Effects of Simulated Trampling on Chlorophyll Fluorescence Characteristics of Sphagnum medium (Postprint)

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Abstract

The effects of human trampling on wetland moss ground cover have long remained unclear. Using red-type and yellow-green-type Sphagnum magellanicum collected from open areas and forest edges of Yueliangwan Wetland in the Changbai Mountains as experimental materials, human trampling was simulated indoors. Chlorophyll fluorescence parameters were measured using a portable modulated chlorophyll fluorometer to investigate the fluorescence parameter responses of the two types of S. magellanicum under different trampling intensities and cycles. Results showed that during the second trampling cycle, the PSII actual photochemical quantum yield [Y(II)] and relative electron transport rate (ETR) of red-type S. magellanicum decreased with increasing trampling intensity, whereas those of the yellow-green type trampling groups were all greater than the control group. At the end of trampling, the Y(II) and ETR values of red-type trampling groups were significantly lower than those of the control group, while for the yellow-green type, only the light trampling group was lower than the control. The non-regulated energy dissipation quantum yield [Y(NO)] of yellow-green type S. magellanicum trampling groups was even lower than that of the control group. The study indicates that although Sphagnum plants can tolerate certain trampling stress, as trampling cycles increase and intensity grows, the cumulative stress effect strongly inhibits their growth. Red-type Sphagnum, commonly found in open areas, exhibits lower tolerance to human trampling than yellow-green type Sphagnum from forest edge habitats. In wetland conservation and management, tourist trampling disturbance should be reduced, and particularly, tourist access to open area habitats should be strictly controlled.

Full Text

Effect of Simulated Trampling on Chlorophyll Fluorescence Characteristics of *Sphagnum magellanicum*

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Abstract

The impact of anthropogenic trampling on wetland bryophyte ground cover remains unclear. Using red and yellow-green morphotypes of *Sphagnum magellanicum* collected from open areas and forest margins respectively in Yueliangwan wetland of the Changbai Mountains, we simulated human trampling indoors and measured chlorophyll fluorescence parameters using a portable pulse-amplitude modulation fluorometer. The study examined fluorescence responses of both morphotypes under different trampling intensities and rounds. Results showed that during the second trampling round, effective PSII quantum yield [Y(II)] and electron transport rate (ETR) of red *S. magellanicum* decreased with increasing trampling intensity, while those of the yellow-green type were higher in trampled groups than in controls. At the end of the experiment, Y(II) and ETR in trampled red morphotypes were significantly lower than controls, whereas for yellow-green types, only light trampling resulted in lower values compared to controls. Non-regulated energy dissipation [Y(NO)] in trampled yellow-green *S. magellanicum* was even lower than in controls. These findings indicate that although *Sphagnum* can tolerate certain trampling stress, cumulative effects become strongly inhibitory as trampling rounds increase and intensity grows. The red morphotype, common in open habitats, shows lower trampling tolerance than the yellow-green morphotype from forest margin habitats. Wetland protection and management should reduce visitor trampling disturbance, particularly by strictly controlling access to open habitats.

Key Words: anthropogenic trampling, bryophyte, chlorophyll fluorescence parameters, wetland, peat

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As natural landscape development intensifies annually, anthropogenic trampling adversely affects vegetation cover and species diversity, increases risks of alien species or weed invasion, and accelerates ecosystem degradation (Pertierra et al., 2013; Barros et al., 2013). Current research on trampling stress primarily focuses on vascular plants (Pescott & Stewart, 2014). *Sphagnum* mosses, as the primary carbon-sequestering plants in most peatlands, play a significant role in global carbon cycling (Mcneil & Waddington, 2003). These plants lack root support, have relatively simple stem cell structures, and lack vascular bundles for conduction, potentially making them more vulnerable to trampling threats. However, the effects of increasing tourist trampling on *Sphagnum* remain unreported.

Photosynthesis is the most crucial physiological process for plant growth and development. Chlorophyll fluorescence contains important information about photosynthesis, including light energy transfer and allocation, photoinhibition, and photodamage status (Gao et al., 2019). Its non-contact, non-invasive measurement characteristics have greatly advanced research on photosynthesis and related protective mechanisms in *Sphagnum* (Proctor & Smirnoff, 2015). Previous studies have shown that vegetation removal (Laine et al., 2015), simulated warming (Gerdol & Vicentini, 2011), and increased nitrogen deposition (Granath et al., 2009) significantly affect chlorophyll parameters in *Sphagnum fuscum*.

In seed plants, the same species can exhibit different morphologies or even ecotypes in different environments due to variations in water, light, and nutrients (Zhou, 2004). Similarly, in bryophytes, the same species shows substantial morphological differences under different habitat conditions. In wetlands, some moss species forming hummocks can display different colors depending on light intensity, appearing green in shaded environments and red or brown in well-lit habitats (Hooijmaijers, 2008). Laine (2011) and Manninen et al. (2011) found that different colored *Sphagnum* exhibit different tolerances to light intensity and nitrogen stress. However, the differential responses of different colored *Sphagnum* to trampling stress remain unknown.

This study used red and yellow-green morphotypes of *Sphagnum magellanicum* from open areas and shaded forest margins of Yueliangwan wetland in the Changbai Mountains to investigate the effects of trampling stress on chlorophyll fluorescence parameters in different morphotypes. We tested two hypotheses: (1) With increasing trampling intensity and rounds, initial fluorescence (F0) would increase, while PSII maximum photochemical efficiency (Fv/Fm), PSII actual quantum yield [Y(II)], and relative electron transport rate (ETR) would decrease. However, plants could reduce damage through regulatory mechanisms including regulated energy dissipation quantum yield [Y(NPQ)], non-regulated energy dissipation quantum yield [Y(NO)], and non-photochemical quenching coefficient (NPQ), potentially even exceeding their original photosynthetic levels. (2) The yellow-green morphotype of *S. magellanicum* would demonstrate stronger trampling stress resistance compared to the red morphotype.

