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DISTRIBUTION AND CHEMOTAXONOMIC SIGNIFICANCE OF ACETYLENIC FATTY ACIDS IN MOSSES OF THE DICRANALES

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Abstract—Thirty-eight moss species from four families of the order Dicranales were analysed for the fatty acid composition of their acyl lipids. In the Ditrichaceae and the Dicranaceae numerous species were found to contain acetylenic fatty acids in their triglycerides. 9,12,15-Octadecatrien-6-ynoic acid was the major component, often accounting for more than 80 mol%, whereas 9,12-octadecadien-6-ynoic acid was found in small amounts of less than 5 mol%. In some genera, all the species examined contained acetylenic fatty acids, e.g. *Dicranella* and *Dicranum*, whereas in the genus *Campylopus* all five species tested were free of acetylenic compounds. Two genera, *Ditrichum* and *Dicranoweisia*, were found to have a non-homogeous distribution of acetylenic fatty acids. The chemotaxonomic significance of the fatty acid composition in relation to morphological characters is discussed.

INTRODUCTION

The most abundant fatty acids of the bryophytes are also common to most other organisms. Typical for many bryophytes, however, is a high content of long-chain polyunsaturated fatty acids, particularly arachidonic acid and eicosapentaenoic acid [1, 2], compounds which are not found very abundantly in the rest of the plant kingdom.

The fatty acid patterns of some moss species are further characterized by the presence of acetylenic fatty acids which are, as far as is known, restricted to the triglycerides [3, 4]. Three compounds have to date been identified: 9,12,15-octadecatrien-6-ynoic acid (18:3A) [3], 9,12-octadecadienoic-6-ynoic acid (18:2A) [5] and 11,14-eicosadien-8-ynoic acid (20:2A) [4, 6]. 18:3A is detected most frequently, 18:2A is found in several species, whereas 20:2A has been isolated from only one moss species.

Although numerous compounds with acetylenic bonds, including fatty acids, have been isolated from plants and microorganisms [7], the occurrence of acetylenic fatty acids identical to those isolated from mosses has not yet been reported. Acetylenic compounds in higher plants are often characteristic for certain taxa and therefore their presence or absence can be of chemotaxonomic significance [8].

From our present knowledge we conclude that acetylenic fatty acids in bryophytes are also restricted to only a few families. The reports of several authors [3, 9–11] and our own studies indicate that acetylenic fatty acids are abundant in the Dicranaceae and related families. The purpose of this study was to analyse the fatty acid composition of a number of species from the order Dicranales which were available to our laboratory, in order to clarify whether the distribution of acetylenic fatty acids can provide chemotaxonomic information.

RESULTS AND DISCUSSION

Not all species which were examined in this study were available as fresh material. Therefore it was necessary to clarify whether lipid extracts from dry samples could be compared with extracts from fresh material. Aliquots of a sample of *Cynodontium strumiferum* (Hedw.) De Not. were extracted fresh and also after dry storage for three days and for one yr. The total triglyceride content decreased markedly on storage (Table 1), probably due to lipid polymerization and peroxidation. Changes in the pattern of the fatty acids (Table 1), whilst obvious were not very striking. Thus even after one yr of storage the characteristic composition, with the acetylenic fatty acid 18:3A being the dominating component, was retained. Almost identical results were obtained with *Dicranum fulvum*, *Orthodicranum montanum* (Hedw.) Loeske and *Rhabdoweisia fugax* (Hedw.) B.S.G. These results show that for studies to confirm only the presence or absence of acetylenic fatty acids, dry material can be used, with certain precautions, i.e. the samples should not be older than one yr. Sub-fractionation of lipid classes can be omitted, too, since the triglycerides are the most abundant acyl lipid fraction and so the fatty acid pattern of the total lipid extract mainly reflects the composition of the triglycerides. Nevertheless the extraction of fresh material and the isolation of the triglyceride fraction is preferable. Table 2 shows the fatty acid patterns of the acyl lipids of *C. strumiferum*, which were extracted from fresh material. Very similar compositions were found in most of the acetylenic fatty acid-containing species. The total amount

