

Carbon and Hydrogen Isotope Ratios of Bryophytes from Arid and Humid Regions

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Summary. Measurements of carbon isotope ratios of nine taxa of arid zone mosses from North America and 24 taxa of European bryophytes show consistent values indicative of C₃ metabolism. Other morphological, physiological and biochemical characteristics provide the mechanism of adaptation to environmental stresses of heat and extended desiccation in these plants. Analyses of D content indicate that values become less negative with increasing aridity of the habitat.

Introduction

Recent interest in the physiological ecology of arid-zone plants has produced a considerable literature on the ecological significance of alternative pathways of CO₂ fixation in vascular plants, particularly with regard to C₄ metabolism. Plants with C₄ metabolic systems utilize a spatial separation of two distinct carboxylation steps, with the PEP carboxylase step limited to outer mesophyll cells and the secondary RuBP-carboxylase reaction occurring in specialized sheaths of thick-walled chlorenchyma around the vascular bundles (Kranz anatomy). Herbaceous C₄ plants have been shown to possess a high temperature optimum for photosynthesis, relatively efficient water utilization and no light saturation in photosynthesis under normal conditions (Björkman et al., 1972), all characteristics associated with adaptation to arid zone conditions. Downton (1975) has surveyed the phylogenetic distribution of C₄ metabolism among angiosperms, but no evidence exists to suggest that this metabolic system is present in non-flowering terrestrial plants.

The general biochemical pathways of C₄ metabolism has been shown in bluegreen algae and green algae (Döhler, 1974a, b). However, the unequivocal establishment of the C₄ syndrome requires that C₄ acids represent true intermediate products of photosynthesis and not just products of isozymes of PEP-carboxylase with no major photosynthetic function. Characteristics of Crassulacean acid metabolism (CAM) were demonstrated in two genera of ferns (Wong and Hew, 1976). *Welwitschia mirabilis*, a highly specialized gymnosperm, exhibits flexible crassulacean acid metabolism (Dittrich and Huber, 1974; Schulze et al., 1976), with similar biochemical pathways.

No previous studies have investigated the photosynthetic sys-

tems of arid zone mosses. While anatomical features corresponding to Kranz anatomy are lacking in this group, highly differentiated chlorophyllous tissues are commonly present. In this paper we report on a survey of $\delta^{13}\text{C}$ values and δD values for nine taxa of the Pottiaceae, an important moss family in arid regions, and 24 bryophyte taxa from humid regions of central and north eastern Europe.

Although mosses are morphologically simple compared with vascular plants, significant differentiation of tissues is present. From an anatomical point of view, the fundamental pattern of organization of moss stems with supportive tissue at the periphery and a simple strand (protostele) of differentiated tissue at the center is similar to that seen in primitive vascular plants. These tissues also appear to be physiologically differentiated. Hebert (1977) has reviewed the literature on conducting tissues in bryophytes and suggests that xylem-like tissues (hydroids) and phloem-like tissues (leptoids) have functions similar to apposite tissues in vascular plants. The lack of such structures in some taxa appears to be a derived condition, following a general trend toward regressive evolution in bryophytes.

Materials and Methods

Sample collections of bryophytes were analyzed for carbon isotope ratio using analysis techniques previously described (Osmond et al., 1975). This survey includes a wide variety of morphological forms representing seven genera of arid zone Pottiaceae from the southwestern United States and Mexico, and 21 genera of European bryophytes, including five liverwort genera.

Results and Discussions

The Pottiaceae, together with Polytrichaceae, represent the most notable families of mosses for possessing gametophyte tissues specialized for photosynthesis. In the most highly developed taxa the ventral (adaxial) surface of the leaf costa is adorned with filaments or lamellae of chlorophyllose parenchyma cells. These excrescences may be tipped distally with one or a row of thick-walled cells that may serve some protective function and the leaf lamina usually closes tightly around this photosynthetic areas when the plant dries. Genera of the Pottiaceae that show morphological differentiation of photosynthetic organs, *Aloina*,

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Table 1. Comparative values of $\delta^{13}\text{C}$, δD , and carbon and hydrogen content (% of organic dry matter) in nine taxa of arid zone Pottiaceae from the southwestern United States and Mexico

