

# Drought stress, water table and photosynthetic activity of peat moss measured by fast fluorescence in alpine peatlands

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## ABSTRACT

Alpine peatlands are highly vulnerable ecosystems worldwide and are endangered by global warming. Peat moss metabolism and growth are governed by rainfall and the level of the water table in the moor. In a protected alpine peatland three sites with different distances from the open water and the water table were chosen to evaluate higher plant diversity and to determine the photosynthetic performance of some plants and of the peat moss layer (mainly *Sphagnum* sp.) at these sites using fast fluorescence kinetics (OJIP-test). The photosynthetic activity of peat moss decreased with greater distance from the water level. In contrast, photosynthesis of *Carex* was impeded at higher water levels. In the context of global warming, if increasing temperature and stronger winds dry the peat moss cover, the differences in observed stress response by a changing water table, we expect that higher plants will overgrow the peatmoss site, a phenomenon already partially observed in recent decades.

**KEYWORDS:** peat moss, peatland vegetation, *Sphagnum*, *Carex*, water level, photosynthetic activity, fast fluorescence, OJIP-test.

## 1. INTRODUCTION

Peatlands are wetlands where dead plant matter often accumulates in a cold climate parallel to a

slow decomposition rate of the organic materials. Peat bogs and moors are important environments and are frequently protected in many countries. A hundred years ago, they were widespread in Europe. Many were drained for agriculture during World War II [1, 2]. Peat bogs and moors are characterized by the presence of water at or near the land surface. They show unique soil conditions and a specialized biota [3]. While accumulating peat, they are an essential carbon sink [4]. In most peatlands, the water originates from precipitation and is low in nutrients. Moreover, the water in *Sphagnum*-dominated peatland is acidic and often brownish in color due to the accumulation of dissolved organic matter and end products of its decay [5, 6]. Plant biodiversity is restricted to species that tolerate low nutrients and water logging, such as sedges and certain grasses. Frequently, bog vegetation includes carnivorous plants, which can supplement the nitrogen deficit. The dominant vegetation is *Sphagnum* moss, also called peat moss, forming thick mats on top of wet peat. Primary net production has been estimated to be in the same high range as tropical rainforests [7-9]. Peatlands are highly dynamic, not only in the vegetation of mosses and higher plants but also in terms of their metabolism, CO<sub>2</sub> assimilation, respiration, and CH<sub>4</sub> emissions [10].

Peat moss plants are formed by the gametophyte in the generation cycle and consist of a stem and branches with fine leaves protruding from both

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parts. The top is shaped by an assembly of young bright green branches or leaves, the capitulum; below, the stem leaves lose chlorophyll and finally transform to hyaline cells, which can store large quantities of water. The photosynthetic activity of mosses is highly dependent on water availability and relative humidity [11-14]. Gas exchange and metabolism are regulated by the level of the water table and by the cover of the ground by vascular plants [15-17]. As peat mosses lack stomata, CO<sub>2</sub> uptake during photosynthesis is not controlled but rather limited by a variable water film on the leaves [12, 18, 19]. As a consequence, climate change lowering the water table is thought to be a major threat to wetlands: they may change from a carbon sink to a carbon source [20]. However, such changed C metabolism may be blocked by vegetation succession [21] or altered by enhanced mineralization and improved nutrient availability [15].

As alpine regions with low direct human intervention are especially susceptible towards global warming, alpine peatlands seem to be good models for studying changes in plant metabolism. The peat bog west of Lake Cadagno examined here is situated in a rock depression formed in a Dolomite area. Its size is approximately 300 m x 350 m (Fig. 1a). In addition to precipitation which annually amounts to between 930 mm (1949) and 2564 mm (1927), the moor is fed not only by low ionic input from the granitic mountains in the North, but also by subsurface springs in the dolomite rock with water of high salt content [22]. The average yearly precipitation in the past decade added up to 1731 mm.

This leads to widely varying ionic concentrations and pH in the brooks within the bog [23, 24]. The area is drained by a small brook into the river Murinascia.

Peat bogs harbor various grasses, sedges and some dicotyledons. The vegetation of the peat bog Cadagno has been studied by Geissler and Selldorf [25]. Various *Sphagnum* species and other peat moss species cover the floor in a completely dense mat and form diverse domed or raised shapes or hummocks. The western boundary of the Cadagno wetland is determined by the rampant alpine meadows towards the mountain Motta.

Thus, the water table of the wetland is more distant for *Sphagnum* sp. growing at the rising edge than for the moss close to the open water. The depth of the water table is important for the evapotranspiration of *Sphagnum* sp. [26], as well as for CO<sub>2</sub> sequestration. In higher plants, it is well established that photosynthesis is regulated by water availability. Drought and salt stress reduce photosynthetic activity as measured by a fast fluorescence rise, a noninvasive measure of plant vitality [27-31]. Also in peat moss, the photosynthetic activity as measured by its CO<sub>2</sub> uptake is highly sensitive to thallus dehydration [11, 12].

We investigated the photosynthetic activity of the head portions or the capitulum of *Sphagnum* sp. using the fast chlorophyll fluorescence technique (OJIP test) to determine whether the initial photosynthetic performance is determined by the distance of the peat moss from the level of the water table below the peat layer and compare it with the activity of higher plants at the same site.