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Abbreviations: 18:2A, 9,12-octadecadien-6-ynoic acid; 18:3A, 9,12,15-octadecatrien-6-ynoic acid; 20:2A, 11,14-eicosadien-8-ynoic acid; DGDG, digalactosyldiacylglycerol; MDGD, monogalactosyldiacylglycerol; SQGD, sulphoquinovosyldiacylglycerol; PG, phosphatidylglycerol; PI, phosohatidylinositol; PE, phosphatidylethanolamine; PC, phosphatidylcholine.

of triglyceride fatty acids is often as much as 20 times the fatty acid content of the galactolipids and the phospholipids.

Samples of *Dicranum scoparium* Hedw. were collected from three different habitats in January, April and October. Variations in the total amount of triglycerides were found in the different samples (from 149 to 239 nmol fatty acids per mg dry wt), but almost no variation in the fatty acid composition was detected. The patterns of all samples were practically identical to the composition listed in Table 3 for *D. scoparium*. The same result was obtained by Karunen and Kallio [12] with *D. elongatum Schwaegr.* The fatty acid pattern of the triglyceride fraction is obviously not influenced drastically by environmental factors. We suppose that the composition of the triglycerides, at least in many mosses, is of taxonomic significance, as predicted by Anderson *et al.* [13] and as it is true for the fatty acid composition of seed oils in higher plants [14, 15].

Table 1. Comparison of the fatty acid patterns of fresh material and air dried samples of *C. strumiferum*

Fatty acid	Fresh material	Material dried and stored at room temperature for 3 days	1 yr
16:0	1.7	2.1	7.3
18:0	1.1	1.3	3.7
18:1ω9	0.8	0.9	3.5
18:2ω6	1.4	1.5	2.7
18:3ω3	2.1	2.5	4.7
20:4ω6	1.1	1.3	2.1
20:5ω3	0.3	0.3	1.4
18:2A	2.9	2.8	1.6
18:3A	88.3	86.3	64.7
Total fatty acids nmol/mg dry wt	514.3	206.7	101.5

The fatty acid compositions of the glycolipids and the phospholipids are not characterized by one dominating fatty acid as in the triglycerides. The common fatty acids palmitic acid (16:0), stearic acid (18:0) oleic acid (18:1), linoleic acid (18:2) and linolenic acid (18:3) were present in varying but more or less similar percentages. Arachidonic acid was most abundant in the phospholipids. The fatty acid patterns of the glycolipids and phospholipids varied from species to species, but no taxon-specific patterns could be found. Similarities to the pattern of the triglycerides were not obvious.

In Table 3 the fatty acid patterns of the triglycerides of all analysed species are listed. The survey clearly shows that the occurrence of acetylenic fatty acids is not characteristic for all members of the order Dicranales. In quite a few species in different families no acetylenic fatty acid could be detected. In acetylenic fatty acid-containing species, 18:3A was, with few exceptions, the major acetylenic component (30–80 mol%). 18:2A, if present at all, was found in small amounts (less than 5 mol%), and always together with 18:3A.

18:2A seems to be an intermediary product, whereas 18:3A is the main constituent of the storage fat in the

Table 2. Fatty acid pattern of the acyllipid fractions of *C. strumiferum*. The values are mol% of the total fatty acids of the respective lipid fraction

