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2 authors:

R. Kelman Wieder
Villanova University

Gerald E. Lang
West Virginia University

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Author(s): R. Kelman Wieder and Gerald E. Lang
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Net Primary Production of the Dominant Bryophytes in a *Sphagnum*-Dominated Wetland in West Virginia

R. Kelman Wieder and Gerald E. Lang
Biology Department, West Virginia University, Morgantown, WV 26506

Abstract. *Measurements of annual net primary production of* Sphagnum magellanicum *Brid.,* Sphagnum recurvum *P.-Beauv., and* Polytrichum commune *Hedw. were 5.4, 6.1, and 7.9 g dry mass* dm^{-2}*, respectively, at Big Run Bog—a wetland in the unglaciated Appalachian Plateau of West Virginia. Production values for these three species were greater than other reported values in the literature. A general increase in annual production of* Sphagnum *spp. with decreasing latitude was documented. This trend is contrary to the progressive declines in the depths and sizes of inland peat deposits with decreasing latitude, suggesting that annual production is less important than annual decomposition in determining peat accumulation.*

About 80 percent of the peat deposits within the United States lie roughly in the area north of 41°N latitude and east of 97°E longitude (Sheridan 1963). This area has, for the most part, been glaciated. Wetland areas with notable accumulations of peat also occur in the unglaciated portion of the Appalachian Mountains, and, along a north to south gradient these peat deposits become fewer, thinner and more highly decomposed (Cameron 1968). The vegetation of several of these small mountain wetlands has been described (Darlington 1943; Rigg & Strausbaugh 1949; Robinette 1964; Gibson 1970; Edens 1973; Fortney 1975; Wieder et al. 1981; Walbridge 1982; Walbridge & Lang 1982) and several species with decidedly boreal distributions are present. However, in contrast to the vast amount of information available on northern peatlands, relatively little is known about the functional attributes of these smaller mountain wetland systems. Of particular importance is the balance between annual net primary production and annual decomposition, which ultimately regulates the accumulation and maintenance of peat in a wetland, regardless of geographic location. Here we report data on the production of one component of the vegetation, the dominant bryophytes, in Big Run Bog—a wetland in the unglaciated Appalachian Plateau of West Virginia.

Study Site and Methods

Big Run Bog (39°07′N, 79°35′W) is a 15 ha *Sphagnum*-dominated wetland located at an elevation of 980 m above sea level within a 280 ha forested watershed of mixed coniferous-deciduous species composition in the Monongahela National Forest. Climatological conditions are estimated from data collected at a national weather station at 991 m in elevation in Canaan Valley, West Virginia, about 15 km west of Big Run Bog. Based on 34 years of observation, mean annual temperature is 7.9°C, with a maximum monthly mean of 18.3°C in July. Mean monthly temperatures are below 0°C during December, January and February. Mean annual precipitation is 133 cm and is fairly well distributed throughout the year, with an average maximum of 12.7 cm in June and an average minimum of 9.0 cm in November. The average number of days between 0°C (32°F) frosts is 97, from 2 June through 7 September, and the average number of days between −2.2°C (28°F) frosts is 130, from 15 May through 22 September.

The vegetation of Big Run Bog has been described by Wieder, McCormick and Lang (1981) and

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by Walbridge (1982). Species of *Sphagnum,* including *S. recurvum* P.-Beauv., *S. magellanicum* Brid., *S. papillosum* Lindb., *S. imbricatum* Hornsch. ex Russ., *S. girgensohnii* Russ., and *S. subsecundum* Nees ex Sturm, cover about 58 percent of the surface of the entire wetland, and species of *Polytrichum,* including *P. commune* Hedw., *P. ohioense* Ren. & Card., and *P. juniperinum* Hedw. cover about 27 percent of the wetland (nomenclature follows Crum 1973). Several distinct plant communities have been characterized at Big Run Bog, and two were selected for measurement of bryophyte production.

