

Record growth of *Sphagnum papillosum* in Georgia (Transcaucasus): rain frequency, temperature and microhabitat as key drivers in natural bogs

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SUMMARY

- (1) Peatmoss (*Sphagnum*) growth has been studied widely, in particular at temperate and boreal latitudes >45 °N, where productivity is mainly controlled by mean annual temperature and precipitation. We studied the growth of *Sphagnum papillosum* and *S. palustre* in four peatlands in the year-round warm and humid Kolkheti Lowlands (Georgia, Transcaucasus, eastern end of the Black Sea, latitude 41–42 °N).
- (2) Productivity, site conditions and climate in Kolkheti are included in a worldwide analysis of studies on the growth of *S. papillosum* to identify driving factors for its growth.
- (3) The productivity of *S. papillosum* and *S. palustre* under natural conditions is extraordinarily high in Kolkheti, reaching 269–548 g m⁻² yr⁻¹ and 387–788 g m⁻² yr⁻¹ (mean of various sites), respectively. Rates of increase in length are up to 30.3 cm yr⁻¹, with the largest values for *S. palustre*.
- (4) Rate of increase in length and biomass productivity differed between years, with better growth being explained by higher number of rain days and shorter periods without precipitation. Regular rainfall is essential for continuous *Sphagnum* growth as low water table prevents permanent water supply by capillary rise.
- (5) The analysis of international studies on *Sphagnum papillosum* productivity confirms the decisive role of rain frequency, next to microhabitat. Productivity increases further with mean temperature during growth periods, the near-largest values being for Kolkheti. As temperature is correlated with latitude, *Sphagnum* productivity may increase towards the equator if the water supply is sufficient.
- (6) Substantial *Sphagnum* growth was observed during winter, confirming year-round growth in the virtual absence of frost. Growth in lawns, rain frequency and almost optimal nutrient availability (N, P, K) were the only site conditions found to explain the high rates of *Sphagnum* growth in Kolkheti.

KEY WORDS: biomass productivity, climate, raised bog, *Sphagnum palustre*, nutrient limitation

INTRODUCTION

The growth of peatmoss species (*Sphagnum*) has been widely studied, in particular in the temperate and boreal zones of the northern hemisphere (Gunnarsson 2005). Only a few studies (e.g. Fukuta *et al.* 2012) relate to the warm temperate zones, while *Sphagnum* growth has been described as increasing towards the equator (cf. Wieder & Lang 1983).

The main climatic factors found to explain differences in growth rates are mean annual temperature (Moore 1989, Vitt 1990, Asada *et al.* 2003, Gunnarsson 2005) and precipitation (Li *et al.* 1992, Asada *et al.* 2003, Nijp *et al.* 2014), but the results of various studies differ greatly. *Sphagnum* growth varies during the year (Clymo 1970, Grigal 1985, Lütt 1992, Asada *et al.* 2003). It is fastest in wet and humid seasons (Wagner & Titus 1984, Schipperges & Rydin 1998), starts at temperatures

above 0 °C (Grigal 1985, Gaberščik & Martiničič 1987, Lindholm 1990, Asada *et al.* 2003) and increases with temperature (tested up to 30 °C) (Moore 1989, Gerdol 1995, Robroek *et al.* 2007, Breeuwer *et al.* 2008, Fukuta *et al.* 2012). On the other hand, increasing temperature may reduce net primary production in peatmosses because of moisture stress and dehydration (Weltzin *et al.* 2001, Gerdol *et al.* 2007) caused by evapotranspiration exceeding capillary transport (Skre & Oechel 1981).

As water retention by *Sphagnum* plants is limited, precipitation is important to keep the peatmosses sufficiently wet to grow, in particular during dry periods with lower water tables (Robroek *et al.* 2009, Nijp *et al.* 2014). At such times *Sphagnum* growth is facilitated by higher amounts of rain and more frequent rainfall (cf. Backéus 1988, Asada *et al.* 2003, Nijp *et al.* 2014), although rain events with large amounts and long durations reduce net CO₂

uptake by peatmosses due to light reduction by clouds (Nijp *et al.* 2015). Alongside climatic factors, site conditions like high water table (Hayward & Clymo 1983, Robroek *et al.* 2009), nutrient availability (Aerts *et al.* 1992, Li *et al.* 1993, Bragazza *et al.* 2004, Limpens *et al.* 2004, Fritz *et al.* 2011) and vascular plant competitors determine *Sphagnum* growth (Malmer *et al.* 2003, Pouliot *et al.* 2011).

The *Sphagnum* peatlands of the warm-temperate, humid Kolkheti Lowlands (Kolkheti) in Georgia (Transcaucasus) with high annual temperature of 14.1 °C and 2,338 mm annual precipitation offer a unique opportunity to test whether higher temperatures combined with high and abundant precipitation increase *Sphagnum* growth. Temperatures below 0 °C and long dry periods are rare, so one may expect high year-round rates of *Sphagnum* growth. This expectation was supported by our pilot studies, which found a productivity for *Sphagnum papillosum* Lindb. of $300 \pm 150 \text{ g m}^{-2}$ over a 127-day period and that high water table was more important for growth than nutrient availability (Krebs & Gaudig 2005).

Here we consider the growth of *Sphagnum papillosum* and *S. palustre* L. in Kolkheti as a function of climate conditions, latitude and main site variables to derive suggested driving factors for *Sphagnum* growth worldwide. Our hypotheses are:

- *Sphagnum* growth rate is high because of high temperatures and frequent and abundant precipitation in Kolkheti; and
- *Sphagnum* grows year-round in Kolkheti.

METHODS

Site description

The Kolkheti Lowlands (Georgia, Transcaucasus, 41° 50' N; 41° 47' E and 42° 09' N; 41° 49' E) on the east coast of the Black Sea (Figure 1a) hold the majority of the Georgian peatlands (450 km², Markow *et al.* 1988). The Lowlands are characterised by a high diversity of ombrotrophic and minerotrophic peatlands (Joosten *et al.* 2003). The ombrotrophic peatlands are dominated by dense *Sphagnum papillosum* and *S. palustre* lawns with accompanying species (all with low total cover < 30 %) including *Sphagnum austinii*, *S. rubellum*, *Molinia arundinacea*, *Rhynchospora alba*, *R. caucasica*, *Rhododendron ponticum*, *R. luteum*, *Vaccinium arctostaphylos*, *Carex lasiocarpa*, *C. rostrata*, *Cladium mariscus* and *Drosera rotundifolia* (Joosten *et al.* 2003, Haberl *et al.* 2006, Kaffke 2008). Mean annual temperature is about 14 °C, precipitation is evenly distributed over the year and the mean ranges from 1,500 mm yr⁻¹ (north) to 2,500 mm yr⁻¹ (south). Air humidity is almost continuously high (70–83 %) and frost is rare (Joosten *et al.* 2003, Figure 1b). We collected meteorological data for the study period from the weather stations at Kobuleti (South Kolkheti) and Poti (Central Kolkheti).

