18:1*§	2.57	—	—
12a-18:1†§	2.26	—	—
19:1 (n-8)	0.31	0.27	0.33
20:1 (n-11)	0.23	0.47	0.70
20:1 (n-9)	0.14	0.11	0.27
21:1 (n-8)	0.14	0.19	0.70
22:1 (n-11)	0.52	0.55	—
22:1 (n-9)	0.12	0.32	0.96
24:1 (n-11)	0.08	0.16	0.27
24:1 (n-9)	0.08	0.08	0.21
25:1 (n-9)	0.17	0.24	—
26:1 (n-11)	0.31	0.43	—

Table 3. *Continued*

	M. polymorpha	*Brachythecium* sp.	*A. angustatum*
Monoenoic	23.97	42.68	40.81
Acetylenic	6.88	—	—
14:2 (n-5)	0.25	0.35	0.33
16:2 (n-4)	0.54	0.11	—
18:2 (n-6)	7.88	13.50	11.09
18:2 (n-3)	0.66	1.37	0.27
6a,9-18:2 ‡§	4.45	0.24	—
9,12a-18:2*§	0.35	—	0.63
9a,12-18:2†§	0.08	0.08	—
20:2 (n-6)	0.25	0.11	—
22:2 (n-6)	1.15	—	—
Dienoic	15.61	15.76	12.32
Acetylenic	4.88	0.32	0.63
16:3 (n-6)	0.66	—	—
16:3 (n-3)	0.69	—	—
18:3 (n-6)	9.42	1.58	2.68
18:3 (n-3)	10.94	2.63	5.73
6a,9,12-18:3‡§	8.89	2.91	—
20:3 (n-9)	0.35	—	—
20:3 (n-6)	0.49	—	—
20:3 (n-3)	0.08	—	0.28
8a,11,14-20:3‡§	0.08	—	—
22:3 (n-6)	0.43	—	—
24:3 (n-3)	0.17	0.35	—
16:4 (n-3)	1.01	—	—
18:4 (n-3)	2.86	—	—
6a,9,12,15-18:4‡§	0.43	1.78	0.81
20:4 (n-6)	0.66	—	—
20:4 (n-3)	0.08	—	0.21
22:4 (n-3)	0.66	—	—
5a,8,11,14-20:4†§	1.69	—	—
20:5 (n-3)	0.17	—	—
Polyenoic	39.76	9.25	9.71
Acetylenic	11.09	4.69	0.81
The sum of acetylenic acids	22.65	5.01	1.44

*Known in nature.
†Prepared only by synthesis.
‡Known in some mosses and/or liverworts, see text.
§Structure confirmed by GC-MS or trimethyl-oxazolines after preseparation.