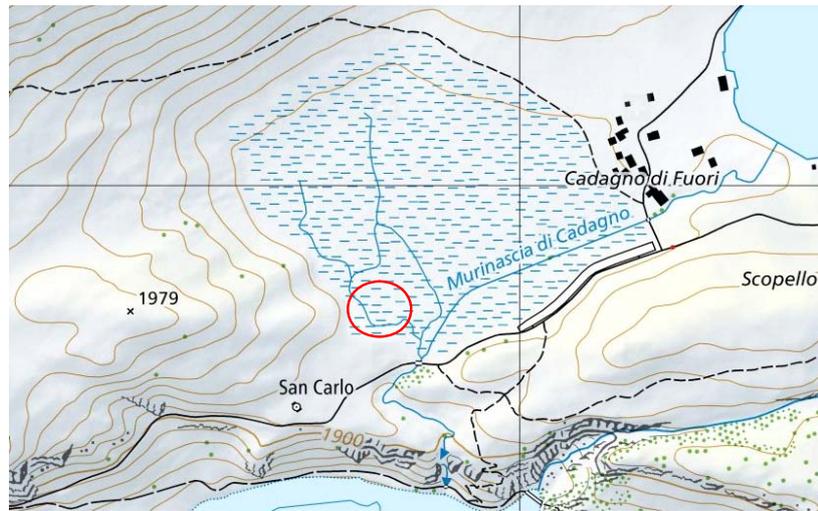
## 2. MATERIALS AND METHODS

### 2.1. Site description

The experimental site is located in the Val Piora (Ticino, Switzerland) (N 46° 54.691 E 8° 70.174, Swiss coordinates 696'855/156'860, 1915 m a.s.l.); the geographical location can be verified under //map.geo.admin.ch, using the search name "Cadagno di Fuori (TI-Quinto)". A map of the site is given in Fig. 1a and a view of the sampling site in Fig. 1b. A schematic illustration in Fig. 1c explains the relation of the 3 sampling sites to the water table in the moor.

### 2.2. Sampling and plant abundance

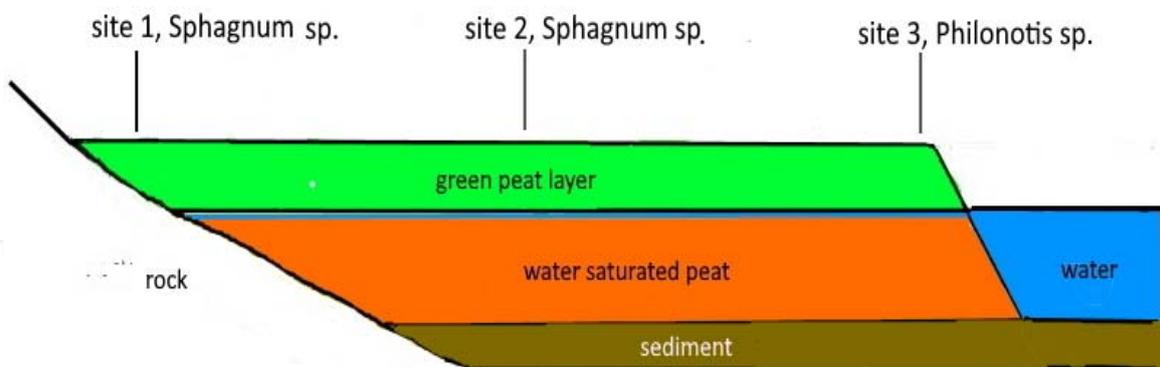
The special geology of the Piora Valley has been described by Peduzzi and Wildi [32]. The cover of the wetland consists of a thick layer of mainly *Sphagnum* species above a band of Dolomite rock. To characterize species diversity, squares of 1 x 1 m around each *Sphagnum* measuring site were drawn, and the composition of higher plant species and their frequency were recorded following the cover abundance scale of Braun-Blanquet [33] (Table 1).



**Fig. 1a.** Map of the wetlands west of Cadagno with the experimental site (circle).



**Fig. 1b.** Photo of part of the experimental site in the wetlands west of Cadagno; left: site 1, right: sites 2 and 3.



**Fig. 1c.** Scheme of a vertical profile at the experimental site, illustrating the height above the water level (horizontal distance between sampling sites - approximately 10 m).

**Table 1.** List of higher plants and their frequencies observed at the three peat moss sites with ecological pH and nutrient indicators (column 2 and 3) according to Landolt *et al.* [35]. The frequency of the species found is given following the cover abundance scale of Braun-Blanquet [33], ranging from +: 2%, 1: 2%-5%, 2: 5%-25%, 3: 25%-50%, 4: 50%-75%, 5: 75%-100%.

Species	Plant pH-index	Plant nutrient-index	Plant frequencies at		
			Site 1	Site 2	Site 3
<b>Moss cover</b>			<i>Sphagnum</i> sp.	<i>Sphagnum</i> sp.	<i>Philonotis</i> sp.
<i>Arnica montana</i>	2	2		2	
<i>Calluna vulgaris</i>	1	2		3	
<i>Carex davalliana</i>	4	2			1
<i>Carex flava</i> s.l.	2 - 4	2 - 4			1
<i>Carex nigra</i>	2	2	1	2	2
<i>Drosera anglica</i>	3	1		4	
<i>Euphrasia rostkoviana</i>	3	2		1	
<i>Equisetum palustre</i>	2	3			3
<i>Festuca rubra</i>		3		2	
<i>Molinia caerulea</i>	3	2	2	3	
<i>Parnassia palustris</i>	4	2	1		
<i>Potentilla erecta</i>	2	2		3	1
<i>Potentilla palustris</i>	2	2	1		
<i>Homogyne alpina</i>	2	2	1		
<i>Tofieldia palustris</i>	3	2	2		1
<i>Trichophorum caespitosum</i>	1	1	3	2	
<i>Vaccinium uliginosum</i>	1	2		3	