Meteorological conditions differed between the two regions (Table 1). Conditions in South Kolkheti were wetter (more rain days, shorter periods without rain) and colder (more days with minimum daily temperature < 0 °C, lower mean annual temperature,

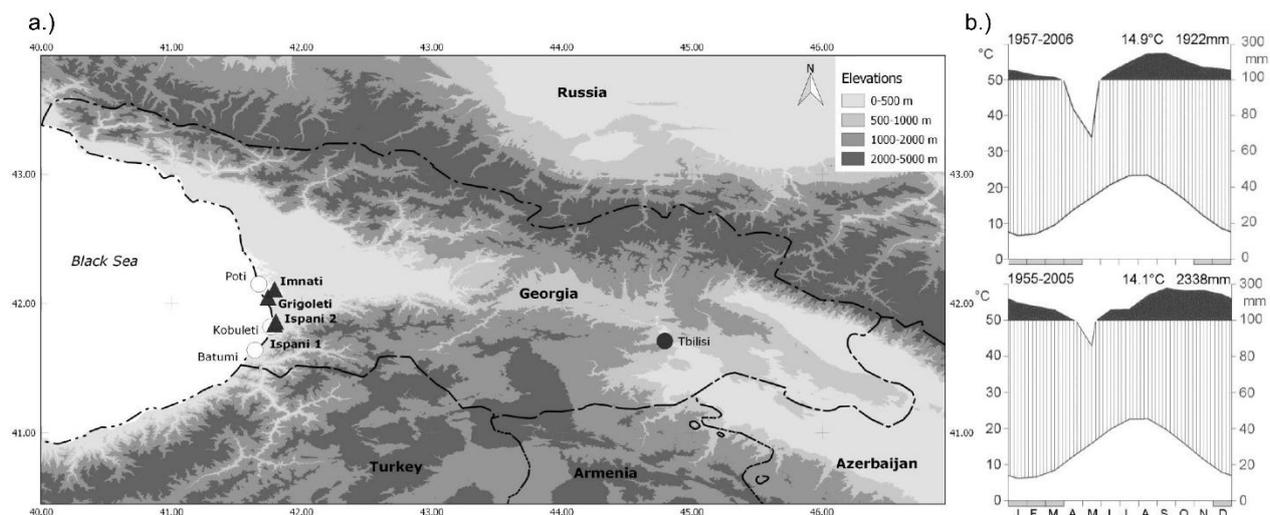


Figure 1. a) Location of Kolkheti showing the study sites (▲) and adjacent cities close to the Black Sea in Georgia and b) climate graphs (Walter & Lieth 1967) of Kobuleti (South Kolkheti, lower graph) and Poti (Central Kolkheti, upper graph). The right-hand axis is precipitation (calendar month)⁻¹. Note the break in scale where the graph is filled.

Table 1. Climate variables for 2007/08 (01.04.2007–31.03.2008) and 2008/09 (01.04.2008–30.04.2009) in South and Central Kolkheti (climate stations Kobuleti and Poti, respectively); with half-year details for South Kolkheti for 2008/09 (summer: 01.04. to 23.09.2008, 176 days and winter: 24.09.2008 to 30.04.2009, 219 days).

Region	South Kolkheti				Central Kolkheti	
	2007–08	2008–09	2008–09		2007–08	2008–09
Study year			summer	winter		
Precipitation sum (mm)	2787	2416	895	1521	2261	2515
Rain days (no.)	167	186	76 (43 %)	110 (50 %)	152	160
Contiguous days without rain (mean)	3.8	2.9	3.1	2.8	4.1	3.4
Contiguous days without rain (max)	16	11	11	9	18	11
Mean temperature (°C)	14.1	14.6	19.7	10.5	14.5	15
Mean relative humidity (%)	81	82	83	81	86	83
Days with mean temperature < 0 °C (no.)	3	1	0	1	7	1
Days with minimum temp. < 0 °C (no.)	35	19	0	19	23	9

Table 1). There were also differences between the study years. Precipitation in South Kolkheti was greater in the first year than in the second year. In Central Kolkheti the opposite was true.

The year 2007/08 was characterised by fewer rain days and longer periods without rain in both regions (Table 1). Mean temperature in the second year was 0.5 °C higher and the number of days with mean or minimum temperatures < 0 °C was smaller (Table 1). The 2008/09 winter in South Kolkheti was wetter (more precipitation, more rain days, shorter dry periods) and colder (lower mean temperature, more days with temperatures < 0 °C) (Table 1).

Growth measurements

We sampled during two study years (04/2007–03/2008, 04/2008–03/2009) in the four peatland sites Ispani 1, Ispani 2 (both near Kobuleti, South Kolkheti), Grigoleti and Imnati (near Poti, Central Kolkheti, Figure 1a).

The unit plot was a 25 × 25 cm square located at random (without deliberate choice) in an even, dense, undisturbed lawn with > 98 % cover of *S. papillosum* or *S. palustre*. We located 15 *S. papillosum* plots in Ispani 1 and Ispani 2, and ten *S. palustre* plots in Ispani 1 and Grigoleti (for Grigoleti in the second study year only). In addition we located 30 more unit plots of *S. papillosum* in Imnati in each of the two study years. We used markers to measure annual *Sphagnum* growth. In each plot ten single *Sphagnum* plants were marked with a nylon cable tie (width 2 mm, length 100 mm) directly below the capitulum (0–1 cm, shoot apex with branches not fully developed, cf. Clymo 1973). The cable tie was fastened between the capitulum and the subjacent

branches. Thus, it was fixed vertically and allowed the continued growth of the moss and measurement at a later time of the distance above it.

We measured growth of the labelled peatmosses as the length (fresh) between the cable tie and the capitulum. In addition, the newly grown parts were weighed after drying for 24 h at 80 °C (accuracy 1 mg; Hendry and Grime 1993). At the sites Ispani 1, Ispani 2 and Imnati, measurements were carried out after 12 and 24 months; at Ispani 2 additionally after 6 months to analyse intra-annual growth rates; and at Grigoleti in the second research year only, after 12 months. Biomass production *per* area (g m⁻²) was calculated from the dry mass of the ten marked peatmosses in each plot and the average number of capitula on three 60 cm² areas close to each plot (cf. Clymo & Hayward 1982).

Site condition measurements

The phreatic water table (Schouwenaars 1995), pH and electrical conductivity (EC, measured with a multi variable tester Hanna Combo HI 98129) of the interstitial water were measured once, at biomass harvest, for each plot. Water table levels in the centres of the peatlands Ispani 2 and Imnati were automatically recorded with data collectors (Keller DCX-22AA) in the first observation year to allow the comparison of water table changes. As the data collectors were installed near the plots in Ispani 2 and Imnati (maximum distance 330 m and 370 m, respectively), these records supplement the water table data from the plots.

Before collecting the biomass samples for annual productivity measurements in March 2008 and 2009, the cover of peatmosses and height of the living

peatmoss (distance between peatmoss surface and peat) were recorded for each plot. The peatmoss was easy to distinguish from the peat below as this peat layer was strongly decomposed creating a sharp black boundary. Selected investigation sites in undisturbed peatland were partly influenced by hunters. Their effects on the plots (trampling, burning) were recorded too. Vascular plants started growing only in March, so the cover of litter in the plots was estimated 'by eye' at that time to assess the effect of vascular plants on *Sphagnum* growth.