Species	Locality	$\delta^{13}\text{C}$ (‰)	δD (‰)	C	H
<i>Desmatodon convolutus</i> (Brid.) Grout	Maricopa Co., Arizona ^a	-26.02	-92.1	47.7	6.43
<i>Hymenostylium recurvirostrum</i> (Hedw.) Dix.	Coconino Co., Arizona ^b	-29.03	-114.2	48.3	5.17
<i>Leptodontium flexifolium</i> (Dicks. ex With.) Hampe in Lindb.	Oaxaca, Mexico ^c	-21.26	-110.08	49.6	5.45
<i>Leptodontium viticulosoides</i> (P. Beauv.) Wijk and Marg.	Durango, Mexico ^d	-25.67	-122.0	48.5	5.92
<i>Pleurochaete luteola</i> (Besch.) Ther.	Nuevo Leon, Mexico ^c	-27.68	-106.7	49.0	5.68
<i>Tortula bartramii</i> Steere	Hidalgo, Mexico ^f	-23.59	-104.7	49.0	5.54
<i>Tortula ruralis</i> (Hedw.) Garth	Gila Co., Arizona ^g	-26.40	-116.2	50.2	6.00
<i>Trichostomopsis australasiae</i> (Hook. and Grev.) Robins.	Mexico, Mexico ^h	-24.44	-106.1	48.2	5.22
<i>Weissia controversa</i> Hedw.	Gila Co., Arizona ^g	-29.56	-95.1	49.9	5.38

^a ca. 33° 30' N 112° 03' W

^b ca. 34° 50' N 111° 40' W

^c ca. 17° 10' N 96° 40' W

^d ca. 23° 40' N 105° 45' W

^e ca. 24° 40' N 100° W

^f ca. 20° 50' N 99° 15' W

^g ca. 34° 15' N 111° 20' W

^h ca. 19° 09' N 99° 50' W

Aloinella, *Crossidium* (Delgadillo, 1975), *Desmatodon* p.p., *Pseudocrossidium*, *Pterygoneurum*, *Tortula* p.p., are all characteristic of arid or otherwise harsh regions. Two species of *Barbula*, *B. aurea* (Bartr.) Zander (= *Tortula aurea* Bartr.) of southwestern United States and Mexico and *B. replicata* Tayl. (= *B. spiralis* Schimp. ex C. Muell.) of the Latin American cordillera, and one species of *Tortula*, *T. velenovsky* Schiffn. of central European mountainous regions, have marginal leaf cells that are extremely thin-walled, hollow-papillose and chlorophyll-rich. These marginal cells are within and protected by the tightly and highly revolute upper leaf margins. Exposed laminal cells are often thick-walled. Certain species of *Pseudocrossidium* of the Andes have both leaf marginal and ventral costal cells differentiated as photosynthetic organs. In some species of *Desmatodon*, *Tortula* and *Barbula* the ventral costal parenchyma cells form a thick chlorophyllose pad several cells in height.

Although no anatomical features corresponding to Kranz morphology are present in the Pottiaceae, the structure of leaf costa is usually complex. The costa may include one or two stereid bands (probably functioning as support cells), large median leptoids and occasionally a hydroid leaf strand, with ventral and/or dorsal layers of superficial parenchyma. The nature of these structures has been widely used as taxonomic characters in this group.

Carbon isotope ratios for the nine taxa of arid zone Pottiaceae investigated all show $\delta^{13}\text{C}$ values typical of normal C_3 plants (Table 1). Carbon isotope ratios for the European bryophytes are in a general very similar; only a few species have very low $\delta^{13}\text{C}$ values. This may be caused by a high lipid content of these species, since the lipid fraction is especially poor in ^{13}C (Park and Epstein,

1961; Smith and Epstein, 1970). *Fontinalis antipyretica* is known to contain larger amounts of lipids (Boresch, 1920). The other taxa with $\delta^{13}\text{C}$ values more negative than -30‰ (*Scapania undulata*, *Scorpidium scorpioides*, *Drepanocladus intermedius*) are, to our knowledge, not analyzed for their lipid content.