Fatty acid	Triglycerides	MDGD	DGDG	SQDG	PG	PI	PE	PC
12:0	—	—	3.0	6.2	1.7	4.5	2.9	0.8
14:0	0.2	1.4	2.0	5.0	1.8	2.4	2.1	0.6
15:0	—	—	0.3	1.8	1.4	—	1.1	1.2
16:0	1.7	16.1	10.4	30.9	38.9	34.2	24.3	25.5
16:1ω9/ω7	—	—	0.7	3.9	3.5	2.0	1.1	—
17:0	—	—	0.6	3.6	1.1	2.2	1.7	0.7
16:2ω6	—	1.8	0.8	—	—	—	—	—
18:0	1.1	32.1	8.8	23.4	7.8	8.9	6.6	2.2
18:1ω9	0.8	2.7	2.9	13.2	4.6	8.9	6.9	3.6
16:3ω3	—	—	0.5	—	—	—	—	—
18:2ω6	1.4	10.6	10.8	4.9	12.7	14.3	14.2	22.4
22:0	—	—	1.5	3.6	0.7	—	—	—
18:3ω6	—	1.5	0.6	—	1.0	—	—	2.1
18:3ω3	2.1	27.1	30.5	3.5	17.5	8.9	7.4	19.8
18:4ω3	—	—	0.5	—	—	—	—	1.1
20:2ω6	0.3	—	—	—	—	—	—	0.4
20:3ω6	—	—	—	—	0.5	0.9	2.4	1.3
20:3ω3	—	—	22.5	—	—	—	—	—
20:4ω6	1.1	2.5	3.5	—	6.0	11.2	24.2	15.5
20:5ω3	0.3	0.9	—	—	0.8	1.6	5.2	2.6
18:2A	2.9	—	—	—	—	—	—	—
18:3A	88.3	—	—	—	—	—	—	—
Total fatty acid content (nmol/mg dry wt)	514.4	7.8	8.4	0.8	2.6	0.8	1.3	5.1

Table 3. Fatty acid composition of the triglycerides of all species examined (only the major components are listed, the values are mol % of the total fatty acids of the triglycerides)