Entire capitula of *S. papillosum* and *S. palustre* were collected at five plots in each peatland for each of the two study years (03/2008 for the first study year, 03/2009 for the second study year), dried and ground in a centrifugal ball mill (rotation speed 18,000 rpm for 1–2 min, FRITSCH pulverisette 14, Idar-Oberstein) to determine total nitrogen (N) and C/N quotient with a C/N-analyser (CHNOS element analyser Vario EL III, elementary analytical systems Hanau). After microwave digestion (START 1500, MLS Enterprises) the solute was treated with acidic molybdate solution containing ascorbic acid ('molybdenum blue method' cf. Murphy & Riley 1962) to measure total phosphorus (P) with a UV/Visible spectrophotometer (Cecil CE 1021, 890 nm wavelength). Potassium (K) was determined directly after the digestion with an atomic absorption flame spectrometer (CD-ContrAA 300, analytic Jena).

The upper 5 cm of peat directly below the living peatmoss was sampled using a 'Russian pattern 'D'-corer made by Eijkelkamp, diameter 5 cm, depth 50 cm. It was analysed for the same elements as the capitula.

Data analysis

We tested the effect of site variables on *Sphagnum* productivity and rate of increase in length of *Sphagnum papillosum* using linear multiple regression (Crawley 2005). Site variables for Central and South Kolkheti (peatlands Ispani 2 and Imnati) were included as they can be confirmed by other studies (Krebs & Gaudig 2005, Haberl *et al.* 2006, Kaffke 2008). The regression models included peatland site, study year, water table, litter cover, pH and EC of the interstitial water and element concentrations in peatmoss capitula (N, P, K) (model 1: biomass productivity, model 2: rate of increase in length).

We explored outliers and collinearity of the explanatory variables with the variance inflation factor (Zuur *et al.* 2009). If the variance inflation factor is below 3, no correlations between the explanatory variables are assumed (Zuur *et al.* 2009)

and they were included in the models. To identify the optimal model we used the Akaike information criterion (AIC) as it measures goodness of fit and model complexity (the lower the AIC value, the better the model). Single explanatory variables were dropped with a backwards selection to determine the lowest AIC (Zuur *et al.* 2009). Statistical data exploration, computation and Figures were made with the R package (R Development Core Team 2009) and the packages AED (Zuur *et al.* 2009), stats (R Development Core Team 2009) and beeswarm (Eklund 2013). Differences between sites were analysed with the non-parametric Kruskal Wallis test and a multiple comparison test after Siegel & Castellan (1988, R package pgirmess, Giraudoux 2010) to accommodate unequal sample sizes (caused by study plots being disturbed by anthropogenic fires, trampling by hunters and cattle grazing).

In a systematic review, field studies of the natural productivity of *S. papillosum* (number of published papers/data for single study periods: $n = 18/44$) and *S. palustre* ($n = 2/3$) were obtained. Our own results, and results from other studies with information on study periods and available climate data for these periods, were used to analyse the global patterns of *Sphagnum* growth with regard to temperature, precipitation and related variables (hereafter referred to as 'global analysis'). Because microhabitat was the only variable mentioned for most studies, it was included in the analysis. The global analysis was carried out for *S. papillosum* only (number of examples of applicable data $n = 44$) as the dataset for *S. palustre* was too small ($n = 6$).

We used boosted regression trees (BRT; Friedman 2001, Elith *et al.* 2008) to test the dependence of *Sphagnum papillosum* biomass productivity on mean temperature, growth duration (number of days with temperature ≥ 0 °C), precipitation sum, quotient of precipitation sum / mean temperature, quotient of rain / dry days, mean number of contiguous days without rain during the single study periods, latitude, altitude, and microhabitat (model 3).

The BRT tool calculates multiple regression models (regression trees) and includes an adaptive method for combining many simple models to give improved predictive performance (boosting) while the final additive regression model is fitted forward with increasing numbers of trees (Elith *et al.* 2008). BRT can fit complex nonlinear relationships, reduces the problem of 'overfitting' (Elith *et al.* 2008), and highly correlated explanatory variables do not cause numerical aberrations (Friedman & Meulman 2003). As this method does not deliver *P*-values, but uses internal validation processes, we used 10-fold cross validation for model development and validation.

Within the BRT model, three terms are used to optimise predictive performance: bag fraction, learning rate, and tree complexity (Friedman 2001, Elith *et al.* 2008). Explanatory variables with explaining deviances below 1 % were removed. We used library *gbm* (version 1.6-3, Ridgeway 2007) implemented in the software R (R Development Core Team 2009).

For international comparison, meteorological data were acquired from the National Climate Data Center (NOAA 2010) and calculated for the growth period of *Sphagnum* in each single study. The growth period included all days with mean daily temperature > 0 °C (cf. Grigal 1985). Days with frost were counted for the study periods.

RESULTS

Sphagnum growth in Kolkheti

Sphagnum biomass productivity in Kolkheti ranges from 126 to 894 g m⁻² yr⁻¹, and the rate of increase in length from 0.1 to 30.3 cm yr⁻¹ (Figure 2).

Sphagnum palustre grows significantly more in length and biomass than *S. papillosum* (Figure 2), but

has mostly smaller capitula and bulk densities of capitula (Table 2). Significant differences in biomass productivity and rate of increase in length were found between study years, with biomass values being up to twofold larger in 2008/09 (Tables 2, 3). When observed for one study period and location, *S. palustre* produced the largest biomass in Ispani 1 by a significant margin during 2008/09. Rate of increase in length differed between sites (Tables 2, 3)

Biomass productivity and rate of increase in length of *S. papillosum* differed between winter and summer half-years (2008/2009), with summer half-year values being on average 366 g m⁻² and 3.6 cm greater than winter values (Figure 3, $P \leq 0.01$).

Site conditions in Kolkheti

Site conditions differed with regard to peatlands and peatmoss species (Table 4). Water table levels at harvest in March 2008 and 2009 were significantly higher in Ispani 2 than at the other sites (Table 4). The water table in Ispani 2 dropped during the first study period to 15 cm below the peat surface, corresponding to 28 cm below the *Sphagnum* capitula (Figure 4). Larger fluctuations were observed in Imnati with a range from 6 cm above to 27 cm below