Net production of *Sphagnum magellanicum* and *S. recurvum*[1] was measured in the *Sphagnum-Eriophorum virginicum* community described by Wieder, McCormick and Lang (1981). *Sphagnum* spp. cover 94 percent of this community compared to only 5.5 percent for *Polytrichum* spp. Hummocks of *S. magellanicum* and to a lesser extent of *S. papillosum* rise above lawn areas of *S. recurvum.* Median peat depth in this community is 67 cm (n = 73), although the deepest peats within the entire wetland (225 cm) are found in this community (Wieder, unpubl. data).

Net production of *Polytrichum commune* was measured in the *Polytrichum*-shrub community described by Wieder et al. (1981). Here hummocks of *P. commune* cover about 75 percent of the surface, with hollows inhabited mainly by *S. recurvum* (about 25 percent cover). Median peat depth is 45 cm (n = 31) although peats up to 80 cm deep are found.

Net production of the two species of *Sphagnum* was measured using the capitulum correction technique (Clymo 1970). On 27 May 1981, 200 individual plants of each species were collected from pure stands in the *Sphagnum-Eriophorum* community. Each plant was cut to a length of 5 cm, individually marked by loosely tying a string around the stem, and replanted in the *Sphagnum-Eriophorum* community. Specifically, *S. magellanicum* plants were replanted on hummocks that rose about 15–20 cm above the surrounding hollows. *Sphagnum magellanicum* formed a complete cover on these hummocks, and a few *Rubus hispidus* runners trailed over the moss surface. *Sphagnum recurvum* plants were replanted in a lawn area that was essentially a pure stand of *S. recurvum*; few individuals of other herbaceous species were present. Individual plants were replanted about 5–10 cm apart from each other, with their capitula at approximately the same level as their immediate neighbors. At no time during the course of the study was it possible to visually distinguish planted individuals from their surrounding neighbors, suggesting that the stress of cutting plants to 5 cm lengths and transplanting was minimal.

Concomitant with the collection of plants for cutting, marking, and transplanting in the field, 50 individual plants of each *Sphagnum* species were returned to the laboratory to determine the empirical relationship between the mass of the dried capitulum (top 1 cm of plant) and the mass of the 3-cm length of dried stem (without branches or leaves) directly below the capitulum (Table 1). Plants were dried for 24 h at 70°C before weighing to the nearest microgram on a Mettler M5 Micro Balance. At approximate monthly intervals from 1 July through 9 November, 20 randomly chosen plants of each species were collected. For each plant, growth in length was measured and net primary production was determined by correcting the mass of the dried plants for the initial capitulum estimated using the relationships in Table 1 (cf. Clymo 1970). On 9 November, only seven *S. recurvum* plants were collected because the lower sections of stem to which the strings had initially been tied had begun to decompose thereby preventing the identification of the marked individuals.

The growth in length of individual *P. commune* plants is indicative of the current year's production, and can be visually identified by changes in leaf density along the stems (Watson 1975; Callaghan et al. 1978). Therefore, at each sampling date, current year's growth was clipped from 20 randomly selected individual plants on each of five hummocks in the *Polytrichum*-shrub community and net production per plant was determined.

For each species, the density of plants in a pure stand was determined in five 1 dm^2 quadrats placed in areas comparable to those in which production for each species was measured. Density values for *S. magellanicum, S. recurvum,* and *P. commune* ranged from 108–143, 96–170, and 257–387 plants per dm^2, respectively. Mean values of 126, 135, and 291 plants per dm^2 for each species, respectively, were used to convert net production per plant to net production per dm^2 of 100% moss cover.

Net production and growth in length between the two *Sphagnum* species were each compared using an analysis of variance, randomized complete block design, where sampling date was the blocked effect.