### 2.3. Defining indicator values for accompanying higher plants

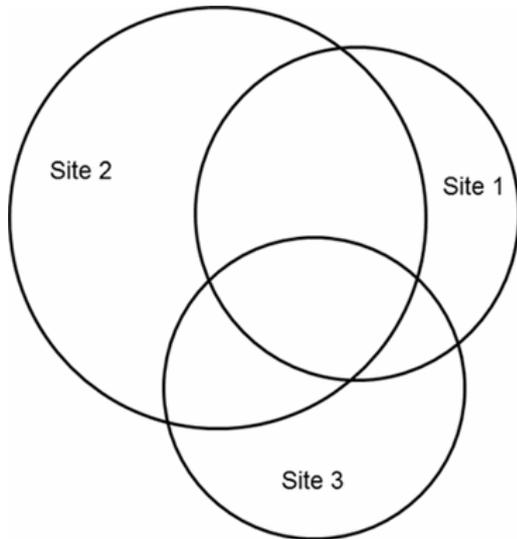
Landolt [34], Landolt *et al.* [35] and Ellenberg *et al.* [36] empirically characterized many plant species by specific indicator values in relation to available nutrients, especially nitrogen, and to the pH in the soil. The indicator values of Landolt are based on a simple ordinal classification of plants according to the position of their realized ecological niche using the ordinal scale of 1 (= very low soil nutrients) to 5 (= very rich soil nutrients, especially nitrogen). Concerning pH, the scale from 1 (soil pH within roots = 2.5 to 5.5) to 5 (soil pH = 6.5 to 8.5) covers the pH range in 5 overlapping sections. Thimonier *et al.* [37] used these indicators later for monitoring the ground vegetation in forests. These literature index values

for the plant species found are listed in columns 2 and 3 of Table 1.

### 2.4. Chlorophyll-*a* fluorescence

Fast chlorophyll-*a* fluorescence kinetics were analyzed using the portable fluorometer Pocket PEA (Hansatech, King's Lynn, England) after a dry week at the end of July 2019. From the peat moss accompanying higher plants, the widely present *Carex* and *Molinia* were selected. Peat moss was analyzed from three sites. Site 1 was situated towards the western side and approximately 30 cm higher in altitude compared to site 2, which was located approximately 10 m apart towards the open water. Site 3 was at the same level as site 2 but another 10 m away and at the edge of a water channel; it consisted of a hump of *Philonotis* sp. (see Fig. 1c).

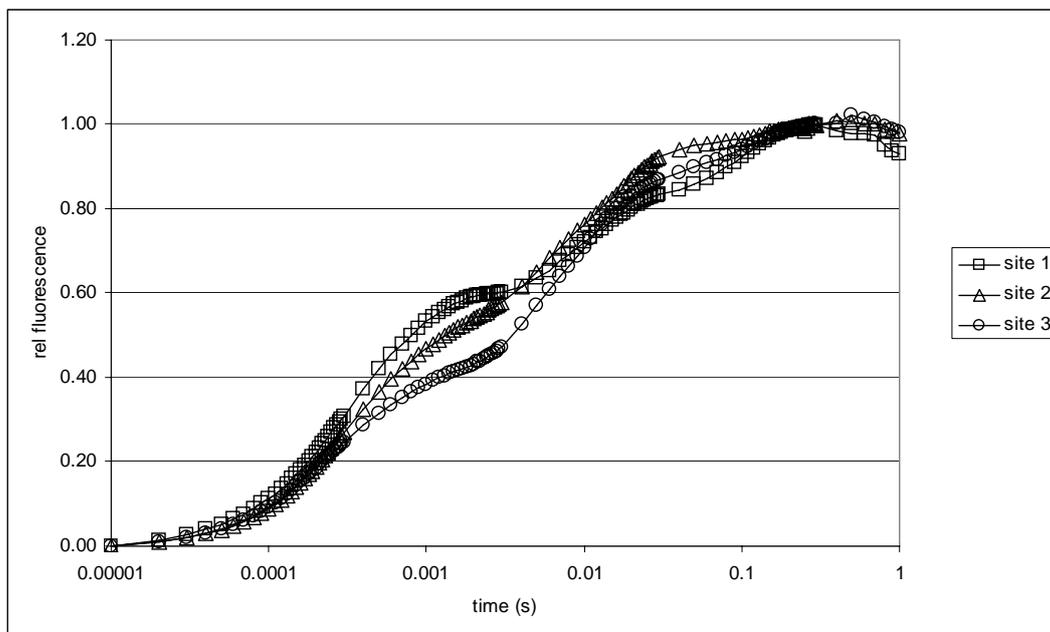
From *Sphagnum* and *Philonotis* moss, the bright green top (1 cm size) was separated from the more faint green part below. The top moss material and the leaves of *Carex* and *Molinia* were fixed in commercial leaf clips [38] and kept in the dark for