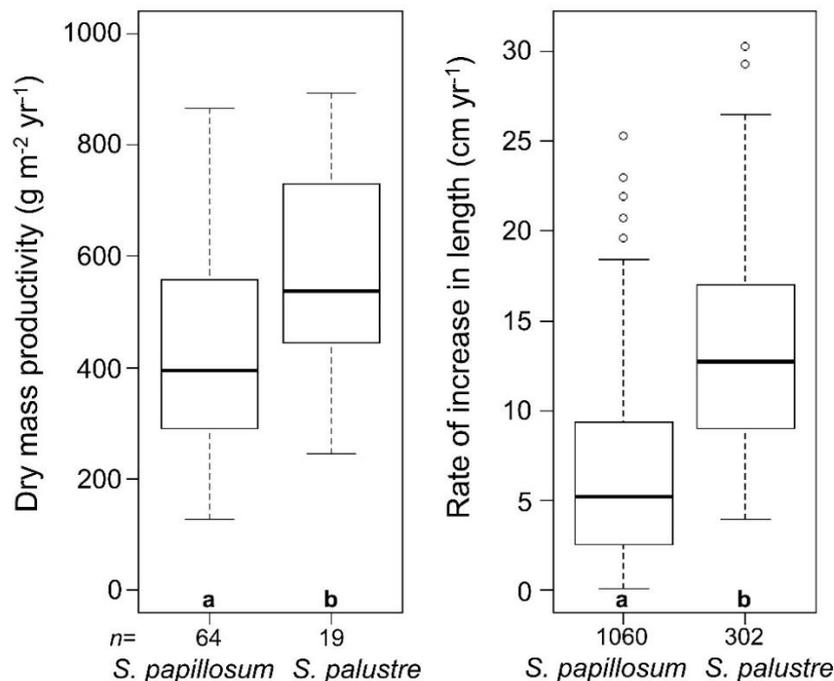


Figure 2. Annual biomass productivity and rate of increase in length of *Sphagnum papillosum* and *Sphagnum palustre* in Kolkheti over the periods 04/2007–04/2008 and 04/2008–04/2009. n = number of measurements. The plot shows the median (bold line), the upper and lower quartiles (including 50 % of the data and creating the box), the whiskers representing the lowest datum still within 1.5 interquartile range (IQR) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile, and the outliers (o), i.e. the values outside these ranges. Values with different letters differ significantly ($P \leq 0.05$). Differences between species were analysed with the non-parametric Kruskal Wallis test after Siegel & Castellan (1988).

Table 2. Biomass productivity, rate of increase in length, and capitulum density for two *Sphagnum* species in four peatlands for two study periods. Values with different letters differ significantly ($P \leq 0.05$). Differences of variables were analysed with the Kruskal Wallis test and a multiple comparison test after Siegel & Castellan (1988).

	Region	South Kolkheti			Central Kolkheti	
	Peatland	Ispani 1		Ispani 2	Imnati	Grigoleti
	<i>Sphagnum</i> species	<i>S.papillosum</i>	<i>S.palustre</i>	<i>S.papillosum</i>	<i>S.papillosum</i>	<i>S.palustre</i>
2007/2008	Number of plots	6	5	13	19	-
	Dry mass productivity (g m ⁻² yr ⁻¹)	269±83 ^a	387±98 ^a	362±89 ^a	359±162 ^a	-
	Rate of increase in length(cm yr ⁻¹)	3.6±2.4 ^b	9.7±2.9 ^d	2.3±1.3 ^a	8.6±4.7 ^c	-
	Capitula density (dm ⁻²)	130±21 ^a	104±39 ^a	157±29 ^{ab}	111±21 ^a	-
	Number of measurements	67	62	197	215	-
	Capitula bulk density (mg cm ⁻³)	15.2±8.0 ^b	13.2±8.0 ^b	22.3±10.1 ^c	9.3±4.5 ^a	-
2008/2009	Number of plots	3	4	8	15	10
	Dry mass productivity (g m ⁻² yr ⁻¹)	548±274 ^a	788±80 ^b	548±49 ^a	499±178 ^a	584±144 ^a
	Rate of increase in length (cm yr ⁻¹)	3.6±1.8 ^a	13.3±6.0 ^c	3.3±1.2 ^a	10.2±3.0 ^b	17.4±3.4 ^d
	Capitula density (dm ⁻²)	166±19 ^b	144±23 ^a	175±22 ^b	125±25 ^{ab}	112±22 ^a
	Number of measurements	66	37	153	112	115
	Capitula bulk density (mg cm ⁻³)	18.1±10.3 ^{bc}	15.0±9.4 ^{ab}	20.6±10.6 ^c	16.4±6.6 ^{bc}	13.6±8.2 ^a

the peat surface, which corresponds to 14–47 cm below the capitula. Water table fluctuations in both peatlands were greater in summer than in winter.

Although there were significant differences in element concentrations between the *Sphagnum* species (P, K), and among the upper peat layers of the different sites (N, P, K) (Table 4), no relationship with *Sphagnum* biomass productivity was observed. Element quotients of the capitula ranged from 18.3 to 41.7 (N/P) and from 2.0 to 4.1 (N/K), respectively, (Table 4) with highest values in Ispani 2. Litter cover was similar between sites. Fires were recorded at all sites, but most frequently in Central Kolkheti (Table 4).

Global growth of *Sphagnum papillosum* and *S. palustre*

Sphagnum papillosum has a mean global productivity ($n=50$) under natural conditions of $204 \text{ g m}^{-2} \text{ yr}^{-1}$ and a range from 29 to $490 \text{ g m}^{-2} \text{ yr}^{-1}$ (Figure 5). Rate of increase in length of *Sphagnum papillosum* ranges globally ($n=40$) from 0.4 to 4.6 cm yr^{-1} . The productivity and rate of increase in length recorded in our study are the global maxima for *Sphagnum papillosum* under natural conditions (Figure 5).

Few studies have addressed productivity and growth in length of *Sphagnum palustre* (cf. Lütt 1992, Fukuta *et al.* 2012). Our results from Kolkheti are greater than reported hitherto (Figure 5).

Table 3. Results of linear modelling of the response variables biomass productivity and rate of increase in length of *Sphagnum papillosum* in the peatlands Ispani 2 (South Kolkheti) and Imnati (Central Kolkheti). Df: degrees of freedom; CI: confidence interval; R^2 : coefficient of determination; ¹: compared with 2007/08; ²: compared with the site Ispani 2. Level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Variable	Factor	Estimate of the slope	95 % CI	P	R^2
Biomass productivity	Model 1 ($n = 54$, Df: 53)				0.22
	2008/09 ¹	156	-81–231	≤ 0.001 ***	
Rate of increase in length	Model 2 ($n = 869$, Df: 867)				0.50
	2008/09 ¹	1.07	-0.73–1.40	≤ 0.001 ***	
	Imnati ²	4.26	-3.96–4.57	≤ 0.001 ***	

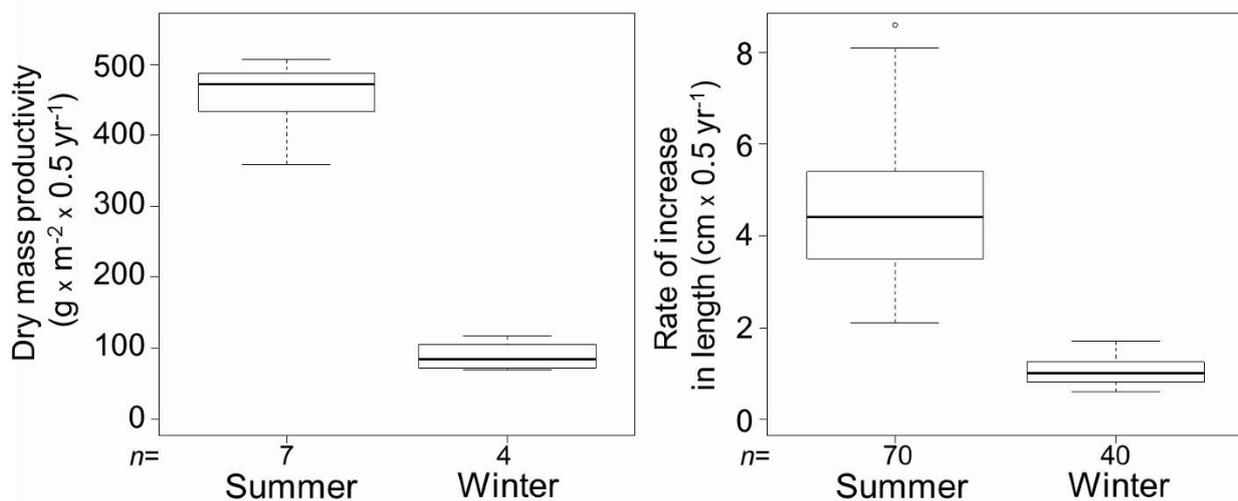


Figure 3. Biomass productivity and rate of increase in length of *Sphagnum papillosum* in Ispani 2 in summer (01.04.–23.09.2008, 176 days) and winter half-year (24.09.2008–30.04.2009, 219 days), standardised to 183 days. Difference is significant ($P \leq 0.01$) following the non-parametric Kruskal Wallis test after Siegel & Castellan (1988).