Species	Fatty acids								
	16:0	18:0	18:1ω9	18:2ω6	18:3ω3	20:4ω6	20:5ω3	18:2A	18:3A
Ditrichaceae									
Ceratodon purpureus (Hedw.) Brid.	6.4	1.3	4.1	12.1	14.9	3.1	4.2	5.0	41.5
Distichum capillaceum (Hedw.) B.S.G.	16.0	12.0	4.7	8.3	27.0	5.7	2.9	—	—
Ditrichum heteromallum (Hedw.) Britt.	14.7	1.6	6.8	16.0	18.9	5.9	3.6	2.9	19.1
D. pusillum (Hedw.) Hampe	10.5	2.9	2.5	13.9	23.7	12.7	4.2	—	19.6
Ditrichum flexicaule (Hedw.) Rabenh.	9.0	4.6	5.0	9.1	27.5	6.9	5.9	—	—
Ditrichum cylindricum (Hedw.) Grout	14.8	2.8	5.1	30.0	15.1	3.1	4.3	—	—
Pleuridium subulatum (Hedw.) Rabenh.	4.3	1.0	1.9	10.2	5.9	2.3	0.8	18.0	47.2
Seligeraceae									
Blindia acuta (Hedw.) B.S.G.	8.7	2.4	3.4	7.5	59.9	4.5	2.5	—	—
Dicranaceae									
Amphidium mougeotii (B.S.G.) Schimp.	15.4	9.5	9.2	5.5	6.6	1.6	0.6	0.3	31.2
Cynodontium polycarpum (Hedw.) Schimp.	1.7	0.5	1.3	3.8	5.0	1.9	0.5	2.3	78.0
C. strumiferum (Hedw.) De Not.	1.7	1.1	0.8	1.4	2.1	1.1	0.3	2.9	88.3
Rhabdoweisia crispata (With.) Lindb.	13.3	5.7	22.4	4.8	3.7	1.8	0.7	3.4	30.8
R. fugax (Hedw.) B.S.G.	6.0	2.5	2.4	8.1	9.7	5.1	1.9	4.0	55.6
Dicranella heteromalla (Hedw.) Brid.	5.8	4.5	3.4	6.6	7.2	3.6	—	—	51.4
D. jamesonii (Mitt.) Broth.	19.3	8.5	5.0	4.5	3.3	1.9	1.0	—	34.9
D. palustris (Dicks.) Crundw. ex Warb.	1.5	0.5	0.6	1.3	2.6	0.8	0.4	2.9	83.7
D. schreberiana (Hedw.) Dix.	17.8	4.4	5.6	11.2	13.4	2.8	—	—	23.7
Dicranum fulvum Hook.	5.2	4.5	4.4	4.6	7.3	3.7	0.4	0.7	61.9
D. fuscescens Turn.	2.5	0.8	1.3	1.7	4.8	2.8	—	—	78.7
D. muehlenbeckii B.S.G.	6.6	3.3	4.7	3.2	6.4	1.5	0.3	1.4	64.9
D. polysetum Sw.	15.3	6.6	4.6	7.6	9.6	7.5	0.9	—	27.1
D. scoparium Hedw.	2.0	0.9	1.1	1.3	3.2	1.6	—	—	83.7
D. spurium Hedw.	1.8	2.1	10.4	4.2	4.8	3.9	0.3	6.6	57.7
D. undulatum Brid.	2.1	0.4	1.5	2.0	5.1	0.5	0.4	4.9	79.6
D. viride (Sull. et Lesqu.) Lindb.	4.6	2.5	6.6	2.8	9.9	3.5	0.5	1.5	62.9
Kiaeria starkei (Web. et Mohr) Hag.	3.0	1.6	1.7	2.9	5.1	—	1.0	—	78.1
Orthodicranum montanum (Hedw.) Loeske	12.5	6.0	5.3	5.1	6.2	2.7	0.9	2.8	47.8
Dichodontium pellucidum (Hedw.) Schimp.	28.6	14.2	11.0	3.0	2.2	—	0.3	—	10.0
Dicranoweisia cirrata (Hedw.) Lindb.	5.3	2.5	3.2	4.9	11.7	1.1	1.1	4.9	57.0
D. crispula (Hedw.) Milde	6.8	4.0	3.6	8.5	56.4	6.5	4.0	—	—
Dicranodontium denudatum (Brid.) Britt.	4.6	0.6	1.9	4.2	68.3	5.4	1.7	—	—
Campylopus atrovirens De Not.	17.8	7.9	9.8	23.3	16.7	4.8	0.5	—	—
C. flexuosus (Hedw.) Brid.	9.8	2.6	7.5	28.4	32.4	7.6	0.8	—	—
C. introflexus Hedw.	26.6	8.2	9.7	17.4	16.4	3.6	0.7	—	—
C. pyriformis (Schultz) Brid.	7.8	2.7	3.6	4.9	56.6	4.6	1.5	—	—
C. substramineus Broth.	16.4	9.5	6.9	7.4	17.4	16.4	3.8	—	—
Paraleucobryum longifolium (Hedw.) Loeske	6.4	1.7	3.1	7.7	54.2	4.1	1.9	—	—
Leucobryaceae									
Leucobryum glaucum (Hedw.) Angstr.	13.5	7.1	5.8	16.1	29.7	7.7	1.1	—	—

moss cells. A study on the metabolism of acetylenic fatty acids in the protonema of the moss *Ceratodon purpureus* (Hedw.) Brid. shows that the content of 18:2A reaches a maximum when the rate of triglyceride synthesis is high and decreases when the rate of triglyceride synthesis slows down in ageing cells (unpublished data).

Almost all the species examined could be classified into three types of fatty acid patterns (Table 3). The first type represents most of the species with acetylenic fatty acids, and in which 18:3A is the over-all dominating component, accounting for up to 80 mol%. In particular, most of the Dicranaceae belong to this type. A second type is also characterized by considerable amounts of 18:3A, but with other fatty acids, particularly 18:2ω6 and 18:3ω3, being present in higher amounts. *C. purpureus* and *Ditrichum pusillum* (Hedw.) Hampe are examples of this type. The third type represents those species without acetylenic fatty acids and which show triglyceride patterns with linolenic acid as the major fatty acid as is found in *Ditrichum flexicaule* (Hedw.) Rabenh., *Blindia acuta Campylopus pyriformis* (Schultz) Brid. and others. The rest of the acetylenic acid-free species more or less resemble the second type, with 18:2ω6 and 18:3ω3 as main components.