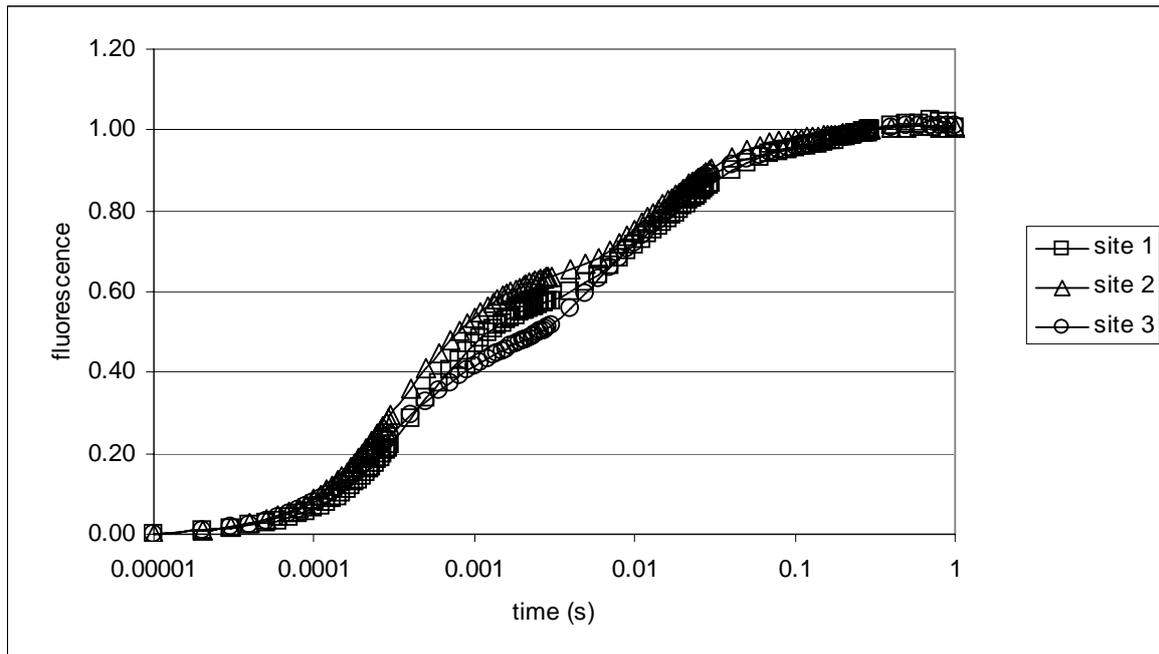
**Fig. 2.** Venn diagram for the distribution of higher plants at the 3 sites.

20 minutes prior to the fluorescence measurement to bring the electron acceptors of photosystem II to a fully oxidized state [38, 39, 40]. At each site, fast fluorescence was measured with 5 leaves from different plants or material from the capitulum of *Sphagnum* or *Philonotis* located at the same site.

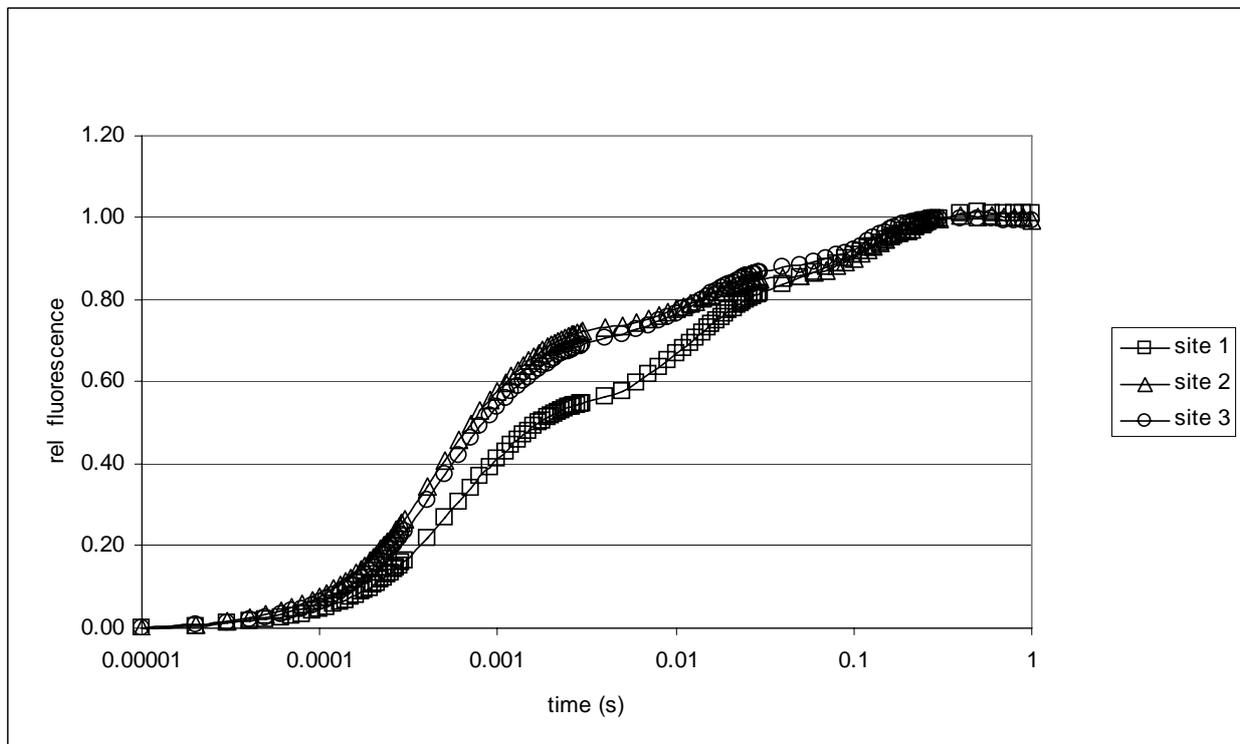
The excitation intensity was  $3500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  with red light of 650 nm for 3 sec. From the fluorescence induction signal with high temporal resolution from 10  $\mu\text{sec}$  to 3 sec, the instrument determined the initial ( $F_0$ ) and maximum ( $F_m$ ) fluorescence and calculated the variable fluorescence ( $F_v$ ) at specified time intervals. It also provided further specific parameters, such as the potential quantum yield of PS II ( $F_v/F_m$ ) or the performance index ( $PI_{\text{ABS}}$ ), as a general vitality measure [39, 40]. For further calculations and visualization, the experimental data were transferred into Excel spreadsheets to determine defined parameters and the mean values of the 5 replicates of the same plant species and location. For comparison of the kinetics, the fluorescence induction curves were normalized by setting  $F_0 = 0$  and  $F_m = 1$ . These results are presented in Figs. 2 to 5. The initial velocity was calculated as  $(F_{0.3\text{ms}} - F_{0.05\text{ms}}) / 0.25$ .