Table 4. Site conditions (mean values with standard deviation) of different peatlands and peatmoss species in Kolkheti, measured or sampled during harvesting of the *Sphagnum* biomass. EC was corrected for pH at 20 °C (ECcorr). Concentrations are calculated on a dry mass basis. Values with different letters differ significantly ($P \leq 0.05$).

Region	South Kolkheti			Central Kolkheti	
Peatland	Ispani 1	Ispani 1	Ispani 2	Imnati	Grigoleti
<i>Sphagnum</i> species	<i>S.papillosum</i>	<i>S.palustre</i>	<i>S.papillosum</i>	<i>S.papillosum</i>	<i>S.palustre</i>
No. of plots	9	9	21	34	10
Mean water table (cm below capitulum; one observation <i>per</i> plot)	31±10 ^b	33±11 ^b	21±5 ^a	27±6 ^b	33±7 ^b
Water (no. of observations)	9	9	21	15	10
pH	4.77 ^a	5.00 ^a	4.89 ^a	4.83 ^a	5.39 ^b
ECcorr (µS cm ⁻¹)	36±26	25±10	25±15	45±24	50±17
Peat (no. of observations)	6	7	10	5	4
Nitrogen (mg g ⁻¹)	19.1±2.9 ^b	16.6±5.0 ^{ab}	18.8±3.9 ^b	14.6±2.2 ^a	21.5±1.1 ^c
C/N quotient	23±5 ^{ab}	30±9 ^{bc}	25±4 ^b	30±6 ^c	19±2 ^a
Phosphorus (mg g ⁻¹)	0.39±0.11 ^a	1.19±0.42 ^b	0.56±0.07 ^a	0.52±0.17 ^a	1.10±0.09 ^b
Potassium (mg g ⁻¹)	0.6±0.1 ^a	0.8±0.3 ^{ab}	1.3±0.2 ^{bc}	0.7±0.02 ^a	1.2±0.1 ^b
Capitulum (no. of observations)	6	7	10	5	4
Nitrogen (mg g ⁻¹)	9.5±0.9	9.4±1.5	10.2±1.1	9.6±1.5	9.4±0.6
Phosphorus (mg g ⁻¹)	0.31±0.15 ^a	0.61±0.26 ^b	0.26±0.06 ^a	0.37±0.04 ^{ab}	0.47±0.10 ^{ab}
Potassium (mg g ⁻¹)	3.0±0.8 ^b	4.7±1.0 ^c	2.6±0.5 ^a	3.3±0.4 ^b	4.9±0.7 ^c
N/P quotient	35.1±7.0 ^{ab}	18.3±8.7 ^a	41.7±8.5 ^b	26.5±4.3 ^{ab}	20.5±4.4 ^a
N/K quotient	3.9±0.3 ^{ab}	2.1±0.4 ^a	4.1±0.4 ^b	2.9±0.4 ^{ab}	2.0±0.2 ^a
Mean cover of litter (%) (one observation <i>per</i> plot)	17±11	13±8	12±10	11±9	5±3
Burned (% of observations)	34–66	0–33	0–33	67–100	67–100

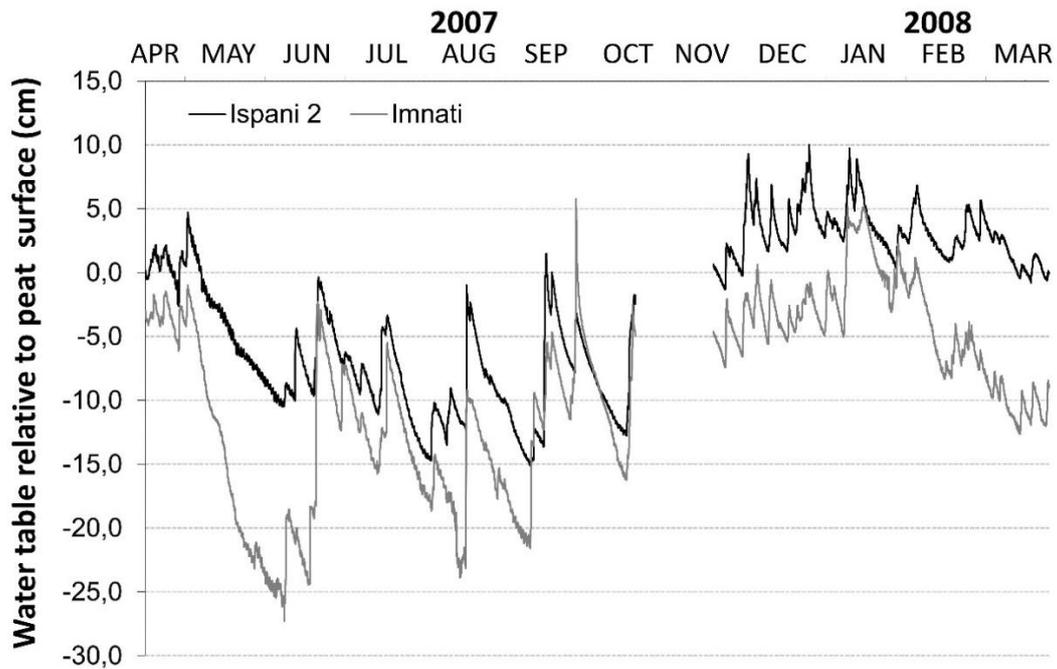


Figure 4. Water table level relative to peat surface (measured at 15-minute intervals) in the centre of Ispani 2 (thin line, *Sphagnum* lawn height at installation time: 13 cm) and Imnati (thicker line, lawn height: 20 cm) for the period 17.04.2007–21.03.2008, with interruption of measurements 18.10.2007–16.11.2007. Water table levels at the two sites are significantly different, $P \leq 0.001$.