In two families (Ditrichaceae and Dicranaceae) acetylenic fatty acids were detected, but not in all species. Several genera were found to be non-homogenous in this respect. The genus *Ditrichum* is obviously divided in two

groups, one including *Ditrichum pusillum* and *D. heteromallum* (Hedw.) Brid. with an acetylenic pattern similar to that of *Ceratodon purpureus*, and a second group including *D. cylindricum* and *D. flexicaule*, two species without acetylenic fatty acids, but otherwise with quite different pattern. These results more or less reflect the morphological characters of these species. *D. heteromallum* and *D. pusillum* are very similar in leaf morphology, leaf cell pattern and capsule morphology [16]. The fatty acid pattern also indicates a close relationship with *Ceratodon*. *D. cylindricum* and *D. flexicaule* are morphologically well differentiated, not only from the two other species, but from each other, which is also expressed in the fatty acid patterns. Differences in habitat requirements, plant size, leaf morphology and anatomy, correlate with the fatty acid composition; in *D. flexicaule*, 18:3ω3 is dominant, whereas in *D. cylindricum* 18:2ω6 is the major component, accompanied by considerable amounts of linolenic and arachidonic acid. The absence of acetylenic fatty acids in *D. capillaceum* is confirmed by other authors [13] who also found *D. inclinatum* to be free of these compounds. *Pleuridium subulatum* has the typical pattern of acetylenic fatty acid-containing species, but with one important exception, in that the amount of 18:2A was much higher than in any other examined species.

No general conclusions can be made about the Seligeraceae and the Leucobryaceae, since only one species of each family was tested.

The Dicranaceae also proved to be non-homogenous in the content of acetylenic compounds. In most of the species examined acetylenic fatty acids were found together with very similar fatty acid compositions. A number of species were tested from the genera *Dicranella* and *Dicranum* and acetylenic fatty acids were detected in all of them. In three more species of *Dicranum* acetylenic fatty acids were found by other authors [3, 10, 11], indicating that the occurrence of acetylenic fatty acids, particularly of 18:3A, can probably be regarded as a genus-specific feature of *Dicranella* and *Dicranum*. The same could be true for the genera *Kiaeria*, *Cynodontium*, *Orthodicranum* and *Rhabdoweisia*, but this will have to be confirmed by the analysis of additional species.

The species of *Campylopus* together with *Dicranodontium denudatum* (Brid.) Britt., *Dicranoweisia crispula* (Hedw.) Milde and *Paraleucobryum longifolium* (Hedw.) Loeske form a group which is free of acetylenic compounds. In the genus *Dicranoweisia* two species which are separated morphologically and by habitat requirements are also distinguished biochemically. In *Campylopus* the absence of acetylenic compounds seems to be typical for the genus. A genus specific fatty acid pattern however could not be found, but final conclusions cannot be drawn because most of the species examined were not available as fresh material. Our results confirm the close relationship between *Campylopus* and *Dicranodontium* [16, 17], and also suggest that the genera *Campylopus*, *Dicranodontium* and *Paraleucobryum* can be regarded as a separate complex within the Dicranaceae, probably forming the link to the Leucobryaceae. The fatty acid pattern of *Amphidium mougotii* (B.S.G.) Schimp., the taxonomy of which is obscure [16], would justify the placement of the species into the Dicranaceae, to which it is not always attributed.

The ability to synthesize acetylenic fatty acids must have existed in the bryophytes for a long time, since the same fatty acids occur in species which are systematically far apart from each other, and it is unlikely that such a character would be formed several times independently. Thus acetylenic fatty acids have been detected in the Bryaceae (unpublished data), the Fontinalaceae [3, 6] and in the Ricciaceae, a family of the Hepaticae [18] (unpublished). The pathway of synthesis was either lost or conserved independently in several lines of evolution, so that the presence or absence of acetylenic fatty acids in two bryophyte species does not necessarily indicate close affinity. The chemotaxonomic details of the fatty acid pattern is only significant when taken together with morphological characters.

