Oecologia (1989) 80:256–262

Oecologia

Limitations on *Sphagnum* growth and net primary production in the foothills of the Philip Smith Mountains, Alaska

K.J. Murray[1], J.D. Tenhunen[1], and J. Kummerow[2]

[1] Systems Ecology Research Group, San Diego State University, San Diego, CA 92182, USA
[2] Biology Department, San Diego State University, San Diego, CA 92182, USA

Summary. In the foothills of the Philip Smith Mountains, Brooks Range, Alaska, tussock tundra occurs on rolling hills and in valleys that were shaped by Pleistocene glaciations. During the 1986 and 1987 summer seasons, *Sphagnum* growth and production were determined in "water tracks" on tundra slopes that acted to channel water flow to the valley bottom stream and in "intertrack tundra" areas that were relatively homogeneous with respect to downslope drainage. Measurements were made under ambient environmental conditions and on mosses receiving supplemental irrigation in each area. Growth rate for *Sphagnum* spp. (cm shoot length increase/day) was low and relatively constant in intertrack tundra and highest but quite variable in water tracks. A strong negative correlation was found between *Sphagnum* spp. growth rate and solar irradiance in the shady environment below *Salix* canopies in the water tracks. Estimates of net annual dry weight (DW) production for *Sphagnum* spp. ranged from 0.10 g DW dm^{-2} yr^{-1} in intertrack tundra vegetation to 1.64 g DW dm^{-2} yr^{-1} in well-shaded water tracks. Experimental water additions had little effect on growth and production in intertrack tundra and well-developed water tracks, but significantly increased growth in a weakly-developed water track community. Low production over large areas of tundra slopes may occur due to presence of slow growing species resistant to dessication in intertrack tundra as opposed to rapidly growing less compact species within the limited extent of water tracks. We hypothesize that species capable of rapid growth occur also in weakly-developed water tracks, and that these are water-limited more often than plants occurring in well-developed water track situations. Where experienced, high light intensity may additionally limit growth due to photoinhibition.

Key words: Tussock tundra – *Sphagnum* – Growth – Tundra

The North Slope of Alaska has been described in terms of three distinct physiographic provinces having unique topographical and biological characteristics: the Coastal Plain, the Foothills, and the Brooks Range (Steere 1978; see Fig. 1). The Foothills Province is floristically most diverse, with 90% of the known vascular plant flora of the Arctic Slope occurring there. Bryophyte species richness is lowest on the Coastal Plain, greatest in the Foothills Province, and intermediate in the Brooks Range.

The Coastal Plain is a region of low relief with relatively high water availability, low mean temperatures, and cloudy weather conditions during most of the summer. Average mid-season moss biomass for the coastal tundra at Barrow is 1.77 g DW dm^{-2}, with highest values in *Carex-Poa* meadows and lowest values in *Salix*-heath vegetation. Average annual net productivity of bryophytes for the coastal tundra at Barrow was estimated from simulation models at 0.66 g DW dm^{-2} yr^{-1}, but with considerable variation depending on vegetation type, ranging from 0.11 to 1.37 g DW dm^{-2} yr^{-1} in *Dupontia* and *Carex-Poa* meadows, respectively (Miller et al. 1980).

Compared with the Coastal Plain, the Foothills Province is a region of moderate topographic relief, greater temporal and spatial variation in water availability, higher average summer temperatures, and increased evapotranspiration. Moderate to well-developed small-scale drainage patterns characterize hillslopes in the Foothills Province. These drainage paths termed water tracks are dominated by a wet *Salix pulchra* – *Eriophorum angustifolium* low shrub, sedge community, and are typically separated by areas of moist, *Eriophorum vaginatum* – *Ledum* spp. dwarf shrub tundra (Walker et al. 1989). These vegetation units occupy 3% and 71% respectively of the current research area (Walker et al. 1989) and are found predominantly on west facing slopes with moderately deep (6–20 cm) winter snow accumulation (Evans et al. 1989).

Bryophytes are very abundant in tussock tundra habitats of the Foothills Province, and contribute significantly to total community aboveground biomass. Moss cover and biomass decrease in dry or disturbed areas such as upslope fellfields or frost boils. Most studies of the ecology of Alaskan arctic bryophytes have been conducted in the Coastal Province near Barrow. Differences in climate and topography between the Coastal and Foothills Provinces may be expected to change the relative importance of environmental factors limiting moss growth and production. This study examines controls on the growth and production of *Sphagnum* spp. within tussock tundra of the foothills of the Philip Smith Mountains. The sensitivity of growth to seasonal variation in water availability, temperature and solar irradiance was investigated. Supplemental irrigation treatments provided additional information on the effects of periodic water availability and periodic supply of nutrients due to rainfall fluctuations.

Offprint requests to: J.D. Tenhunen

Materials and methods

Site description and irrigation system

Field studies were conducted adjacent to Material Site 117 (MS 117) on the Dalton Highway (68 degrees 38 min N, 149 degrees 22 min W) at ca. 900 m elevation. This is a region of moderate relief characterized by generally south to north trending drainage systems separated by rounded interfluves. The primary study site is located approximately 20 km north of the Brooks Range in the upper watersheds of Imnavait Creek and the Toolik River (Fig. 1). Growth measurements were conducted both in the Toolik River watershed (WTC), and in the Imnavait Creek watershed (IT, WT 1, WT 3). Water supplementation was carried out in the Imnavait Creek watershed only.