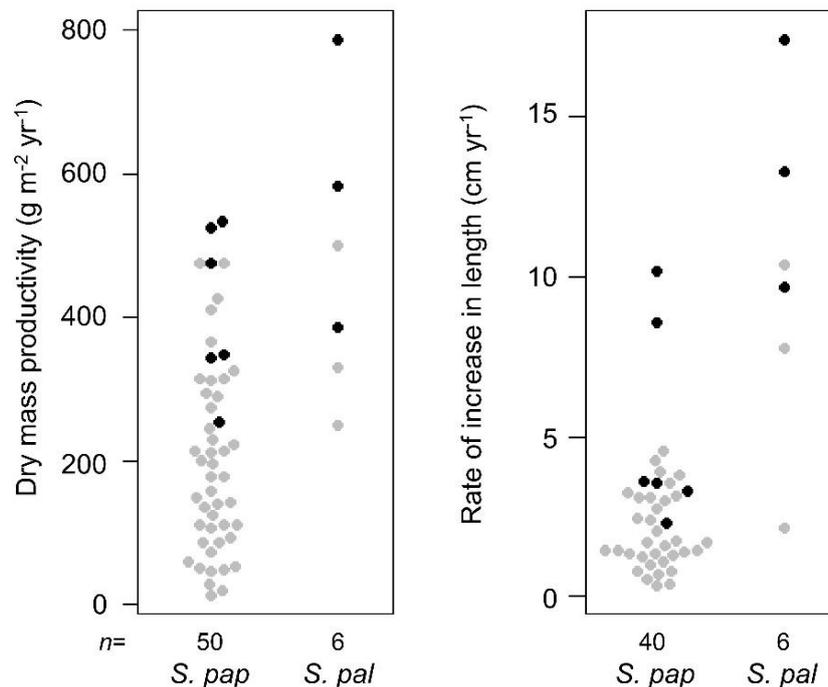


Figure 5. Annual biomass productivity and rate of increase in length of *Sphagnum papillosum* and *Sphagnum palustre* in Kolkheti (●: mean of the different peatlands) compared with literature references (●: Newbould 1960, Chapman 1965, Clymo 1970, Clymo & Reddaway 1971, Ilomets 1974, Forrest & Smith 1975, Pedersen 1975, Ilomets 1976, Hulme & Blyth 1982, Gaberščik & Martiničič 1987, Moore 1989, Lindholm & Vasander 1990, Li *et al.* 1992, Lütt 1992, Fukushima *et al.* 1995, Shiraishi *et al.* 1996, Grabovik 2002, Asada *et al.* 2003, Grabovik 2003, Fukuta *et al.* 2012). Graphs are displayed in bee swarm plots (Eklund 2013) for concise presentation of single data points while avoiding overlap.

Moreover, *Sphagnum palustre* (244–894 g m⁻² yr⁻¹, 3.9–30.3 cm yr⁻¹) had a greater productivity and rate of increase in length in Kolkheti than *S. papillosum* (126–867 g m⁻² yr⁻¹, 0.1–25.3 cm yr⁻¹, Tables 2, 3).

The statistical analysis of literature and field study data shows that biomass production of *Sphagnum papillosum* decreases with longer dry periods, from hollow and lawn to hummock sites, and with decreasing temperature during the growth periods (Figure 6). The mean productivity of *Sphagnum papillosum* growing in a hollow or lawn microhabitat is 140 g m⁻² yr⁻¹ greater than its mean productivity in hummocks. Moreover, its productivity decreases if

the mean duration of contiguous days without rain is longer than 3 days during the growth period; there is a decrease in growth rate of 110 g m⁻² yr⁻¹ if the mean duration changes from 3 to 3.5 days. Raising mean temperatures during the growth periods from 10 °C to 13 °C increased the productivity of *Sphagnum papillosum* by almost 50 g m⁻² yr⁻¹. Moreover, we find that the biomass productivity of *Sphagnum papillosum*, related to the quotient of precipitation sum / mean temperature during the growth period, increases with increasing quotient values (Figure 6). The temperature is positively correlated with the latitude ($R^2=0.44$; $P \leq 0.001$).

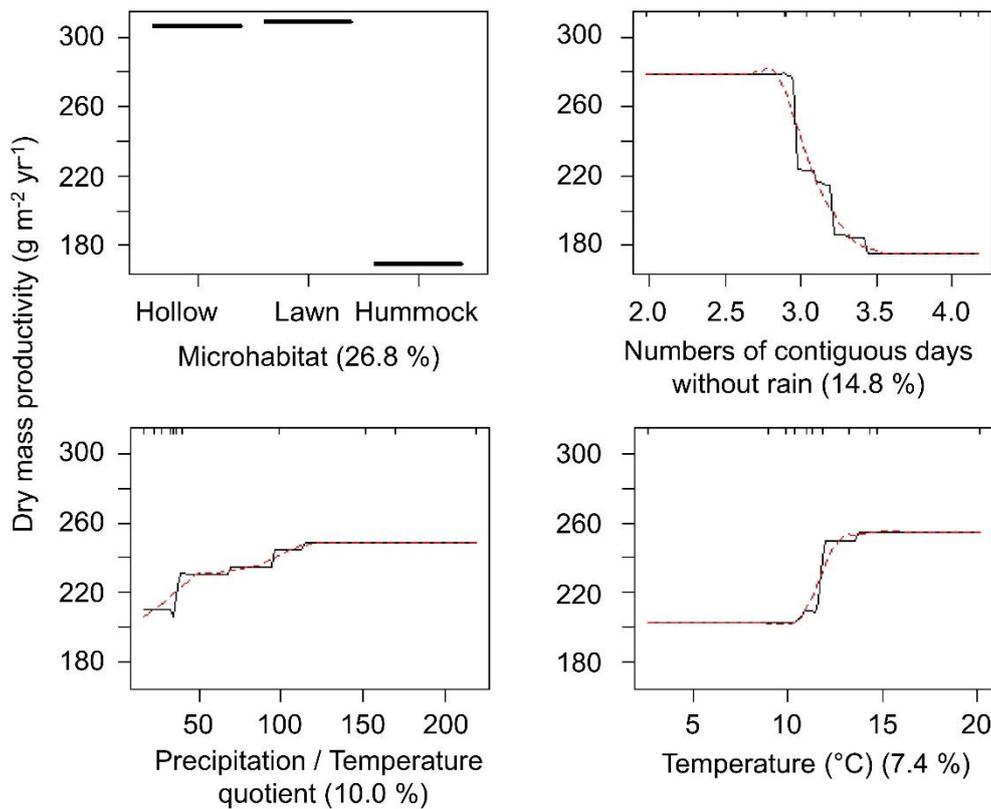


Figure 6. Boosted regression tree model of modelled global biomass productivity of *Sphagnum papillosum* (response variable) and its predictor/ explanatory variables microhabitat (hollow $n = 8$, lawn $n = 12$, hummock $n = 21$, not specified $n = 3$), mean numbers of contiguous days without rain, the quotient of precipitation sum and mean temperature and mean temperature during the growth period from Newbould 1960, Chapmann 1965, Clymo 1970, Clymo & Reddaway 1971, Forrest & Smith 1975, Pedersen 1975, Ilomets 1976, Lindholm & Vasander 1990, Li *et al.* 1992, Lütt 1992, Fukushima *et al.* 1995, Shiraishi *et al.* 1996, Grabovik 2002, Grabovik 2003, Asada *et al.* 2003 and the present study). Percentages in the abscissa labels are the absolute contribution of the variable to the biomass productivity. The red (dashed) line is the smoothed relationship of the biomass productivity and the single explanatory variables. The vertical markers on the ‘box’ line at the top are single-study values. The boosted regression tree model was performed with 38 observations and 3 predictors, using the Poisson distribution, with tree complexity = 2 (sets the complexity of individual trees, interaction order), learning rate = 0.001 (sets the weight applied to individual trees, shrinkage factor), bag fraction = 0.75 (sets the proportion of observations used in selecting variables). The final model was fitted with 1500 trees with explained deviance = 0.59.