Our results are not sufficient to cause major rearrangements in the taxonomy of the Dicranales, but we think that we have shown that the fatty acid patterns provide valuable taxonomic information. This, however, has still to be augmented by the analysis of additional species, in order to support a reexamination of the relationships within the families and within several genera.

EXPERIMENTAL

Plant material. Most of the moss samples were collected in southwest Germany and Austria. Some species were obtained from other sources: *Campylopus pyriformis* from Belgium, *C. substramineus* from Rwanda, Africa, and *C. atrovirens* from Scotland. *Ditrichum cylindricum*, *Ditrichum pusillum*, *Dicranella schreberiana* and *Dicranella jamesonii* were supplied by Dr H. L. K. Whitehouse, Cambridge, UK, and grown in axenic culture. The nomenclature is that of ref. [17]. Voucher specimens are deposited in the herbarium of the Institut für Spezielle Botanik (MJG), University of Mainz, FRG.

Lipid extraction. As far as possible fresh material was used for extraction, otherwise air-dried material was used. The moss samples were carefully selected and freed from soil and other contaminants. Only the upper green parts of the gametophores were used for lipid extraction. The moss samples were treated with boiling *iso*PrOH to avoid lipid degradation by lipases. Dry material was wetted with distilled water immediately before the treatment. Homogenization was carried out in the still hot *iso*PrOH with quartz sand in a mortar with a pestle. The homogenate was extracted with $CHCl_3$–MeOH (2:1) following the procedure of [19]. The extract was evaporated to dryness, the residue dissolved in hexane and stored at $-20°$.

Separation and identification of lipids. The hexane extract was fractionated by CC on silicic acid as described in [20]. The purity of the fractions and the identity of the lipids was verified by TLC.

Fatty acid analyses. The acyl lipid fractions from the CC were *trans*-esterified with 5% H_2SO_4 in MeOH (v/v) for 4 hr at 80°. The resulting methyl esters of the fatty acids were analysed by GC on a WCOT fused silica capillary column, (50 m × 0.23 mm i.d.), with FID and split injector (split ratio 1:100). The stationary phase of the column was CP Si188 (Chrompack) with a film thickness of 0.20 μm. N_2 was the carrier gas (flow rate 1.1 ml/min), with an oven temp. of 200°.

Fatty acids were identified by co-chromatography of known standards and by GC-MS [18, 20]. The GC was equipped with a 180 cm × 2 mm i.d. column packed with 15% DEGS-PS (Supelco) on Chromosorb WAW. The oven temp. was 200°. The electron energy of the mass spectrometer was set to 70 keV, and the temperature of the ion source was 250°.

Reference substances of acetylenic fatty acids were isolated from moss species from which they had been originally identified. 18:3A was obtained from *Ceratodon purpureus* [3], and 18:2A and 20:2A were extracted from *Fontinalis antipyretica* [5, 6]. The methyl esters of the suspected acetylenic fatty acids were isolated by preparative GC on a GC fitted with a stream splitter. A 180 cm

× 4 mm i.d. column, packed with 15% DEGS-PS on Chromosorb W-AW was used at 200°. The carrier gas flow (N_2) was 200 ml/min, and the split ratio between FID and the solvent trap was 1:25.

The effluent peaks were trapped in cold hexane. The identity and purity of the fractions was checked by GC-MS. Parts of the fractions were dissolved in 0.5 ml MeOH, transferred into a 3 ml septum vial and mixed with platinum asbestos as a hydrogenation catalyst. The vial was flushed with excess H_2 and shaken for 3 hr at room temp. The hydrogenation products were extracted into hexane and analysed by GC. Stearic acid was obtained from 18:2A and 18:3A fractions, eicosanoic acid from 20:2A [18].

The fatty acid contents were calculated on a dry wt basis and the fatty acid composition is given in mol% of the total fatty acid content of the respective lipid fraction. All values listed in the tables are mean values of at least three determinations.

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