During the summer months, precipitation is often the result of brief but intense convective storms (Figs. 3 and 4). Relatively long drought periods can occur as was experienced during the 1986 and 1987 summer seasons. Summer temperatures are mild. Daily mean air temperatures ranged from 0 to 20° C during the study (Figs. 3 and 4).

Sphagnum mosses occupy a wide spectrum of habitats at the study site, from submerged sites in valley bottom streams, throughout the hillslope vegetation, and to the perimeter of up-slope frost boil/fell-field sites. Studies reported here were restricted to vegetation types characteristic of hillslope communities in the Foothills Province (Walker et al. 1989), i.e. water tracks (WT) and intervening intertrack tundra (IT) interfluves. Water tracks are mainly ombrotrophic and dominated bryologically by *Sphagnum girgensohnii* Wils., *S. angustifolium* C. Jens., *S. squarrosum* Crome, *S. warnstorfii* Russow., *Aulacomnium palustre* Hedw., *Hylocomium splendens* Hedw., and *Polytrichum* spp. In intertrack tundra, *Sphagnum fuscum* Klinggr., *S. rubellum*, and *S. warnstorfii* Russow. were prevalent in association with *Aulacomnium turgidum* Schwaegr., *Hylocomium splendens* Hedw., and *Dicranum elongatum* Schleich. On a ground surface area basis, cover values for *Sphagnum* in these selected habitats varied considerably (Table 1).

An irrigation system was used to pump water (250 l min^{-1}) approx. 55 m above Imnavait Creek to a water storage reservoir (70000 l capacity). Irrigation water was applied to the treatment plots by gravity feed (approximately 20 liter hr^{-1} per linear meter in 1986 and 5 l hr^{-1} per linear meter in 1987) from a drip irrigation line located along the upslope perimeter of the plots. The length of irrigation line parallel to the slope contours was approximately 15 m in each plot. Irrigation was begun on June 18 and water was applied continuously and at a constant rate through August 16 in 1986, and from June 8 until July 28 in 1987. The water drained downslope through the active layer above the permafrost. Due to irregularities of the frozen sub-surface (cf. Murray et al. 1989), it is not possible to determine the area over which the added water spreads. The application resulted in standing water in depressions between *Sphagnum* hummocks that was similar in extent and magnitude to that observed after moderate rain events. Nutrient concentrations in the stream water added in irrigation treatments are reported by Everett et al. (1989).

Sphagnum growth measurements

Growth (cm shoot extension) of *Sphagnum* mosses was measured by the "cranked wire" method (Clymo 1970) at approximately 8 day intervals during the period June 23 to August 15, 1986, and June 23 to August 13, 1987. Wires were firmly embedded in the moss cushions which averaged 10 cm in depth to the base of the brown moss layer. Elongation was measured relative to the cranked-wire reference point to the nearest 0.1 cm.

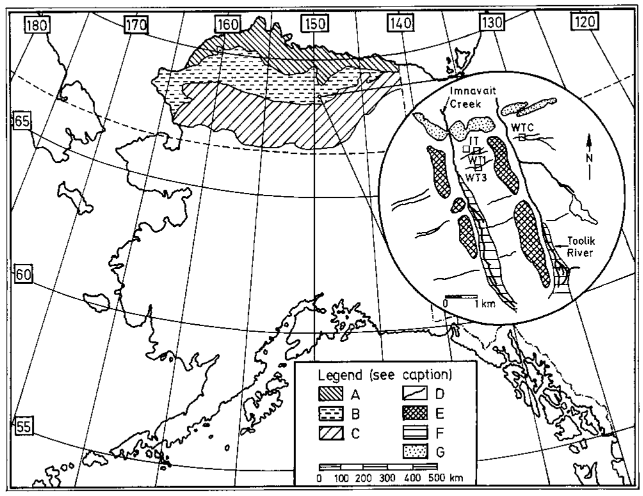

Fig. 1. The Philip Smith Mountains study site with respect to three physiographic provinces of Northern Alaska. A = Coastal Province. B = Foothills Providence. C = Brooks Range. Detailed inset shows location of intertrack tundra (*IT*) and water track (*WT*) moss production study plots in the paired watersheds of Imnavait Creek and the Toolik River. Major vegetation types of the study site include: D: tussock shrub tundra with west facing water tracks, E: *Cassiope* dwarf shrub tundra, F: wet sedge meadows (basin colluvium). G: sedimentary bedrock outcrops shown north of study site. Detailed description of the vegetation is reported by Walker et al. 1989