**Fig. 3.** Fast fluorescence rise with *Sphagnum* sp. (sites 1 and 2) and *Philonotis* sp. (site 3) on 30.7.2019 after normalization ( $F_0 = 0$ ,  $F_{\text{max}} = 1$ ); mean of 5 measurements.



**Fig. 4.** Fast fluorescence rise with *Sphagnum* sp. (sites 1 and 2) and *Philonotis* sp. (site 3) on 31.7.2019 after normalization ( $F_0 = 0$ ,  $F_{\max} = 1$ ); mean of 5 measurements.



**Fig. 5.** Fast fluorescence rise with *Carex nigra* at the 3 sites on 30.7.2019 after normalization ( $F_0 = 0$ ,  $F_{\max} = 1$ ); mean of 5 measurements.

## 2.5. Statistical treatment

To calculate the mean values, standard deviation and significance with t-test analysis, the software MaxStat was used. All data points presented in the figures are the means of 5 consecutive measurements.

## 3. RESULTS

### 3.1. Biodiversity of higher plants within the *Sphagnum* and *Philonotis* vegetation

The wetlands near Cadagno di fuori are protected by Swiss federal law. Geissler and Selldorf [25] mapped the vegetation of wetlands and characterized different communities. The moor is fragmented in small-area patches, has a high biodiversity and there are many areas worthy of protection. As there is no water reservoir, such as glaciers or snowfields, the water table varies, and even in years of high precipitation over the seasons, parts of the moor may become dry. Large areas are covered with a thick carpet of peat moss; up to more than a dozen different species have been counted [25, 41]. For our investigation, we sampled square plots of 1 m<sup>2</sup> within the *Sphagnum* and *Philonotis* mats on the west side of the wetland (Fig. 1a). At three sites, each consisting of one m<sup>2</sup>, the higher plants within the peat moss-covered ground were determined and their frequencies estimated (Table 1).

Table 1 presents 17 higher plant species, typical for an alpine peat bog [25, 41] with frequency and plant indices for nutrients and pH. The frequency data presented as a Venn diagram (Fig. 2) demonstrated a substantial overlap. Concerning nutrient indices, all plants except *Drosera* prefer the range 2 to 4, moderately poor to moderately rich in nutrients. The pH preference covers indices 1 to 4, giving a broad range between pH 3 and pH 7. This fits well with measured values in the open brooks by Wiggli *et al.* [24]. The widespread *Carex nigra* is found at all three sites, while other species are present only in one of the experimental plots.

The Jaccard index [42] indicates the similarity between sites. The highest similarity of 21% is seen between sites 1 and 2, with a total number of 3 higher plant species being present at both sites, followed by 18% similarity between sites 1 and 3 and 14% between sites 2 and 3.

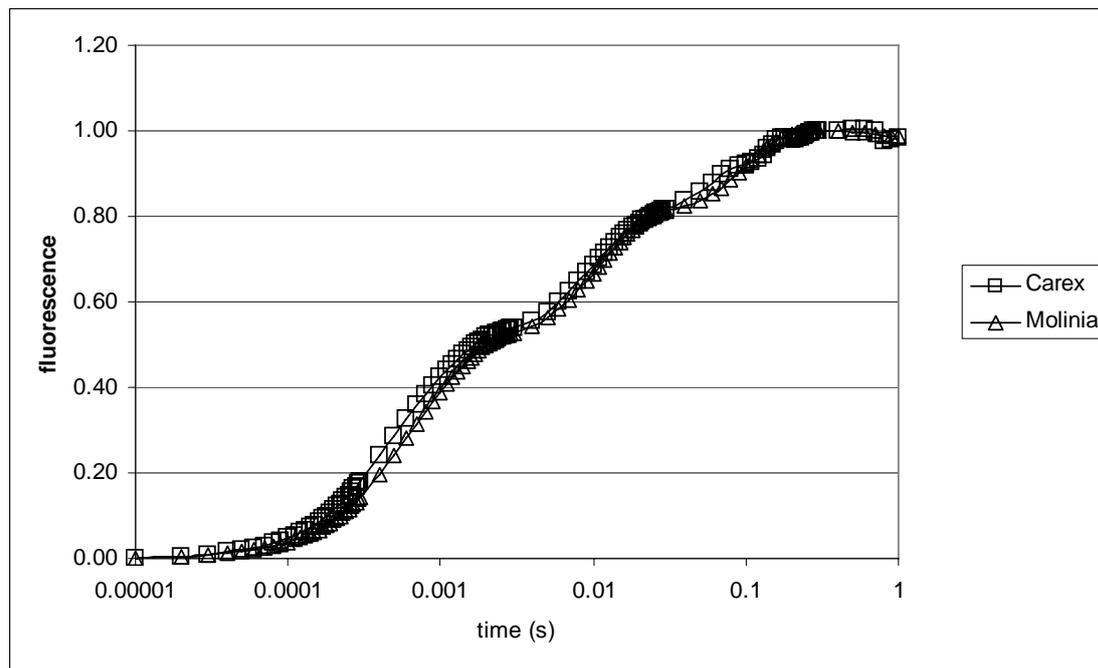
### 3.2. Fluorescence measurements

Here we present data collected during two days which follow a dry and sunny period, with a strong rain in the night within the measurements (see 'Discussion' section). All peat moss samples from the 3 sites showed the typical multistep induction kinetics of fast fluorescence rise as observed in higher plants and first described by Strasser and Strasser [39], (Figs. 3 and 4). The maximum  $F_m$  is reached after approximately 0.3 sec and the J and I steps are present at 0.003 and 0.03 sec, respectively.