Table 4. Fatty acid composition of glycolipid fractions

	M. polymorpha	*Brachythecium* sp.	*A. angustatum*
12:0	0.58	0.57	0.94
13:0	0.02	0.02	—
14:0	0.10	0.10	0.05
15:0	0.56	0.55	0.58
16:0	9.62	6.34	7.39
17:0	0.54	0.53	0.52
18:0	3.06	3.10	4.35
19:0	0.26	0.06	0.16
20:0	0.28	0.14	0.16
21:0	0.72	0.21	0.60
22:0	—	0.84	—
23:0	0.50	0.59	0.39
24:0	0.10	0.02	0.09
25:0	0.28	0.27	0.26
26:0	0.54	0.53	0.47
iso-12:0	0.02	0.02	—
iso-13:0	0.10	0.10	0.05
iso-14:0	0.40	0.39	0.63
iso-15:0	0.08	0.08	0.05
iso-16:0	0.06	0.06	—
iso-17:0	0.16	0.16	0.16
anteiso-13:0	0.14	0.14	0.10
anteiso-15:0	0.34	0.33	0.26
anteiso-17:0	0.04	0.04	—
anteiso-19:0	0.14	—	0.05
Pristanic	0.06	0.06	0.05
Phytanic	0.16	0.45	0.42
Saturated	18.86	15.70	17.73
Iso-	0.82	0.81	0.89
Anteiso-	0.52	0.51	0.41
12:1 (n-5)	0.40	0.39	0.63
13:1 (n-5)	0.58	0.57	0.94
14:1 (n-5)	0.14	0.14	0.10
15:1 (n-9)	0.53	0.51	0.52
15:1 (n-7)	0.18	0.18	0.16
16:1 (n-9)	3.19	4.76	5.65
16:1 (n-7)	1.78	2.01	2.75
trans-16:1 (n-13)	0.14	0.14	0.37
iso-17:1 (n-9)	0.24	0.23	0.16
anteiso-17:1 (n-9)	0.14	0.14	0.10
17:1 (n-9)	0.61	0.59	0.63
17:1 (n-7)	0.34	0.33	0.31
18:1 (n-11)	0.74	1.19	0.87
18:1 (n-9)	5.17	10.97	9.27
18:1 (n-7)	0.80	0.94	0.94
19:1 (n-8)	0.28	0.10	0.13
20:1 (n-11)	0.26	0.10	0.21
20:1 (n-9)	0.10	0.10	0.13
21:1 (n-8)	0.10	0.02	0.05
22:1 (n-11)	0.62	0.80	1.05
22:1 (n-9)	0.02	0.10	0.08
24:1 (n-11)	0.06	0.10	0.08
24:1 (n-9)	0.02	0.06	0.03
25:1 (n-9)	0.18	0.18	0.16
26:1 (n-11)	0.26	0.25	0.10
26:1 (n-9)	0.15	0.16	0.42

are characterized by the presence of acetylenic acids which are, as far as is known, restricted to the acylglycerols [1, 2, 5]. Some compounds which have been identified include 6a,9-18:2 from *Riccia fluitans* [6] and *Fontinalis antipyretica* [3], 6a-18:1, 9a-18:1, 12a-18:1, 6a,9,12-18:3, 6a,9,12,15-18:4, 8a,11,14-20:3 and 5a,8,11,14-20:4 from other mosses [2, 3, 7, 38].

EXPERIMENTAL

Marchantia polymorpha L., *A. angustatum* (Brid.) Bryol. eur. and *Brachythecium* sp. were sampled in May 1992 in

Table 4. *Continued*

	M. polymorpha	*Brachythecium* sp.	*A. angustatum*
Monoenoic	17.03	25.06	25.84
14:2 (n-5)	0.20	0.20	0.16
16:2 (n-4)	0.48	0.47	0.26
18:2 (n-6)	8.41	8.86	8.96
18:2 (n-3)	0.85	0.98	0.94
20:2 (n-6)	0.53	0.64	0.81
22:2 (n-6)	4.21	—	0.50
Dienoic	14.68	11.15	11.63
16:3 (n-6)	0.69	0.66	0.58
16:3 (n-3)	0.62	0.60	0.37
18:3 (n-6)	11.40	0.90	7.39
18:3 (n-3)	15.47	16.48	17.30
20:3 (n-9)	0.34	1.03	0.63
20:3 (n-6)	0.50	0.59	0.39
20:3 (n-3)	0.06	0.10	0.08
22:3 (n-6)	2.85	2.11	4.66
22:3 (n-3)	0.72	1.19	0.60
24:3 (n-3)	0.18	0.33	0.29
16:4 (n-3)	1.18	1.15	1.26
18:4 (n-3)	3.46	2.40	2.70
20:4 (n-6)	7.76	6.81	4.12
20:4 (n-3)	0.02	0.74	0.03
22:4 (n-3)	2.42	6.81	4.12
20:5 (n-3)	1.96	6.19	0.29
Polyenoic	49.63	48.18	44.81

the Zhiguli nature reserve near Togliatti. Freshly collected specimens were thoroughly cleansed of extraneous matter and homogenized in a high-speed unit.