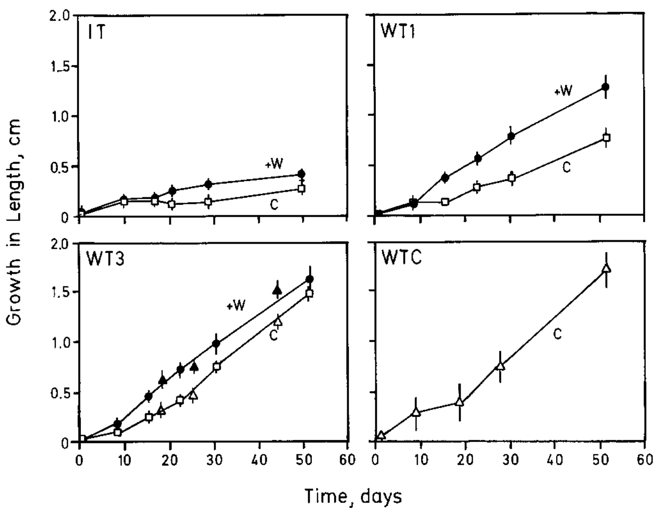

Fig. 2. Seasonal course of total elongation of new shoots of *Sphagnum* spp. during the measurement period of 23 June to 15 August. Data illustrate growth in length under ambient (C – *open squares* and *triangles*) and irrigated (+W – solid squares and triangles) conditions in intertrack tundra (IT) and water tracks 1 and 3 (WT 1 and WT 3). Data are from 1986 (*squares*) and 1987 (*triangles*). Bars indicate standard errors of the mean

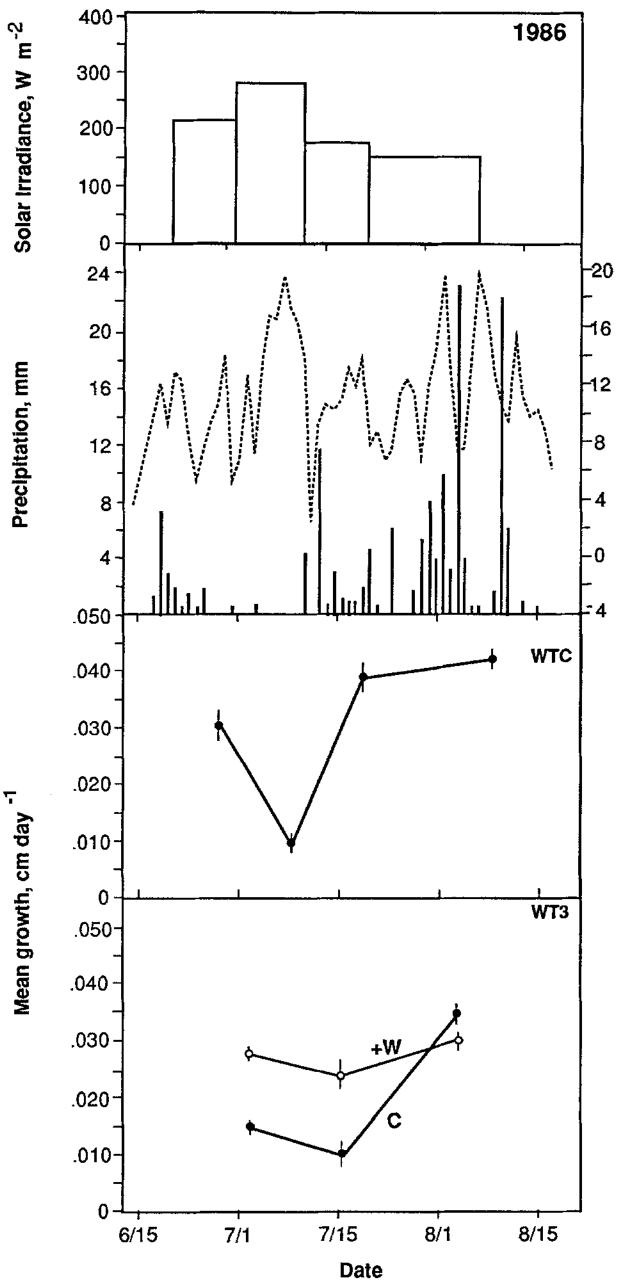

Fig. 3. Variation in mean *Sphagnum* growth rate (cm/day) observed during different periods of the 1986 season. Mean growth rates are indicated with symbols plotted at the end of each measurement period (see text) in control plots (C) and irrigated plots (+W). The periods of measurement are indicated by the bars in the upper box of the figure which illustrate average daily (9:00 to 21:00 h) total solar radiation input for the period. In the case of WT3, the periods of observation are different than in WTC to which the light bars correspond (see text). Vertical bars indicate standard errors of the mean. Also plotted are actual recorded daily mean temperature and daily total precipitation