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[1] *Sphagnum recurvum* taxonomy is somewhat problematical and controversial. Andrus (pers. comm.) has verified that by using Crum's (1973) key our plants would be identified as *S. recurvum*; however, using Andrus's (1980) key the same plants would be identified as *S. fallax* (Klinggr.) Klinggr. Andrus (pers. comm.) also noted that in the mountain wetlands of West Virginia within *S. recurvum* sensu lato, the species *S. recurvum* sensu stricto, *S. angustifolium, S. flexuosum,* and *S. fallax* occur.

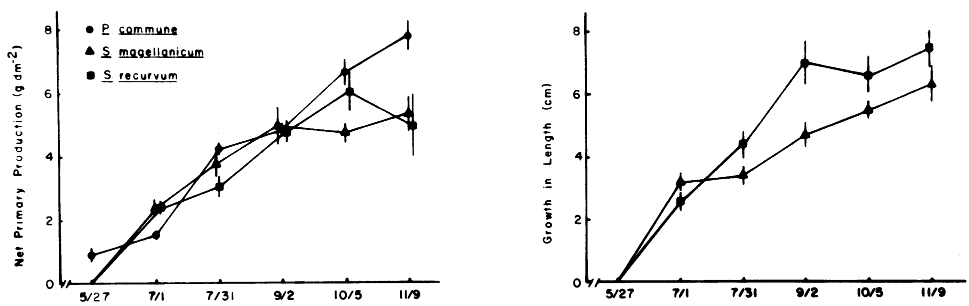

FIGURE 1. Productivity (g dry mass dm^{-2}) of *Sphagnum magellanicum, S. recurvum,* and *Polytrichum commune,* and growth in length of the two *Sphagnum* spp. at Big Run Bog. Values are means ± one standard error.

RESULTS AND DISCUSSION

Net primary production for all three species and growth in length of the two species of *Sphagnum* are shown in Figure 1. Over the course of the study, net production of the two *Sphagnum* species was not significantly different ($p = 0.85$); however, growth in length was considerably greater for *S. recurvum* than for *S. magellanicum* ($p = 0.0009$). This pattern seems to be typical for hummock and hollow dwelling *Sphagnum* species (Clymo 1970; Pedersen 1975; Pakarinen 1978). Clymo (1970) has suggested that in hollow-inhabiting species the chlorophyll is typically distributed over a greater horizontal surface than in hummock species, allowing the former to obtain relatively greater growth in length.

Most of the *Sphagnum* production occurred prior to 2 September (Fig. 1). The subsequent decline in *Sphagnum* productivity may be related to a variety of factors, including moisture, temperature, and to a lesser extent snow cover. Wieder and Lang (1982) examined the balance between precipitation and potential evapotranspiration for the Big Run Bog area and calculated regional water deficits of 6 and 35 mm for July and August 1981, respectively. Because of its low-lying topographic position on the landscape, Big Run Bog itself is less susceptible than the surrounding upland forest to variation in the regional water balance. Field observations indicate that water table levels within the wetland remained fairly constant over most of the study except during late August when an approximate 10 cm drop in the water table level was observed after a two-week period without precipitation. Individual plants of both *Sphagnum* species noticeably dried out during this period. Several studies have reported either a reduction or a cessation of *Sphagnum* productivity in response to desiccation (Overbeck & Happack 1956; Neuhausl 1976; Damman 1978). Although water table levels had returned to normal by 9 September, possible damage to individual plants from desiccation coupled with progressively declining temperatures may have precluded a vigorous resumption of *Sphagnum* productivity. Minimum daily

TABLE 1. Linear regressions of capitulum mass (y) as a function of the mass of the 3-cm length of stem directly below the capitulum (x).

Species	Regression	r^2	*p*
Sphagnum magellanicum	y = 6.554x − 0.007	0.65	0.0001
S. recurvum	y = 5.214x − 0.004	0.83	0.0001

temperatures of 0.6°C (33°F) were recorded in Canaan Valley, West Virginia on 17 and 18 August and on 10 and 18 September. Because Big Run Bog is located in a frost-pocket (cf. Hough 1945), it is likely that below-freezing temperatures also occurred on these days at Big Run Bog.