The extraction of lipids, their analyses and quantification and the identification of individual phospholipid classes are described elsewhere [7, 22, 39]. The total lipid extract was sepd on a silica gel column according to the method of ref. [40] into neutral, glyco- and phospholipid frs. PLs were isolated by silica gel TLC using the following solvents [7, 22]: system 1: $CHCl_3$–MeOH–C_6H_6–NH_4OH (65:30:10:6), system 2: $CHCl_3$–MeOH–C_6H_6–Me_2CO–HOAc–H_2O (70:30:10:5:4:1).

DGTS was checked chromatographically by comparison with that isolated from the microphytic alga *Nephrochloris salina* [41]. DGTS and PE were determined according to the method of ref. [42] using DGTS and PE as standards. When carrying out qualitative determination of phospholipids as well DGTS and PE 3–5 parallel determinations were made.

Fatty acids as trimethylsilyl-oxazoline derivatives were prepd and analysed by capillary GC-MS as described elsewhere (the data shown in Tables 3–5 were obtained from 3 experiments) [7, 43].

Table 5. Fatty acid composition of phospholipid fractions

	M. polymorpha	*Brachythecium* sp.	*A. angustatum*
12:0	0.76	0.85	0.63
13:0	0.06	0.06	0.12
14:0	0.10	0.10	0.20
15:0	0.46	0.42	0.63
16:0	8.02	8.83	13.88
17:0	0.48	0.55	0.72
18:0	2.56	6.81	5.75
19:0	0.18	0.14	0.37
20:0	0.28	0.51	0.75
21:0	0.28	0.48	0.67
22:0	0.15	0.82	—
23:0	0.25	0.24	—
24:0	0.12	0.14	0.35
25:0	0.25	0.27	0.37
26:0	0.36	0.41	0.60
iso-12:0	0.06	0.06	0.12
iso-13:0	0.10	0.10	0.20
iso-14:0	0.46	0.51	0.35
iso-15:0	0.10	0.10	0.18
iso-16:0	—	—	0.07
iso-17:0	0.10	0.17	0.23
anteiso-13:0	0.10	0.10	0.18
anteiso-15:0	0.25	0.27	0.45
anteiso-17:0	—	0.04	0.10
anteiso-19:0	0.06	0.06	0.25
Pristanic	0.03	—	0.05
Phytanic	0.25	0.06	0.10
Saturated	15.82	22.10	27.32
Iso-	0.82	0.94	1.15
Anteiso-	0.41	0.47	0.98
12:1 (n-5)	0.46	0.51	0.35
13:1 (n-5)	0.76	0.85	0.63
14:1 (n-5)	0.10	0.10	0.18
15:1 (n-9)	0.43	0.48	0.60
15:1 (n-7)	0.10	0.10	0.15
16:1 (n-9)	4.02	5.23	4.85
16:1 (n-7)	0.68	3.56	3.07
trans-16:1 (n-13)	0.21	—	—
iso-17:1 (n-9)	0.15	0.20	0.37
anteiso-17:1 (n-9)	0.06	0.24	0.37
17:1 (n-9)	0.46	0.51	0.60
17:1 (n-7)	0.25	0.27	0.37
18:1 (n-11)	0.46	1.24	1.20
18:1 (n-9)	5.21	15.22	11.09
18:1 (n-7)	0.33	1.10	1.07
6a-18:1*§	0.88	—	—
9a-18:1*§	0.57	—	—
12a-18:1†§	0.30	—	—
19:1 (n-8)	0.10	0.20	0.42
20:1 (n-11)	0.21	0.38	0.47
20:1 (n-9)	0.12	0.14	0.15
21:1 (n-8)	0.12	0.14	0.35
22:1 (n-11)	0.40	0.92	0.45
22:1 (n-9)	0.10	0.31	0.40
24:1 (n-11)	0.06	0.10	0.15
24:1 (n-9)	0.06	0.04	0.07
25:1 (n-9)	0.10	0.10	0.15
26:1 (n-11)	0.06	0.06	0.22
26:1 (n-9)	0.24	0.27	—