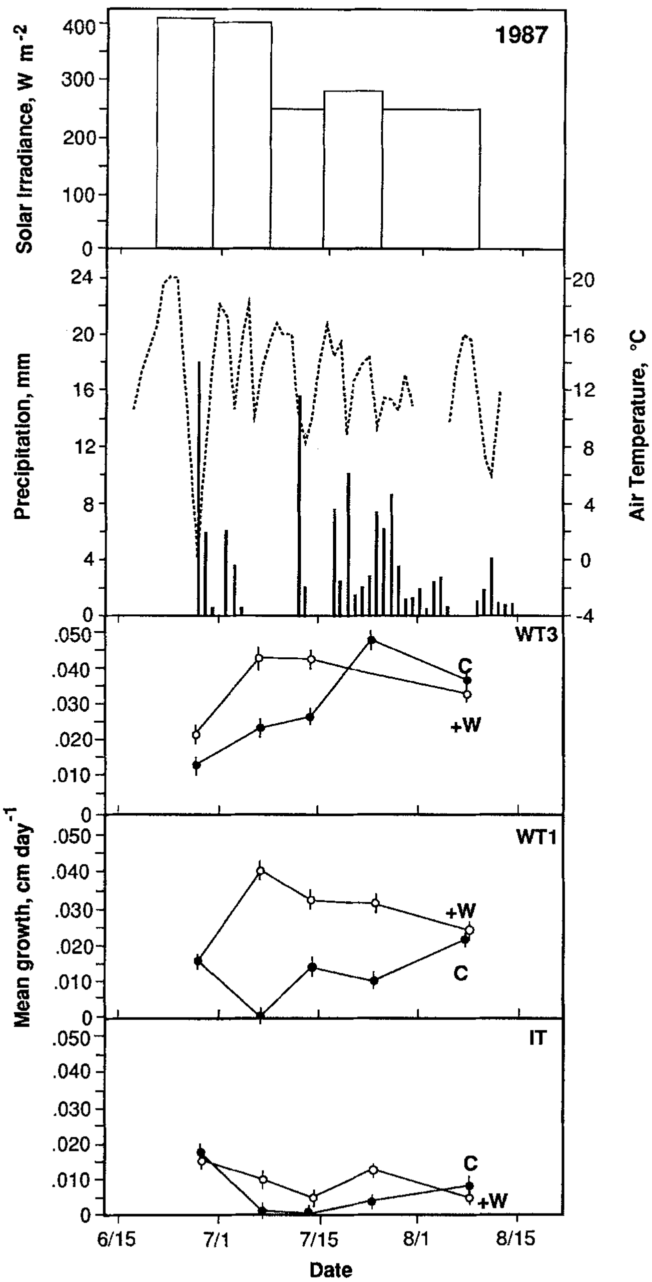

Fig. 4. Variation in mean *Sphagnum* growth rate (cm/day) observed during different periods of the 1987 season. Results presented as in Fig. 3

Control plots to determine moss growth under ambient conditions (C) in both intertrack and water track habitats were located 2 to 3 meters upslope from the areas receiving irrigation (+W). This ensured that irrigation water did not enter the controls. The species composition of both control and irrigated plots was similar. Additional plots were established to test for "slope" effects under ambient conditions, but no significant differences were found. In intertrack tundra, 30 growth wires were located in each of the three replicate control and irrigated plots. Because only two water tracks could be reached by piping from the irrigation system, 45 growth wires were located above and below the water addition line in each.

Water content of the uppermost 2 cm layer of *Sphagnum* was determined at intervals during the growing season both above and below the water addition line. The samples were collected as close to the growth wire locations as possible without disturbing those measurements. Samples were cleaned of visible vascular plant parts and other mosses, placed in plastic bags and weighed in the field within 30 min of collection. Samples were oven dried at 70° C for 36 h

Table 1. Percent cover, shoot density, and shoot mass (g) values for *Sphagnum* growing in intertrack tundra and water tracks. Location abbreviations as in the text. Estimates of net annual moss production in water tracks and intertrack tundra. All values are in g DW dm^{-2} yr^{-1} and take into account differences in moss % cover at each site. Production rates are adjusted for a 70 day growth period in each case. C = production under ambient conditions, +W = production with supplemental irrigation

Location:	IT		WT1		WT3		WTC
% cover	16.8		20.9		40.0		38.2
shoots/dm^2	346		542		542		542
mass/shoot	0.02		0.01		0.01		0.01
Treatment:	C	+W	C	+W	C	+W	C
Production estimate:							
1986					1.14	1.54	1.64
1987	0.10	0.17	0.40	0.65	1.46	1.60	

before dry weight measurements were made; water contents are expressed as g H_2O/g DW moss. The samples were dried, ground to pass a 40 mm mesh and were subjected to a Kjeldahl digest. Total N and P were determined colorimetrically using a Technicon autoanalyzer, while K was determined by flame emission spectrometry.

Correlations between *Sphagnum* growth rates and natural variations in precipitation, temperature, and solar irradiance were examined. Weather data were obtained from a meteorological station located on a ridge top approximately 150 m from the study plots. Climate data used in the correlation analysis were mean precipitation (mm day^{-1}), mean daily temperature (degrees C), and mean solar irradiance (W m^{-2} measured between 09:00 to 21:00 h calculated for time periods corresponding to consecutive growth estimates.

Annual production estimates

Total increase in shoot length measured for *Sphagnum* was used to estimate annual net production at the study locations in each vegetation type, expressed as grams dry weight per square decimeter surface area. These net production values illustrate the extreme range in production that may occur due to microclimate differences as well as due to vegetation development (species abundances). Average *Sphagnum* shoot densities appropriate for the mixture of species in each area were estimated from 32 cores (6.25 cm^2) in intertrack tundra, and 31 cores in WT3. Average mass per unit stem length (4 cm immediately below capitula) was determined from shoots taken randomly from the cores. Dry weight per unit moss area increases during the measurement period were then adjusted for the percent cover of *Sphagnum* in each vegetation type (Table 1).

Total seasonal dry weight per unit ground area estimates were adjusted for an approximate 70 day growing season. Growth is assumed to begin in late June (due to observed inactivity of photosynthesis early in the season – until approx. June 20 during 1985 – Murray et al. 1989) and to continue until the end of August. The 70 day estimate may be conservative and better studies of the seasonal course of growth and development are needed.