*Philonotis* at site 3, close to the open water, showed a slower fluorescence rise and a lower J-value than *Sphagnum* at both sites 1 and 2 and did not differ between the two days. The traces of *Sphagnum* at these sites stayed rather close together. However, on July 30<sup>th</sup>, the rise of *Sphagnum* at site 1 was slightly more rapid than that of *Sphagnum* at site 2 (Fig. 3); in contrast, the following day, the graph indicates a faster rise at site 2 (Fig. 4).

To compare higher plants with peat moss, *Carex nigra*, the only species present in all 3 plots was chosen. Measurements of *Carex* leaves resulted in a different presentation of the 3 curves compared to peat moss. At site 1, at the edge of the wetland, a slower rise was observed compared to the waterlogged sites 2 and 3 (Fig. 4). The fluorescence rise of another frequent wetland plant, *Molinia*, was practically identical to *Carex* at site 1 (Fig. 6) and similar to *Carex* the day before, as shown in Fig. 5.

The kinetic differences between *Sphagnum*, *Philonotis*, *Carex* and *Molinia* at the 3 sites are numerically summarized in Table 2. Statistical significance is indicated for  $p = 0.05$ . These data strengthen the interpretations of the kinetics in Figs. 3 to 6 and present statistical evidence of ecologically important differences between site 1 and site 2. On 30.7.2019 *Sphagnum* presented a lower  $F_v/F_m$  at site 1, while on the following day, the peat moss at all 3 sites showed maximum  $F_v/F_m$  values close to 0.8. Similarly, the PI was lower at site 1 at 30.7, while at 31.7, no significant differences were observed among the 3 sites. This holds for all the measurements with peat moss, except for  $F_j$ , where the water-saturated *Philonotis* showed a value clearly lower than



**Fig. 6.** Fast fluorescence rise with *Carex nigra* and *Molinia caerulea* at site 1 on 31.7.2019 after normalization ( $F_0 = 0$ ,  $F_{\max} = 1$ ); mean of 5 measurements.

*Sphagnum* at both sites 1 and 2. For *Carex*, except for  $F_v/F_m$ , plants at site 1 showed a better photosynthetic performance than plants from the more flooded sites 2 and 3, and no difference was observed between *Carex* and *Molinia* at site 1.

#### 4. DISCUSSION

Today, global warming is one of the most important issues that will change landscapes, environments and biomes. Increasing temperatures and lacking precipitation will lead to droughts in many regions. Peat bogs are especially vulnerable, as their plant species are highly adapted to water logging and low nutrient conditions. Geissler and Selldorf [25] distinguished 4 main groups of vegetation types: acid hummocks covered with more or less dwarf-shrubs, acid and wet fens, more alkaline moore manures and humid to more dry marshes. Our site of measurements may be indexed as Trichophoretum, at the transition from a humid to a dry site. Already 35 years ago, parts of the moor were described as threatened and suffered from drought, with lacking precipitation in the summer months in the decades before. The fragment studied at the west border of these wetlands (Fig. 1)

is fully covered by several species of peat moss *Sphagnum* and *Philonotis* and contains various grasses and sedges. The indicator values for nutrient conditions and pH (Table 1) of the latter at the three plots supplement the description of the peat vegetation [25] and the data on the water chemistry in the brooks nearby [23, 24]. Global warming with its consequences, increased evaporation, less precipitation and a lowered water level in peatland would increase the burden on the dense moss cover. Waterlogged bogs store high amounts of organic carbon; a lowering of the water table could lead to massive carbon loss [15, 43, 44] by higher fluxes of  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  [45, 46, 47, 48, 49].

Photosynthesis, the primary process for growth of plants, is well known to be sensitive to many environmental effects, such as light, temperature, water and nutrient availability. For peat moss the water content, defined by precipitation and the distance from the water table, is of main importance. The noninvasive fluorescence induction technique (OJIP-test) allows an extensive interpretation of the effects of many environmental stress factors (50 and references there). For our alpine peatland the measurement of the fluorescence kinetics gave

interesting information on the photosynthetic activity with regard to the water table in the peat bog. For *Carex*, we observed that on July 30<sup>th</sup>, the less humid site 1 was different from sites 2 and 3 for the parameters  $F_j$ ,  $V_{init}$  and PI, while the  $F_v/F_m$  values did not differ statistically. These data show that *Carex* performs better when its roots are not submerged. Possibly the oxygen supply to the roots is limiting in the thick peat layer. The lack of significant differences in  $F_v/F_m$  at the 3 sites confirms the frequently reported observation that  $F_v/F_m$  is generally less sensitive to external stress than other markers. The fluorescence kinetics of *Carex* and *Molinia* at the same site were practically identical (Fig. 6), and the data in Table 2 indicated no significant difference between the two species or to the *Carex* results the day before.