Table 5. *Continued*

	M. polymorpha	*Brachythecium* sp.	*A. angustatum*
Monoenoic	17.00	32.27	27.73
Acetylenic	1.75	—	—
14:2 (n-5)	0.15	0.17	0.28
16:2 (n-4)	0.15	0.54	0.47
18:2 (n-6)	6.73	7.05	10.18
18:2 (n-3)	0.58	0.65	0.70
6a,9-18:2‡§	4.70	—	—
9,12a-18:2*§	0.36	—	—
9a,12-18:2†§	0.06	—	—
20:2 (n-6)	0.51	0.48	0.23
22:2 (n-6)	6.10	0.34	2.50
Dienoic	19.34	9.50	14.36
Acetylenic	5.12	—	—
16:3 (n-6)	0.33	0.83	0.58
16:3 (n-3)	1.29	0.79	0.60
18:3 (n-6)	8.50	1.24	8.49
18:3 (n-3)	14.31	12.99	9.93
6a,9,12-18:3‡§	0.54	—	—
20:3 (n-9)	0.15	0.65	0.30
20:3 (n-6)	0.25	0.42	0.42
20:3 (n-3)	0.06	0.10	0.15
8a,11,14-20:3‡§	0.06	0.06	—
22:3 (n-6)	1.44	4.48	2.37
22:3 (n-3)	0.28	0.48	0.67
24:3 (n-3)	0.10	0.27	0.15
16:4 (n-3)	0.73	0.82	0.88
18:4 (n-3)	2.25	1.26	2.67
6a,9,12,15-18:4‡§	0.46	—	—
20:4 (n-6)	10.34	3.38	1.58
20:4 (n-3)	0.06	1.24	0.07
5a,8,11,14-20:4†§	0.54	—	—
22:4 (n-3)	1.77	3.38	1.58
20:5 (n-3)	4.38	4.01	0.15
Polyenoic	47.84	36.40	30.59
Acetylenic	1.60	—	—
Sum of acetylenic acids	8.47	—	—

*Known in nature.
†Prepared only by synthesis.
‡Known in some mosses and/or liverworts, see text.
§Structure confirmed by GC-MS of trimethyl-oxazolines after preseparation.