Results

Moss growth and production

Sphagnum growth (shoot length increase) varied at the different locations studied (Fig. 2). Total shoot elongation over the 50 day observation period was least in intertrack tundra (IT) and reached highest values in water tracks (WT), with a maximum in WTC. In 1986, total shoot length increase in WT3 was 1.02 cm and 1.75 cm in WTC (open triangles in Fig. 2). Average shoot length increase in control areas during 1987 was 0.24 cm in IT, 0.77 cm in WT1, and 1.48 cm in WT3 (open squares in Fig. 2). Average shoot length increase in irrigated plots was 1.52 cm in WT3 in 1986 (solid triangles in Fig. 2); and 0.43 cm in IT, 1.28 cm in WT1, and 1.60 cm in WT3 during 1987 (solid circles in Fig. 2).

Considering the complex of species sampled from the two habitats, average *Sphagnum* shoot densities were less in intertrack tundra than in water tracks, while the mass per unit stem length was greater in intertrack tundra than in water tracks (Table 1). Working from the growth data of Fig. 2, *Sphagnum* net seasonal production estimates on a ground surface area basis varied greatly according to vegetation type (Table 1). In 1986, production in control areas of WT3 was 1.14 g DW dm^{-2} yr^{-1} and was 1.64 g DW dm^{-2} yr^{-1} in WTC. *Sphagnum* production in control plots in 1987 ranged from 0.10 g DW dm^{-2} yr^{-1} in intertrack tundra, to 0.40 g DW dm^{-2} yr^{-1} in WT1, and 1.46 g DW dm^{-2} yr^{-1} in WT3. WT1 is a weakly defined water track with many characteristics of both vegetation units. From Table 1, simple differences in *total Sphagnum* abundance (approximately twice as abundant in well developed water tracks) are inadequate to account for the increases in production in water track areas.

Nutrient contents of *Sphagnum* from water tracks and intertrack tundra were similar. Total Kjeldahl nitrogen varied between 0.9 and 1.6% of dry weight. Phosphorus content averaged approximately 0.07% of dry weight. Potassium content was approximately 0.5% of dry weight. Irrigation resulted in a 24% and 17% increase in nitrogen and phosphorus content, respectively.

Correlations between moss growth rate and environmental variables

Figures 3 and 4 illustrate variation in mean *Sphagnum* growth rate (shoot length increase in cm/day) observed during different periods of the 1986 and 1987 seasons. These mean growth rates are indicated with symbols plotted at the end of each measurement period but are not to be interpreted as indicating rates on any particular day. This method of presentation is chosen only to permit easy comparisons of growth in control plots (C) and irrigated plots (+W). The periods over which the elongation measurements are valid are indicated by the bars in the upper box of the figure, which illustrates average daily (9:00 to 21:00 h) solar radiation input for the period. One exception to this is found in the case of WT3 in 1986 (Fig. 4). Here the periods of observation are different than in WTC to which the light bars correspond. Nevertheless, symbols are plotted at the end of each observation period. The first period was initiated on June 23, 1986. Also plotted are daily mean temperature and total precipitation.

Growth rates (cm shoot extension/day) were low early

Table 2. Correlation coefficients (r) between *Sphagnum* growth rates and environmental parameters at various sites. C = control plots, + W = plots with supplemental irrigation. Location abbreviations as in the text

	Environmental factor					
	Precipitation[a]		Temperature[b]		Solar irradiance[c]	
Treatment:	C	+W	C	+W	C	+W
Location:						
WTC	0.79	–	−0.60	–	−0.97	–
WT3	0.85	0.08	−0.65	0.18	−0.69	−0.44
WT1	0.18	−0.04	−0.80	0.42	−0.42	−0.15
IT	−0.12	0.16	−0.05	0.34	0.61	0.69

[a] Total precipitation during growth measurement interval
[b] Mean ambient air temperature during growth measurement interval
[c] Mean daily total radiation during growth measurement interval

in the season compared to the maximal extension observed, but decreased to even lower values during mid-season warm, dry periods. Growth rates were highest and most variable in shaded mesic habitats such as in WTC and WT3, and were lowest in open habitats (e.g. IT). *Sphagnum* growth rates increased below the point of slope irrigation and remained high during periods of reduced precipitation, with the largest irrigation growth response in WT1, and smallest response in intertrack tundra (IT). The irrigation response was relatively greater in WT3 in 1986 than in 1987, probably because of more frequent precipitation in 1987.

In 1986 the average moss water content above the water addition in WT3 ranged from 3 to 6.6 g H_2O/g DW during the mid-summer period (Murray et al. 1989). Due to more regular rainfall in 1987, average moss water content above the water addition in WT3 ranged from 8.6 to 9.6 g H_2O/g DW and from 11.7 to 12.6 below the irrigation treatment. During mid-summer 1987, ambient *Sphagnum* water contents in intertrack tundra ranged from 6.8 to 10.5 g H_2O/g DW above the irrigation and from 9.6 to 10.7 g H_2O/g DW in adjacent irrigated plots.