For the peat mosses *Sphagnum* and *Philonotis*, all fluorescence rises were close together on July 31<sup>st</sup> and the parameters  $F_v/F_m$ ,  $F_j$ ,  $V_{init}$  and PI showed no statistical difference between the three sites despite the different levels of the water table (Table 2). In contrast, on the day before, site 1 with the largest distance to the water level was

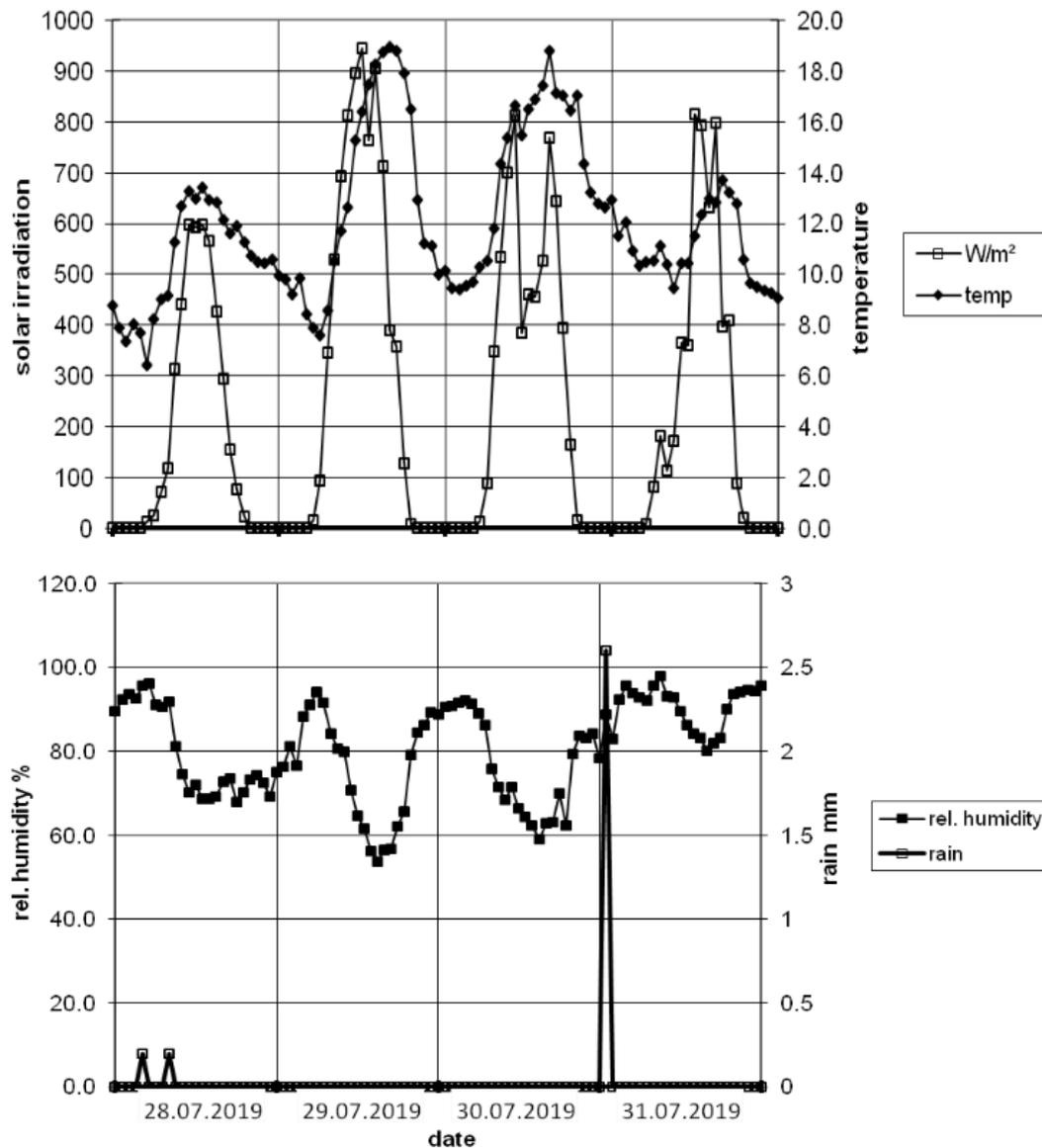
different compared to sites 2 and 3 for  $F_v/F_m$  and PI. The  $F_j$  values at sites 1 and 2 were similar but differed ( $p < 0.05$ ) from site 3, while for  $V_{init}$ , the values showed no difference. This last observation is possibly due to the signal-to-noise ratio of the fluorescence signals which is much greater in the early  $\mu\text{sec}$  phase of the measurement. These data show that *Sphagnum* performs better at sites closer to the water table below the peat-layer or when wetted by rain, similar to *Philonotis* at site 3 near the open water. It must be noted that *Philonotis* was not found at the edges of the wetland.

These results agree with many reports on the strong dependence of peat metabolism on the water level and water content of peat moss with different methods [12, 13, 14, 15, 16, 17, 47, 51, 52, 53]. In contrast to most techniques used, the fast fluorescence kinetics or the OJIP-test is noninvasive and results are obtained within minutes.

To explain the different results with *Sphagnum* obtained at the two sites and days, we have to consult the meteorological data. Both days were rather sunny, with clouds on July 30<sup>th</sup> and in the morning of July 31<sup>st</sup> and lower temperatures on

**Table 2.** Mean of important parameters characterizing the fast fluorescence rise (n=5). Letters indicate statistically significant differences within the same data collection ( $p < 0.05$ ).