DISCUSSION

Sphagnum growth rates

We hypothesised that *Sphagnum* productivity would be high in Kolkheti. Including all species, global productivity ranges from 8 to 1,450 g m⁻² yr⁻¹ with an overall mean of 259 g m⁻² yr⁻¹ (\pm 206, SD) (Gunnarsson 2005). Values from Kolkheti are large in this context, with a mean of 453 g m⁻² yr⁻¹ (\pm 182, SD). The global maxima for all species of *Sphagnum* are reached by the species *S. cristatum* and *S. falcatulum* at a hyper-oceanic peatland site in New Zealand (Stokes *et al.* 1999). *Sphagnum papillosum* is a slow-growing species (Lütt 1992), and reaches its global maximum under natural conditions in our study in Kolkheti (Figure 5). The largest value reported in literature is 610 g m⁻² yr⁻¹, associated with a transplantation experiment (Clymo 1970) and consequently not included in the analysis because of modified growth conditions. The highest growth rates of *Sphagnum palustre* previously reported were a dry mass productivity of 501 g m⁻² yr⁻¹ (Fukuta *et al.* 2012) and a rate of increase in length of 10.41 cm yr⁻¹ (Lütt 1992). Our work found new global maxima for *S. palustre* growth rates under natural conditions and confirms our hypothesis of high *Sphagnum* productivity in Kolkheti (Figure 5).

Sphagnum palustre grows faster than *S. papillosum* in Kolkheti. Lütt (1992) also found that *S. palustre* grows better than *S. papillosum*, although in North Germany, with productivities of 250–332 g m⁻² yr⁻¹ and 172–220 g m⁻² yr⁻¹ and rates of increase in length of 7.8–10.4 cm yr⁻¹ and 2.8–3.8 cm yr⁻¹, respectively. *Sphagnum palustre* in Kolkheti has a smaller capitulum density than *S. papillosum*, except in Imnati in 2007/08 (Table 2), thus allowing light to penetrate deeper into the *Sphagnum* lawn, which increases the active assimilation area (Sliva 1997, cf. Robroek *et al.* 2009) resulting in faster growth in terms of both length and biomass (Pedersen 1975). Moreover, Fukuta *et al.* (2012) suggest physiological traits for *Sphagnum palustre* that suit it to production under warm conditions, identifying an optimum temperature for net photosynthetic rate at 20 °C.

Site conditions responsible for *Sphagnum* growth in Kolkheti

Nutrient supply

Major nutrients for *Sphagnum* growth are N, P, and K. Their concentrations in the peat and in the *Sphagnum* capitula in Kolkheti peatlands correspond to values reported from other studies in natural bogs (Aerts *et al.* 1992, Succow & Joosten 2001, Bragazza *et al.* 2004, Fritz *et al.* 2011). Nitrogen is described

as the primary limiting nutrient in ombrotrophic bogs (Succow & Joosten 2001) and *Sphagnum* growth is N-limited at N/P quotients < 10 in the capitula (Aerts *et al.* 1992). With a nitrogen deposition rate of around 5.4 kg ha⁻¹ yr⁻¹ (data for 2008 and 2009 from European Monitoring and Evaluation Programme, EMEP 2015) the N/P quotients of the *Sphagnum* capitula in Kolkheti (> 18) exceed this threshold and indicate no N limitation. *Sphagnum papillosum* growth in the Ispani 1 and 2 peatlands seems to be P and K co-limited as the N/P and N/K quotients are larger than the thresholds of 30 and 3.3, respectively, derived by Bragazza *et al.* (2004). This contradicts the results of a fertilisation experiment in the Ispani 2 peatland, where additional P did not increase *Sphagnum papillosum* productivity (Krebs & Gaudig 2005). Moreover, as the N/P values are close to the threshold, a P limitation seems unlikely. Therefore, we assume a K limitation of *Sphagnum* growth similar to the findings of Krebs & Gaudig (2005). In contrast, the results for *Sphagnum papillosum* in the Imnati peatland and for *Sphagnum palustre* indicate optimal nutrient supply in Kolkheti, corresponding with the higher growth rates of the latter species.

Vascular plants

Vascular plants can facilitate *Sphagnum* growth (e.g. Pouliot *et al.* 2011). However, the role of vascular plants could not be assessed sufficiently accurately because frequent peatland fires in spring (Table 4) prevented collection of adequate data. We assume that vascular plants support *Sphagnum* growth by providing shade, and thus preventing excessive (> 31 °C) surface temperatures (Pedersen 1975) and photoinhibition (cf. Murray *et al.* 1993). This will be especially relevant in Kolkheti where mean temperatures during the growth period were the highest recorded in all similar studies worldwide. The combination at Grigoleti of significantly larger rate of increase in length of *Sphagnum palustre* with significantly lower biomass productivity than at Ispani 1 may be attributable to the higher cover of vascular plants providing ‘scaffolding’ to support elongating moss shoots in Grigoleti, leading to looser and higher *Sphagnum* lawns (Sliva 1997) but not necessarily more biomass production (Pouliot *et al.* 2011).

Microhabitat

Peatmosses in Kolkheti grow mainly in lawns, i.e. in a microhabitat that has been described as wetter (Sjörs 1948, Hayward & Clymo 1982) and more productive than hummocks (Clymo & Reddaway 1971, Gunnarsson 2005). Our review confirmed the overriding importance of microhabitat for *Sphagnum*

growth (Figure 6), with habitat being the best explanatory factor. The productivity of *Sphagnum papillosum* in wetter microhabitats is double that in hummocks (Figure 6). Since microhabitats are seldom defined in detail in the literature, the reasons for differences in growth rates remain unclear. A comparison of data from hollows with water table depths between 2 and 28 cm (Lütt 1992) and data from a lawn with water table 3 to 33 cm below the capitula (Pedersen 1975) shows that the distinguishing features of microhabitats are more than differences in water table. They also differ, for instance, in nutrient status (Gunnarsson 2005) or global solar irradiation (Bragazza 2008). Even though it may be difficult to differentiate between peatmoss hollows and lawns, hummocks may at least be identified as 'higher up' (associated with a lower water table).