We know of only two other reports of $\delta^{13}\text{C}$ values in bryophytes in the literature, both showing C_3 values too. Troughton (1971) reported ratios of -31.4‰ for "mosses" and -32.3‰ for "liverwort", while Smith and Epstein (1971) reported -26.0‰ for *Sphagnum magellanicum* Brid.

The δD values of the organic dry substance in plants are influenced by many exogenous and endogenous variables (cf. Ziegler, 1979). One of the most important of the exogenous factors is the D-content of the precipitation or soil water respectively. In general this D-content increases with increasing aridity of a region. This is reflected clearly in our values (Table 2; Fig. 1). The δD value in the arid zone mosses is on average less negative than in the more humid central Europe and much less negative than in the very humid Kola-Peninsula. In *Aulacomnium palustre* this difference is shown in the two localities for this species.

It is apparent that the species with very low $\delta^{13}\text{C}$ values also have exceptionally low δD values in comparison with other species from the same biotope. This may again be caused by a high lipid content (cf. Smith and Epstein, 1970).

Since C_4 metabolism does not appear to be present in arid zone mosses, other morphological, physiological and biochemical strategies of adaptation to environmental stresses of heat and desiccation must be present. Morphological features of mosses that may be inferred as possible adaptations to periodic drying

Table 2. Comparative values of $\delta^{13}\text{C}$, δD and carbon and hydrogen content (% of organic dry matter) in humid zone bryophytes from West Germany, Austria and the USSR

Species	Family	Site	$\delta^{13}\text{C}$ (‰)	δD (‰)	C (%)	H (%)
<i>Hepaticae</i>						
<i>Saccobasis polita</i> (Nees) Buch	Epigoniaceae	Kola-Peninsula, USSR ^a	-22.69	-161.1	48.7	5.61
<i>Gymnomitrium obtusum</i> (Lindb.) Pears.	Marsupellaceae	Rhön, W. Germany ^b (Meissner)	-24.04	-114.4	51.0	5.78
<i>Scapania undulata</i> (L.) Dum.	Scapaniaceae	Kola-Peninsula, USSR	-37.26	-190.3	50.2	5.65
<i>Harpanthus flotovianus</i> (Nees) Nees	Harpanthaceae	Kola-Peninsula, USSR	-23.10	-147.5	47.7	5.42
<i>Musci</i>						
<i>Andreaea rupestris</i> Hedw.	Andreaeaceae	München, W. Germany ^c München, W. Germany	-22.34 -22.54	-144.5 -123.2	49.8 50.2	5.71 5.76
<i>Sphagnum palustre</i> L.	Sphagnaceae	Osterseen, W. Germany ^d	-28.38	-116.6	47.4	5.36
<i>Dicranella cerviculata</i> (Hedw.) Schimper	Dicranaceae	Rhön, W. Germany	-26.43	-102.7	52.4	5.75
<i>Paraleucobryum longifolium</i> (Hedw.) Loeske	Dicranaceae	Rhön, W. Germany	-26.83	-92.0	49.0	5.56
<i>Racomitrium canescens</i> (Timm) Brid.	Grimmiaceae	Pfälzer Wald, W. Germany ^e SW of Kaiserslautern	-27.62	-126.9	50.2	5.92
<i>Racomitrium heterostichum</i> Brid.	Grimmiaceae	Niedere Tauern, Austria ^f Moaralm, ca. 1,350 m	-24.02	-128.5	54.1	6.42
<i>Racomitrium lanuginosum</i> (Hedw.) Brid.	Grimmiaceae	Rhön, W. Germany Rhön, W. Germany Niedere Tauern, Austria Maralmsee, ca. 1,800 m	-23.03 -23.57 -23.23	-119.3 -120.5 -124.5	49.7 49.0 50.4	5.51 5.59 6.02
<i>Racomitrium ramulosum</i> Lindb.	Grimmiaceae	Petrosavodsk ^g (Karelia), USSR	-24.88	-137.8	50.5	5.77
<i>Bryum pseudotriquetrum</i> (Hedw.) Schwaegr.	Bryaceae	Kola-Peninsula, USSR	-28.62	-159.4	50.2	5.70
<i>Mnium pseudopunctatum</i> Bruch and Schimp.	Mniaceae	Kola-Peninsula, USSR	-22.4	-	43.2	-
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	Aulacomniaceae	Osterseen, W. Germany Kola-Peninsula, USSR	-28.73 -26.0	-114.2 -156.8	50.1 48.5	5.51 5.25
<i>Climacium dendroides</i> (Dill. ap. L.) Weber and Mohr	Climaciaceae	Osterseen, W. Germany	-29.82	-119.3	49.7	5.68
<i>Fontinalis antipyretica</i> Hedw.	Fontinalaceae	Osterseen, W. Germany Schwarzach, W. Germany ^h Pfreimd, W. Germany ^h Grünau, W. Germany	-37.49 -37.28 -36.04 -27.46	-125.7 -158.6 -151.8 -101.3	47.1 51.3 52.3 49.2	5.95 6.05 6.49 5.49
<i>Homalia trichomanoides</i> (Schreber) B.S.G.	Neckeraceae					
<i>Acrocladium cuspidatum</i> (L.) Lindb.	Amblystegiaceae	Osterseen, W. Germany	-28.78	-114.2	49.1	5.58
<i>Calliergon cordifolium</i> (Hedw.) Kindb.	Amblystegiaceae	Kola-Peninsula, USSR	-25.47	-152.6	49.6	5.53
<i>Campylium protensum</i> (Brid.) Kindb.	Amblystegiaceae	Kola-Peninsula, USSR	-23.61	-145.1	48.8	5.64
<i>Cratoneurum commutatum</i> (Hedw.) Roth	Amblystegiaceae	Kola-Peninsula, USSR	-26.45	-152.9	50.4	5.47
<i>Drepanocladus intermedius</i> (Lindb.) Warnst.	Amblystegiaceae	Kola-Peninsula, USSR	-30.30	-149.0	50.4	5.55
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	Amblystegiaceae	Kola-Peninsula, USSR	-34.77	-181.4	49.2	5.47