Moss growth rate data from 1986 and 1987 were analyzed with respect to variations in mean precipitation, mean temperature, and solar irradiance (Table 2) during the observation periods. Although the number of seasonal growth rate observations ($n = 5$) limits the statistical significance of the analysis, negative correlations were found between moss growth rate and solar radiation input (W/m^2) in water tracks and positive correlations were found with precipitation. Based on the current data, seasonal changes in precipitation and solar irradiance may strongly influence seasonal vaiation in moss growth in well developed water tracks (WTC and WT3), but have less influence in weakly developed tracks (WT1) and no effect in intertrack tundra.

Discussion and conclusions

Previous studies have demonstrated that high water availability, delivery of nutrients in flowing water, and maintenance of low pH are important factors supporting maximal *Sphagnum* growth (Clymo and Hayward 1982). These conditions are found in the water tracks on tussock tundra slopes and measured shoot elongation of *Sphagnum* mosses growing in the shaded water track habitat (0.8–1.8 cm/50 day measurement period) is very similar to the maximum reported for *Sphagnum* at other sites. For the water track species *Sphagnum angustifolium* growing in moist sites of a subarctic bog near Fairbanks, Alaska, Luken and Billings (1983) reported annual shoot extension of 1.12 cm/90 day. Pakarinen (1978) recorded a higher annual shoot extension of 3.2 cm/yr for *S. balticum* and *S. majus* in wet microsites of a southern Finnish bog. Forrest and Smith (1975) measured an annual shoot elongation of 1.49 cm for *S. magellanicum* growing in wet "lawn" situations in the northern Penines. The estimates for annual *Sphagnum* production on a ground surface area basis in WT3, WT3 irrigated, and WTC, along with the highest values observed for total moss production at other high latitude sites advantageous for *Sphagnum* growth (Washington Creek – taiga; Moor House – wet blanket bog), provide upper limits on the range that may be expected with high water availability (cf. Fig. 5). In terms of ecosystem function, high potential rates of *Sphagnum* production in well-developed water tracks are probably important in regulating nutrient release to the stream system and in terms of stabilizing otherwise erodable areas.

The results obtained in a weakly developed water track (WT1) suggest that the conditions associated with high *Sphagnum* production are gradually lost as the degree of channeling of water flow decreases. The level of production observed for *Sphagnum* in intertrack tundra areas is low and in striking contrast to that found in water tracks (Fig. 5). Such situations, in which *Sphagnum* production is decreased, have most often been associated with decreased water availability. For *Sphagnum* in a subarctic bog near Fairbanks, Alaska, Luken and Billings (1983) found lowest annual shoot extension (0.43 cm/90 day) in *S. fuscum*, a hummock-forming moss characteristic of the driest bog microsites (also prevalent in intertrack tundra). Pakarinen (1978) also reported annual shoot elongation of 1.15 cm/yr in *S. fuscum* from hummock tops as opposed to the high growth rates found in hollows. Decreased water availability and possibly shading were cited a causes of lowered *Sphagnum* production in several blanket bog sites at Moor House (cf. Fig. 5; Smith and Forrest 1978).

Clymo and Hayward (1982) examined the effects of variation in light climate and water availability on growth of a number of *Sphagnum* species. The following general conclusions were drawn. Species such as *S. capillifolium, S. rubellum*, and *S. papillosum* (slow-growth species) exhibited maxima in length growth that were only 25% to 50% of the maxima found for *S. recurvum* and *S. cuspidatum* under the same conditions (rapid-growth species). All species exhibited maximum growth at less than full sunlight intensity. Considerable variation in potential response to water availability were found to exist. *S. rubellum* (slow-growth species), a species common in intertrack tundra, and *S. capillifolium* showed a weak to intermediate response to higher water table, while *S. recurvum* and *S. cuspidatum* (rapid-growth species) were strongly stimulated as water table rose. Clymo and Hayward (1982) concluded that the differences in response to water table depth reflect the fact that slower growing species were also better able to control water supply to the capitula.

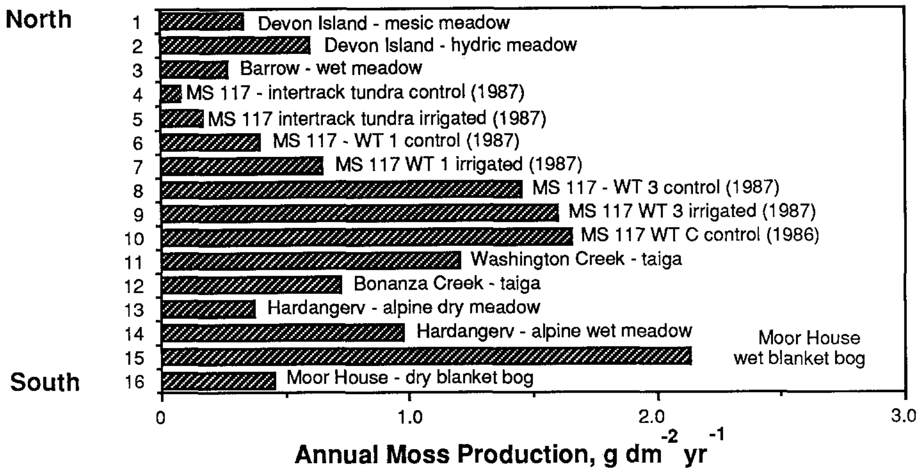

Fig. 5. Comparison of measured moss community annual production in a series of northern latitude sites including MS 117 (Table 1). Production values at Devon Island are reported by Pakarinen and Vitt (1972); at Barrow by Rastorfer (1978); at Washington Creek and Bonanza Creek by Oechel and Van Cleve (1986); at Hardangerv by Wielgolaski and Kjelvik (1973); and at Moor House by Smith and Forrest (1978)