In contrast to the patterns exhibited by the *Sphagnum* species net productivity in *Polytrichum commune* continued through 9 November. The presence of water conducting tissues in *P. commune* allows individual plants to obtain water from submerged stems even during times of relatively low water table (Bayfield 1973). Skre and Oechel (1981) determined that optimal net photosynthesis in *P. commune* occurred at a water content of about 100 percent of dry mass, compared to about 725 percent for *Sphagnum subsecundum*. In addition, *P. commune* can maintain a positive CO_2 exchange at water contents as low as 45 percent (Sveinbjornsson & Oechel 1981). While the net photosynthetic rate in *P. commune* shows a strong temperature dependence, plants submerged in snowmelt water still can photosynthesize (Sveinbjornsson & Oechel 1981). In using regression equations for prediction purposes, Sveinbjornsson and Oechel (1981) assumed a complete cessation of CO_2 exchange in *P. commune* at temperatures below −2°C. Thus the continued production of *P. commune* throughout the summer and well into the autumn months may be a reflection of this species' abilities to withstand dry periods and to photosynthesize at near freezing temperature.

Snow cover was probably not a major factor in influencing productivity of any of the three species examined. Several small snowstorms were reported at Canaan Valley in October and early November, but continuous snow cover did not become established until late November.

The maximum production values obtained by *S. magellanicum, S. recurvum* and *P. commune* in Figure 1 are taken to represent the annual net primary production for each species. In using these values, we are assuming that minimal productivity occurred prior to 27 May or after 9 November. For *P. commune,* the data indicate that about 12 percent of the annual net production occurred prior to 27 May, suggesting that some *Sphagnum* production may have also occurred prior to the initiation of the study. It is likely that after 9 November, productivity of all three species was relatively insignificant because of the cold temperatures and constant snow cover. Thus, our values of annual net primary production may be slight underestimates. Other values of *Sphagnum* and *Polytrichum* production in Table 2 represent the annual net production of a potentially pure stand of each particular species, such that those studies that measured production in mixed species stands have been corrected by percent cover values provided by the authors. Therefore, all of the values in Table 2 are directly comparable. Because the amount of data available on *Sphagnum* production is considerably greater than that available for *Polytrichum* production, the ensuing discussion of Table 2 focuses mainly on *Sphagnum.*

It is apparent from Table 2 that considerable variation exists in the estimates of production. Some of the sources of variation are relatively obvious including the fact that individual species may have characteristically different growth rates and that estimates of net production may vary depending on the method of measurement (Clymo 1970). In addition, a particular species may exhibit quite different amounts of production when placed in different habitats, i.e., hummocks vs. lawns vs. mud bottoms (Clymo 1970; Clymo & Reddaway 1971), or under different nutrient conditions (Clymo 1973). Pakarinen (1978) notes that even within small geographic areas variability in production can result from a variety of factors including distance to water table, degree of dwarf shrub cover, presence of lichens or hepatics, occasional trampling by birds or moose, depth and duration of snow cover, and degree of exposure to wind and solar radiation. Nonetheless, the four

TABLE 2. Comparison of annual net production values for *Sphagnum* and *Polytrichum*.