^a The locality was a bog near the Khibiny Mountains, ca. 67° 36' N lat.; 37° 40' E long. The δD value of the water in the bog was -98.1‰

^b ca. 51° 48' N; 10° 30' E

^c 48° 09' N; 11° 34' E

^d ca. 47° 48' N; 11° 18' E. The δD value of the water was -74.4‰

^e ca. 49° 24' N; 7° 38' E

^f ca. 47° 17' N; 13° 30' E

^g ca. 62° N; 34° 30' E

^h ca. 49° 32' N; 12° 10' E

of the habitat were listed by Watson (1913). Many of these features are present in the Pottiaceae, for which gametophyte characteristics include: cushion-forming habit; leaves that may be long-pointed, with hyaline hairs or apices; margins that are incurved, revolute, bordered by thick-walled cells; cucullate apices; imbricate leaves on drying, appressed and twisted; small and papillose leaf cells, often with collenchymatous walls; thickened costa, bearing lamellae or filaments; inflated and thin-walled basal cells; asexual reproductive bodies present; and cortex of cells with thickened walls in stem. Patterson (1964), however, in a review of experimental evidence, concluded that physiological responses, including variation in tolerance to desiccation and in compensation point, are most important in determining range of possible habitat. The morphological features associated with xerophily were considered by him to be of little significance in this regard.

Although data are very limited, physiological adaptations in desert mosses do not appear to be unusual. Rundel and Lange (1979) have shown that desert moss compensation points for light and moisture are similar to those of taxa from other habitats. They also demonstrated for *Barbula aurea* that wetting with liquid water was necessary to provide significant levels of net CO₂ uptake to occur. Unlike desert lichens, water vapor uptake from a saturated atmosphere will not raise thallus water content much beyond the moisture compensation point. Conservation of polyribosomes during total desiccation and their subsequent reactivation are biochemical adaptations in arid zone mosses (Bewley 1972, 1973a, b) that may provide the single most significant aspect of their survival in these regions.

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