The decreased rates of *Sphagnum* production observed in intertrack tundra are not accounted for by decreased total abundance (compare Fig. 5 and Table 1). While water availability is a limitation, the results obtained with irrigation demonstrate that other factors must be responsible for the large production differences between intertrack tundra, the weakly developed water track 1, and well-developed water track 3. Decreased growth ability observed in intertrack areas suggest that this habitat is occupied by slow-growth species, that they are outcompeted (overtopped) in moist situations such as under *Salix* canopies in water tracks, but that they have the ability to survive in the open intertrack tundra. Conversely, large fluctuations in elongation growth of *Sphagnum* that occur in water tracks in response to natural precipitation events, suggest that these are species of the rapid-growth type which are sensitive to water table depth.

Eco-physiological studies on *Sphagnum* mosses from MS-117 water tracks (Murray et al. 1989) have indicated a reduction in photosynthetic rate at water contents below approximately 6.0 g H_2O/g DW, with little change in rate at water contents between 6.0 and 15.0 g H_2O/g DW. When average water content decreased as low as 6.0 g H_2O/g DW, many areas sampled for growth in 1986 would have considerably lower water contents. The data suggest that observed decreases in *Sphagnum* growth during mid-summer dry periods are in part due to drought effects on carbon fixation. In irrigated plots, water availability was near optimal for photosynthesis.

The largest effects of irrigation were observed in the weakly-developed water track 1. Natural water supplies may be sufficient here to ensure that "rapid-growth species" coexist with "slow-growth species". Irrigation leads to expression of high growth potentials but total production is limited due to the high presence of "slow-growing" individuals. In well-developed water tracks such as WT 3, irrigation does not affect production dramatically because the natural water supply is often sufficient to support maximum rates of growth.

Due to leaching and leaf fall from the willow canopy and to longer periods of water flow after rain events, it is likely that *Sphagnum* spp. growing in the water track habitat are better supplied with nutrients than *Sphagnum* found in open intertrack tundra. Nevertheless, growth and production in the differently vegetated areas seem not to be as strongly limited by nutrient supply as by physical environment and genetic factors. Tissue nutrient contents increased with irrigation, suggesting that greater than normal quantities were available. The additional nutrients supplied by the irrigation water (considering the total supplied over time and potential movement of materials in the irrigated area) did not lead to strong growth stimulations in either WT 3 or IT.

While the surface temperature of moss cushions in water tracks and intertrack tundra differ, measured temperature maxima remain within a broad range permitting maximal photosynthetic activity (Harley et al. 1989). Irrigation resulted in an approximate 4 degree C decrease in daily maximum temperature measured with thermocouples at 1 cm depth. Based on those physiological processes for which we have information, such temperature effects should be of minor importance.

As in the experiments of Hayward (1980), negative correlations were found here between *Sphagnum* growth rate in water track habitats and solar irradiance. It seems probable that inhibitory effects of high irradiance occur in both water tracks and intertrack tundra, with greatest variability in expression of these effects in water tracks where the vascular plant canopy significantly reduces light intensities incident on the moss. *Sphagnum squarrosum*, the most abundant bryophyte found in WTC, has been described as an exclusively shade species in studies by Horton et al. (1979) and Vitt and Andrus (1977). Reduced growth rate of *S. squarrosum* may be the result of lowered photosynthetic capacity owing to photoinhibition as has been described in other shade plants (Powles 1984).

The period of reduced growth rate corresponding to high solar input found in this study occurred before the vascular plant canopy was fully expanded. Harley et al. (1989) showed that net photosynthesis in *S. squarrosum* declined soon after the removal of all vascular plant cover, with the reduced photosynthetic capacity being paralleled by obvious chlorosis of exposed capitula. Results from the correlation analysis must be viewed with caution however, since precipitation during the sunny period was very low, and water stress may also have contributed to reduced photosynthetic capacity.

In studies attempting to correlate moss growth and habitat environmental parameters, Busby et al. (1978) suggested that high solar radiation may have had deleterious effects on growth of the feather moss *Hylocomium splendens*. These authors suggested that feather moss growth in boreal fen habitats may be limited by an interacting complex of factors including radiation damage and water stress. Our data for tundra *Sphagnum* indicate the sensitivity of these mosses to a similar complex of factors. Other workers have discussed the potential for photoinhibition in arctic and alpine environments (Caldwell et al. 1978; Oechel and Sveinbjornsson 1978; Kallio and Valanne 1975). Oechel and Sveinbjornsson stated that even though environmental factor in the Barrow area are particularly appropriate for moss growth and production, there is still a tendency for high light levels to result in reduced rates of photosynthesis, presumably through photoinhibition or photooxidation.

Low production over large areas of tundra slopes may occur due to presence of slow growing species resistant to dessication in intertrack tundra as opposed to rapidly growing less compact species within the limited extent of water tracks. We hypothesize that species capable of rapid growth occur in weakly-developed water tracks, and that these are water-limited more often than plants occurring in well-developed water track situations. Where experienced, high light intensity may additionally limit growth due to photoinhibition. Future studies must critically examine species-specific potentials and apparent adaptations expressed in the habitats described.