REFERENCES

1. Anderson, B., Anderson, W. H., Chipault, J. R., Ellison, E. C., Fenton, S. W., Gellerman, J. L., Hawkins, J. M. and Schlenk, H. (1974) *Lipids* **9**, 506.
2. Anderson, W. H., Gellerman, J. L. and Schlenk, H. (1975) *Lipids* **10**, 501.
3. Jamieson, G. R. (1975) *J. Chrom. Sci.* **13**, 491.
4. Jamieson, G. R. and Reid, E. H. (1976) *J. Chromatogr.* **128**, 193.
5. Kohn, G., Demmerle, S., Vandekerkhove, O., Hartman, E. and Beutelmann, P. (1987) *Phytochemistry* **26**, 2271.
6. Kohn, G., Vierengel, A., Vandekerkhove, O. and Hartman, E. (1987) *Phytochemistry* **26**, 2101.
7. Dembitsky, V. M., Rezanka, T., Bychek, I. A. and Afonina, O. M. (1993) *Phytochemistry* **33**, 1021.
8. Huneck, S. (1983) in *New Manual of Bryology* (Schuster, R. M., ed.), pp. 1–116. Hattori Botanical Laboratory, Nichinan.
9. Gellerman, J. L., Anderson, W. H., Richardson, D. G. and Schlenk, H. (1975) *Biochim. Biophys. Acta* **388**, 277.
10. Gellerman, J. L., Anderson, W. H. and Schlenk, H. (1972) *Bryologist* **75**, 550.
11. Hartmann, E., Beutelmann, P., Vandekerkhove, O., Euler, R. and Kohn, G. (1986) *FEBS Letters* **198**, 51.
12. Hansen, C. E. and Rossi, P. (1990) *Phytochemistry* **29**, 3749.
13. Alam, M., Ckakravarti, A. and Ikawa, M. (1971) *J. Phycol.* **7**, 267.
14. Leim, P. Q. and Laur, M. H. (1974) *Biochimie* **56**, 925.
15. Eichenberger, W. (1982) *Plant Sci. Letters* **24**, 91.
16. Smith, K. L. and Harwood, J. L. (1983) *Biochem. Soc. Trans* **21**, 394.
17. Smith, K. L., Douce, R. and Harwood, J. L. (1982) *Phytochemistry* **21**, 569.
18. Eichenberger, W. and Boschetti, A. (1978) *FEBS Letters* **88**, 201.
19. Janero, D. R. and Barrnett, R. (1982) *J. Lipid Res.* **23**, 307.
20. Evans, R. W., Kates, M. and Wood, G. W. (1982) *Chem. Phys. Lipids* **31**, 331.
21. Freid, A., Tietz, A., Ben-Amotz, A. and Eichenberger, W. (1982) *Biochim. Biophys. Acta* **713**, 419.
22. Dembitsky, V. M. and Rozentsvet, O. A. (1989) *Phytochemistry* **28**, 3341.
23. Khotimchenko, S. V., Klochkova, N. G. and Vaskovsky, V. E. (1990) *Biochem. Syst. Ecol.* **18**, 93.
24. Brown, A. E. and Evolson, J. (1974) *Biochemistry* **13**, 3476.
25. Sato, N. and Furuya, M. (1983) *Plant Cell. Physiol.* **24**, 1113.
26. Furlong, S. T., Leary, J. A., Costello, C. E. and Dawidowicz, E. A. (1986) *J. Lipid Res.* **27**, 1182.
27. Sato, N. and Furuya, M. (1984) *Phytochemistry* **23**, 1625.
28. Sato, N. and Furuya, M. (1985) *Plant. Sci.* **38**, 81.
29. Jamieson, G. R. and Reid, E. H. (1972) *Phytochemistry* **11**, 1423.
30. Dembitsky, V. M., Pechenkina-Shubina, E. E. and Rozentsvet, O. A. (1991) *Phytochemistry* **30**, 2283.
31. Khotimchenko, S. V. and Svetashev, V. I. (1983) *Biol. Morya (Vladivostok)* **5**, 45.
32. Radwan, S. S., Shaalan, A. S. and Gebreel, H. M. (1988) *Z. Naturforsch.* **43c**, 15.
33. Kato, M. and Ariga, N. (1982) *Kyoyobu Kenkyu Hakoku (Gifu Gaigaku)* **18**, 53.
34. Karunen, P. (1982) *J. Hattori Bot. Lab.* **53**, 255.

35. Anderson, W. H., Gellerman, J. L. and Schlenk, H. (1972) *Lipids* **7**, 710.
36. Karunen, P. and Aro, E.-M. (1979) *Physiol. Plant.* **45**, 265.
37. Al-Hasan, R. H., El-Saadawi, W. E., Ali, M. A. and Radwan, S. S. (1989) *Bryologist* **92**, 178.
38. Jamieson, G. R. and Reid, E. H. (1976) *Phytochemistry* **15**, 1731.
39. Dembitsky, V. M., Bychek, I. A., Rozentsvet, O. A. and Shustov, M. V. (1992) *Cryptogamic Bot.* **2**, 391.
40. Rouser, G., Kritchevsky, G. and Yamamoto, A. (1976) in *Lipid Chromatographic Analyses* (Marinetti, G., ed.), Vol. 3, pp. 715–734. M. Dekker, N.Y.
41. Dembitsky, V. M. (1988) *Khim. Prir. Soed.* **4**, 589.
42. Kabara, J. J. and Chen, J. S. (1976) *Analyt. Chem.* **48**, 814.
43. Dembitsky, V. M., Rezanka, T. and Bychek, I. A. (1992) *Phytochemistry* **31**, 851.