30.7.2019	<i>Sphagnum</i>		<i>Philonotis</i>	<i>Carex nigra</i>			<i>Molinia caerulea</i>
site	1	2	3	1	2	3	1
Fv/Fm	0.64 a	0.77 b	0.79 b	0.80 a	0.76 a	0.79 a	
Fj	0.60 a	0.58 a	0.47 b	0.55 a	0.72 b	0.69 b	
Vinit	1.02 a	0.92 a	0.82 a	0.58 a	0.93 b	0.86 b	
PI	0.44 a	1.15 b	1.70 b	2.40 a	0.83 b	1.09 b	
31.7.2019	1	2	3	1	2	3	1
Fv/Fm	0.79 a	0.80 a	0.79 a	0.83 a			0.83 a
Fj	0.62 a	0.63 a	0.53 b	0.53 a			0.53 a
Vinit	0.87 a	1.00 a	0.87 a	0.63 a			0.51 a
PI	1.53 a	1.16 a	1.67 a	3.25 a			3.39 a



**Fig. 7.** Global insolation, temperature, relative humidity and rainfall on the two experimental days and two days before (Swiss meteo and Alpine Station Piora).

the 2<sup>nd</sup> day (Fig. 7). More importantly, a short rain event covered the Piora Valley at night from July 30<sup>th</sup> to 31<sup>st</sup>, resulting in nearly 100% relative humidity in the morning of July 31<sup>st</sup>. This allowed the *Sphagnum* mats at site 1 to become highly saturated with water. A similar restoration process was observed in field and laboratory experiments, when water was sprayed on partially dried *Sphagnum* samples (unpublished observations).

Air humidity has been described as an important driver of moss metabolism in Tibetan grasslands [54].

Our results fit well with the observations cited above, where growth and CO<sub>2</sub> uptake by peat moss depended on the water content and the level of the water table.

Dry weight determinations on July 30<sup>th</sup> resulted in 35% dw. for the top 3 cm of *Sphagnum* at site 1 and 11% at site 2, resulting in water contents of approximately 190% and 860%, respectively. Optimal water contents for New Zealand green moss samples as high as 1200 to 2000% have been reported [12], while Van Gaalen *et al.* [52]

reported maximal photosynthesis between 800 and 900% water content. In lab experiments,  $F_v/F_m$  dropped rapidly below 1000% water content from about 0.55 down to less than 0.3 [52]; our field experiments displayed values of 0.64 at site 1, but 0.77 at site 2. The alpine peat moss in the Piora valley seemed to be better adapted to these changes under natural conditions compared to these lab experiments.

In a study to simulate the effects of global warming, a long-term large field experiment started in a peatland in Poland [55, 56]. Warming, reduced precipitation or the combination of both in large peat areas had a strong negative effect on the chlorophyll concentration in *Sphagnum*, while in *Carex* or *Oxycoccus*, the effect was negligible. Similarly, the quantum yield of PSII dropped in *Sphagnum*, but showed no change in higher plants except in *Menyanthes* [55]. Additionally, due to the different treatments even morphological changes within *Sphagnum angustifolia* and *Sphagnum fallax* were observed ( $p < 0.05$ ) [56]. This shows that species of higher plants as well as species within the *Sphagnum* genus are differently tolerant to stress induced by warming or limited precipitation. In contrast, Flanagan and Syed [21] found that photosynthesis and respiration were stimulated in a boreal peatland ecosystem in response to warmer and dryer conditions. Studying the succession of different species of *Sphagnum* when wet meadows develop into bogs, a decrease in photosynthetic activity by *Sphagnum* species was observed [57], parallel to an increase in stress tolerance and species richness [58]. It seems that the *Sphagnum* group has a high capability to respond and adapt to short- and long-term changes in the environment.

## CONCLUSIONS

Peat mosses as well as higher plants in peatlands react sensitive to changes in the water table. While the photosynthetic metabolism of mosses, mainly *Sphagnum* sp., is highest when the cells are supersaturated at high water level, in higher plants such as *Carex* and *Molinia*, photosynthesis is hindered, possibly due to anoxic conditions in the root system. The fast fluorescence technique (OJIP-test) has been confirmed as an ideal tool to monitor changes in plant activity in field work.

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## ETHICS APPROVAL AND CONSENT TO PARTICIPATE

No endangered plants were involved; furthermore, the Center for Alpine Biology, Piora, has permission for environmental and ecological experiments in the Piora valley.

## CONSENT OF PUBLICATION

Not applicable.

## AVAILABILITY OF DATA AND MATERIALS

The original PEA data files can be obtained from the corresponding author (<https://www.botinst.uzh.ch/en/research/emeriti/rbachofen.html>).

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## AUTHORS' CONTRIBUTIONS

The project was designed by J.S and R.B. and the experimental work, collection and classification of plant material, measuring fast fluorescence emission and processing the data was carried out by A.SH, E.H., L.I. and S.H. The manuscript and the figures were prepared by R.B. and J.S. All authors read, reviewed and approved the final manuscript.

**CONFLICT OF INTEREST STATEMENT**

The authors declare no conflict of interest.

**ABBREVIATIONS**

OJIP	fast fluorescence rise from $F_0$ to $F_m$
$F_0$	initial fluorescence
$F_m$	maximal fluorescence P after 1 sec
$F_v$	variable fluorescence, = ( $F_m - F_0$ )
PI	photosynthetic performance index
J-step	variable fluorescence at 2 ms, = $F_j$
RC	reaction center
PS II	photosystem II
PS I	photosystem I
PEA fluorimeter	photosynthetic efficiency analyzer

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