Species	Latitude	Net production g dm^{-2} yr^{-1}	Reference
Sphagnum balticum	68°22′N	1.7	Rosswall et al. 1975
S. fuscum		0.7	
S. fuscum	63°09′N	2.5	Silvola & Hanski 1979
S. balticum/majus	60–62°N	2.1–4.1	Pakarinen 1978
S. fuscum		0.7–3.3	
S. cuspidatum	58°50′N	2.6	Pedersen 1975
S. fallax		5.0	
S. magellanicum		0.7	
S. papillosum		0.7–1.6	
S. pulchrum		3.0–3.5	
S. fuscum	56°05′N	0.9	Damman 1978
S. magellanicum		1.0	
S. magellanicum	55°09′N	0.5–1.0	Chapman 1965
S. papillosum		0.8–1.0	
S. cuspidatum	54°46′N	1.8–1.9	Clymo 1970[1,2]
S. papillosum		2.4–3.3	
S. recurvum		2.3–4.8	
S. rubellum		2.4	
S. recurvum	54°46′N	2.1–3.5	Clymo & Reddaway 1971[2]
S. rubellum		0.5–3.0	
S. papillosum		2.1–3.0	
S. rubellum	54°46′N	0.8–1.4	Clymo & Reddaway 1974[2]
S. cuspidatum	54°46′N	4.0	Forrest & Smith 1975[2]
S. magellanicum		2.3	
S. papillosum		3.0–3.9	
S. recurvum		2.4–3.3	
S. rubellum		1.6–2.4	
S. fuscum	54°28′N	2.7	Bellamy & Rieley 1967
S. cuspidatum	51°09′N	3.6	Clymo 1970[1]
S. papillosum		3.1–4.0	
S. recurvum		3.6–4.8	
S. rubellum		3.2–4.3	
S. fuscum	49°53′N	0.2	Reader & Stewart 1971
S. magellanicum	39°07′N	5.4 ± 0.5	This study
S. recurvum		6.1 ± 0.6	
Polytrichum commune	51°09′N	8.0	Clymo 1970
P. juniperinum	49°54′N	1.7	Reader & Stewart 1971
P. commune	39°07′N	7.9 ± 0.4	This study
P. alpestre	60°43′S	4.3–6.5	Collins 1976
P. alpestre	60°43′S	4.5	Fenton 1978
P. alpestre	54°17′S	4.5–5.1	Longton 1970
	60°43′S	3.4	
	65°15′S	3.8–4.2	

[1] Hummock and hollow areas only; pool areas excluded.
[2] Study conducted at the Moor House National Nature Reserve.

studies carried out at the Moor House National Nature Reserve in different years and using different methods provided reasonably consistent estimates of net production for a given species of *Sphagnum* (Table 2), suggesting that variability at a particular site may be considerably less than the total variability exhibited across all sites in Table 2.

In discussing the influence of climate on the geographic patterns of peatland development in eastern North America, Damman (1979) presents arguments to suggest that *Sphagnum* production should increase along a gradient from continental to maritime climates and along a gradient from northern to southern latitudes. Pakarinen's (1978) data for growth in length support this trend in production along the continental to maritime gradient, although his actual production data do not show this trend. Our values for *Sphagnum* and *Polytrichum* production are generally greater than the other values in Table 2, which are listed in order of decreasing latitude. Moreover, regardless of species, the genus *Sphagnum* shows a trend of increasing production with decreasing latitude that is significant ($p = 0.003$, Daniels Test for Trend, midpoints were used for production values expressed as ranges, Conover 1980). Admittedly the *Sphagnum* species composition of the sites along this latitudinal gradient is quite variable. However, given that most studies examine the production of the dominant bryophytes at a particular site, it appears that the overall production of the dominant *Sphagnum* species increases with decreasing latitude. This trend is supported by production values for individual species, e.g., *S. magellanicum* and *S. recurvum,* albeit the sample sizes are small. Although Damman's (1979) arguments focused on the peatlands north of about 45°N latitude, we suggest that the trend of increasing *Sphagnum* production with decreasing latitude may prevail over a much wider geographic range.

Sphagnum-dominated wetlands and associated peat deposits occur throughout the Appalachian Mountains. Despite a general increase in *Sphagnum* production with decreasing latitude, these peat deposits become progressively fewer, thinner and more highly decomposed. These apparently opposing trends lend support to another of Damman's (1979) contentions—that the latitudinal effect on decomposition may be stronger than the effect on production.

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