Water table

As *Sphagnum* cannot actively control its water loss and is affected by prolonged desiccation, especially in summer (Clymo 1973, Pedersen 1975, Hayward & Clymo 1982, Rydin & Jeglum 2009), the water table is important for the water supply of peatmosses (cf. Hayward & Clymo 1982). In Kolkheti (Ispani 2), a high and constant water table has been identified as a major factor for high productivity of *Sphagnum papillosum* in summer (Krebs & Gaudig 2005). The mean water table level of 21.4 cm below the peatmoss surface from Krebs & Gaudig (2005) corresponds to records obtained from Ispani 2 in the present study (Table 4, Figure 4). However, water tables are deeper in other Kolkheti peatlands and may drop to almost 0.5 m below the capitula (Figure 4). If the water table falls, evapotranspiration may continue to such a degree that the photosynthetically active parts of the peatmosses cannot maintain sufficient water content for growth, as capillary water transport also decreases (McCarter & Price 2014). The same article reports a substantial dewatering of the upper 5 cm of *Sphagnum magellanicum* at water tables of -40 cm. This *Sphagnum magellanicum* had a capitulum density of $100 \pm 20 \text{ dm}^{-2}$ and a capitulum bulk density of $18 \pm 5.4 \text{ mg cm}^{-3}$, i.e. the values are comparable with our results for *S. papillosum* and *S. palustre* from Kolkheti (Table 2). Thus we assume that capillary water transport is insufficient to keep the peatmosses wet enough for optimal growth during periods with deep water tables. Moreover, Li *et al.* (1992) associated water table levels 3–6 cm below the capitulum with highest productivities for *Sphagnum papillosum*. Thus we conclude that the position of the water table cannot explain the high growth rates of *Sphagnum* in Kolkheti.

Precipitation/rain frequency

Sphagnum growth differed substantially between the study years (Table 2). When found in other studies, this has been ascribed to meteorological differences, usually in precipitation and temperature (Wallén *et al.* 1988, Moore 1989, Lindholm & Vasander 1990, Lütt 1992, Gerdol 1995, Asada *et al.* 2003).

Sphagnum growth depends strongly on the water supply from precipitation (Clymo 1973, Pedersen 1975, Hayward & Clymo 1982). As the water table does not ensure permanent water supply to the peatmosses, it seems that *Sphagnum* growth in Kolkheti must be governed by precipitation. Precipitation compensates for reduced water tables by keeping the water content of the mosses sufficiently high for CO₂ assimilation (Robroek *et al.* 2009, Nijp *et al.* 2014). Indeed, the growth of *Sphagnum papillosum* has been reported to correlate with precipitation (Li *et al.* 1992, Asada *et al.* 2003), although Moore (1989) failed to identify a significant relationship between total precipitation and productivity whilst Gunnarsson (2005) identified only a weak positive effect. The better overall growth in our second study year cannot be explained by the precipitation sum, as the South Kolkheti rainfall was less than in the first year. However, the rain frequency was greater in the second year, as rainfall was more evenly distributed with a higher number of rain days and shorter periods without precipitation (Table 1). The larger number of long dry periods in the first year may have affected *Sphagnum* growth, which decreases with increasing length of the dry period (Li *et al.* 1992, Asada *et al.* 2003), perhaps because *Sphagnum* is slow in re-starting photosynthesis after prolonged desiccation (Wagner & Titus 1984, Robroek *et al.* 2009). Our global analysis is consistent with our hypothesis, in that the length of periods without rainfall is significantly related to the productivity of *Sphagnum papillosum* (Figure 6). Evenly distributed precipitation seems to determine the continuous *Sphagnum* growth in Kolkheti. This is confirmed by growth chamber experiments, where frequent simulated precipitation (once *per* 2 days) partly offset the negative effects of deep water table (Nijp *et al.* 2014). However, among species of *Sphagnum*, *S. papillosum* and *S. palustre* are relatively resistant to water stress (Clymo & Hayward 1982, Li *et al.* 1992, Lütt 1992) so additional factors may have caused the differences in *Sphagnum* productivity between the study years.

Temperature

Mean temperatures during the growth periods were 0.5 °C higher in both regions during the second study year (Table 1), i.e. the year with greater *Sphagnum*

growth. Mean annual temperature is an important explanatory variable for *Sphagnum* productivity (Moore 1989, Vitt 1990, Asada *et al.* 2003), as our global analysis confirms for mean temperature during the growth period of *Sphagnum papillosum* (Figure 6). Also, increasing mean daytime temperatures (up to 21.4 °C, Breeuwer *et al.* 2008) lead to increased *Sphagnum* growth.

We found productivity of *Sphagnum papillosum* to increase with higher temperatures and higher values of the quotient of precipitation sum / mean temperature during the growth periods (Figure 6). With increasing temperature, a near-constant water supply in the form of frequent rainfall (cf. contiguous days without rain) is essential for *Sphagnum* growth (Figure 6, cf. Bragazza 2008) to avoid a reduction of net primary production by moisture stress and dehydration (Weltzin *et al.* 2001, Gerdol *et al.* 2007) resulting from higher evapotranspiration (Skre & Oechel 1981). Clymo (1970) found that biomass productivity of *Sphagnum papillosum* more than doubled (from 240 g m⁻²yr⁻¹ to 610 g m⁻²yr⁻¹) after transplantation to an area with more rain days, higher precipitation and 4 °C warmer summer temperatures. Similarly, Asada *et al.* (2003) found *Sphagnum* growth to correlate strongly with precipitation and temperature, with precipitation playing the major role. These studies corroborate our findings that temperature is a driving factor for *Sphagnum* productivity and precipitation frequency is more important than precipitation amount, in accordance with our hypothesis.

Seasonal growth pattern

Temperature, alongside water supply, also determines seasonal growth patterns. The fourfold higher productivity and length growth of *Sphagnum papillosum* in summer compared with winter illustrates its distinct seasonal growth pattern in Kolkheti (Figure 3), which was also observed in North Germany by Lütt (1992) for both *S. papillosum* and *S. palustre*. Even so, the winter growth of *Sphagnum papillosum* at Ispani 2 (mean 106 g m⁻², Figure 3) exceeded the annual productivities reported from several other studies (Figure 5), illustrating the year-round growth of *Sphagnum* in Kolkheti (cf. Asada *et al.* 2003), as our hypothesis suggests.

Although both precipitation and water tables are higher and dry periods are shorter in winter, the main growth occurs during summer, which is 9 °C warmer with a mean temperature of 19.7 °C (Table 1, Figure 3). At temperatures below 0 °C, *Sphagnum* photosynthesis is interrupted by water freezing at the plant surface (Gaberšček & Martiničič 1987, cf. Grigal 1985, Moore 1989, Lindholm 1990, Asada *et*

al. 2003). Thus, *Sphagnum* growth in Kolkheti is halted for at least 1–7 days *per year* (Table 1). Minimum daily temperature drops below 0 °C on an additional 9–35 days (Table 1). Accordingly, *Sphagnum* growth in Kolkheti will to some extent be constrained by low temperatures in winter.

Global growth pattern

Sphagnum growth is assumed to increase towards the equator (cf. Wieder & Lang 1983). In our global analysis for *Sphagnum papillosum* we did not find that latitude explained *Sphagnum* growth. However, we identified a negative correlation between temperature and latitude; mean temperature during the growth period increased with decreasing latitude (i.e. moving towards the equator). As *Sphagnum* productivity increases with temperature, it may increase towards the equator if the water supply is sufficient. Moreover, higher photosynthetically active incident radiation at lower latitudes may explain higher *Sphagnum* productivity in Kolkheti (cf. Wieder & Lang 1983, Loisel *et al.* 2012).

In Kolkheti high and (in particular) evenly distributed precipitation, short duration of dry periods and high temperatures cause the annual productivities and year-round growth rates of *Sphagnum palustre* and *Sphagnum papillosum* to reach the highest values reported for these species growing under natural conditions worldwide. Our study demonstrates that it is not the amount of precipitation, but the frequency of rainfall in combination with high temperature that is decisive for peatmoss growth.

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