Acknowledgement. The research was supported by the U.S. Department of Energy OHER/ERD as part of the R4D program in arctic tussock tundra (Grant No. DE-FG03-84ER60250).

References

Busby JR, Bliss LC, Hamilton D (1978) Microclimate control of growth rates and habitats of the boreal forest mosses *Tomenthypnum nitens* and *Hylocomium splendens*. Ecol Monogr 48:95–110

Caldwell MM, Johnson DA, Fareed M (1978) Constraints on tundra productivity: Photosynthetic capacity in relation to solar radiation utilization and water stress in arctic and alpine tundras. In: Tieszen LL (ed) Vegetation and Production Ecology of an Alaskan Arctic Tundra, Springer, Berlin Heidelberg New York, pp 323–342

Clymo RS (1970) The growth of *Sphagnum*: methods of measurement. J Ecol 58:13–49

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In Smith AJE (ed) Bryophyte Ecology, Chapman and Hall, London and New York, pp 229–289

Evans BM, Walker DA, Benson CS, Nordstrand EA, Petersen GW (1989) Spatial interrelationships between terrain, snow distribution, and vegetation patterns at an arctic Foothills site in Alaska. Hol Ecol (in press)

Everett KR, Marion GM, Kane DL (1989) Seasonal geochemistry of an arctic tundra drainage basin. Hol Ecol (in press)

Forrest GI, Smith RAH (1975) The productivity of a range of blanket bog types in the northern Pennines. J Ecol 63:173–202

Harley PC, Tenhunen JT, Murray KJ, Beyers J (1989) Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia (in press)

Hayward PM (1980) Effects of Environment on the Growth of *Sphagnum*. Ph.D. Thesis, Univ. of London

Horton DG, Vitt DH, Slack NG (1979) Habitats of circumboreal-subarctic sphagna: I. A quantitative analysis and review of species in the Caribou Mountains, northern Alberta. Can J Bot 57:2283–2317

Kallio P, Valanne N (1975) On the effects of continuous light on photosynthesis in mosses. In: Wielgolaski FE (ed) Fennoscandian Tundra Ecosystem Part I. Plants and Microorganisms, Springer, Berlin Heidelberg New York, pp 149–162

Luken JO, Billings WD (1983) Changes in bryophyte production associated with a thermokarst erosion cycle in a subarctic bog. Lindbergia 9:163–168

Miller PC, Webber PJ, Oechel WC, Tieszen LL (1980) Biophysical processes and primary production. In: Brown J, Miller PC, Tieszen LL, Bunnell FL (eds) An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska, Dowden, Hutchinson and Ross, Inc., Stroudsberg, Pa, pp 66–101

Murray KJ, Harley PC, Tenhunen JT, Walz H (1989) Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia (in press)

Oechel WC, Cleve K Van (1986) The role of bryophytes in nutrient cycling in the Taiga. In: Van Cleve K, Chapin FS, Flanagan PW, Viereck LA, Dyrness CT (eds), Forest Ecosystems in the Alaskan Taiga. Springer, Berlin Heidelberg New York, pp 121–137

Oechel WC, Sveinbjornsson B (1978) Primary production processes in arctic bryophytes at Barrow, Alska. In: Tieszen LL (ed) Vegetation and Production Ecology of an Alaskan Arctic Tundra, Springer-Verlag, Berlin Heidelberg New York, pp 269–298

Pakarinen P (1978) Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. Ann Bot Fenn 15:15–26

Pakarinen P, Vitt DH (1972) The ecology of bryophytes in Truelove Lowland, Devon Island. In: Bliss LC (ed) Devon Island IBP Project. High Arctic Ecosystem, Project Report 1970 and 1971, Dept. of Botany, University of Alberta, pp 185–196

Powles SB (1984) Photoinhibition of photosynthesis induced by visible light. Ann Rev Plant Phys 35:15–44

Rastorfer JR (1978) Composition and bryomass of the moss layers of two wet-tundra-meadow communities near Barrow, Alaska. In: Tieszen LL (ed) Vegetation and Production Ecology of an Alaskan Arctic Tundra, Springer, Berlin Heidelberg New York, pp 169–181

Smith RAH, Forrest GI (1978) Field estimates of primary production. In: Heal OW, Perkins DF (eds) Production Ecology of British Moors and Montane Grasslands, Springer, Berlin Heidelberg New York, pp 17–37

Steere WC (1978) The mosses of arctic Alaska. Cramer-Ganter Verlag, Germany. pp 12–31

Vitt DH, Andrus RE (1977) The genus *Sphagnum* in Alberta. Can J Bot 55:331–357

Walker DA, Binnian E, Evans BE, Lederer ND, Nordstrand E, Webber PJ (1989) Terrain, vegetation, and landscape evolution of the R4D research site, Brooks Range Foothills, Alaska. Hol Ecol (in press)

Wielgolaski FE, Kjelvik S (1973) Production of plants (vascular plants and cryptogams) in alpine tundra, Hardangervidda. In: Bliss LC, Wielgolaski FE (eds) Primary Production and Production Processes, Tundra Biome, Edmonton-Oslo: IBP Tundra Biome Steering Committee, pp 75–86

Received May 25, 1988