1.1 Study Site Description

Yueliangwan wetland in Erdaobaihe Town, Changbai Mountains, experiences a temperate monsoon climate with long winters and short summers. The annual mean temperature is only 2.2 °C, with the hottest month (July) averaging 27.9 °C and the coldest month (January) averaging -26.6 °C. Annual precipitation is approximately 780 mm, the frost-free period lasts only about 110 days, and the freezing period is extensive with maximum frozen soil depth exceeding two meters (Guo, 2007). The wetland is dominated by *Sphagnum magellanicum*, which forms relatively low hummocks with coverage exceeding 90%. Associated sedges (*Carex* sp.) form a herbaceous layer, while in some areas near forests, *Sphagnum fuscum* forms larger hummocks with sparse herbaceous plants and occasional low-growing *Larix olgensis*.

In December 2016, we selected red morphotype *S. magellanicum* from open areas and yellow-green morphotype from shaded forest margins as experimental materials. After removing snow cover, intact *Sphagnum* blocks were excavated with spades and transported to the laboratory. Indoors, we selected healthy specimens of both morphotypes with similar growth conditions, cut the upper 8 cm sections, and placed them uniformly into vinyl cups (7 cm height, 12 cm top diameter, 7 cm bottom diameter) according to natural field density. Samples were placed in an artificial climate chamber on the same day.

1.3.1 Indoor Simulation of Trampling

Excavated *Sphagnum* blocks were placed in large plastic basins. After the ice and snow between plants melted, a person weighing 50 kg randomly trampled on them. We measured and calculated the mean ratio of *Sphagnum* subsidence depth to footprint length under each trampling event, recorded as A (A 1/3). For the 8 cm *Sphagnum* samples in cups, we simulated trampling using a custom trampling device until the subsidence depth to moss height ratio approximated A. The resulting weight equivalent represented a 50 kg person' s body weight. Testing revealed the trampling device mass was approximately 331 g, applied about 3 cm from the moss capitulum.

1.3.2 Indoor Trampling Experiment

In Changbai Mountain wetlands, severe anthropogenic trampling occurs primarily during summer economic crop harvesting periods. Based on field day-night conditions, climate chamber settings were: 14 h/10 h photoperiod with corresponding light intensity of 7500 lx/0 lx, temperature of 20 °C, and relative humidity of 73%. Distilled water was added to maintain a water level of 2 cm. Sample positions were randomly changed daily to ensure uniform light exposure across all cups. After 9 days of indoor acclimation, trampling treatments were applied using weights. Four trampling treatment levels were established: no trampling (control), light trampling (trampled once every 7 days), moderate trampling (trampled 4 times every 7 days), and severe trampling (trampled 8 times every 7 days). Three trampling rounds were conducted with three replicates per treatment. Trampling occurred at 9:30 AM each time, with chlorophyll fluorescence parameters measured using a portable pulse-amplitude modulation fluorometer (PAM2500) starting at 10:00 AM, then every 2 hours for a total of 5 measurements per round. Means were calculated, with 360 measurements accumulated throughout the experiment.

Measured parameters included initial fluorescence (F0), PSII maximum photochemical efficiency (Fv/Fm), PSII actual quantum yield [Y(II)], regulated energy dissipation quantum yield [Y(NPQ)], non-regulated energy dissipation quantum yield [Y(NO)], relative electron transport rate (ETR), and non-photochemical quenching coefficient (NPQ).

1.4 Data Processing and Analysis

SPSS 19.0 was used for data processing and statistical analysis. Repeated measures ANOVA was applied to analyze changes in chlorophyll fluorescence parameters across different trampling rounds, with data grouped by trampling intensity for pairwise comparison using Least Significant Difference (LSD) tests. One-way ANOVA was used to analyze effects of trampling intensity on fluorescence parameters within the same round, and height changes of different *S. magellanicum* types under different intensities after trampling. Significance level was set at =0.05.

2.1 Effects of Trampling Stress on Morphological Characteristics of *Sphagnum magellanicum*

After the trampling experiment, no visible leaf damage was observed in either morphotype, but plant height was significantly compressed without recovery [Figure 1: see original paper]. Control group red morphotype *S. magellanicum* grew shorter than yellow-green morphotype (P=0.013). With increasing trampling intensity, plant height of both morphotypes continuously decreased, with significant differences among intensities (P<0.001) .

TABLE:1 Height of red and yellow-green *Sphagnum magellanicum* under different trampling intensities (mean±SD) (cm)

Type	Control	Light trampling	Moderate trampling	Severe trampling
Yellow-green	8.97±0.15 Aa	6.30±0.17 b	5.47±0.12 c	4.70±0.17 d
Red	8.57±0.06 Ba	6.37±0.15 b	5.60±0.10 c	4.90±0.10 d

Note: Different lowercase letters indicate significant differences among trampling intensities for the same S. magellanicum* type (P<0.01). Different capital letters indicate significant differences between the two *S. magellanicum* types under the same trampling intensity (P<0.05).*

2.2 Effects of Trampling Stress on F0 and Fv/Fm of *Sphagnum magellanicum*

Red morphotype F0 increased with trampling rounds ($P<0.05$). During the second round, F0 was highest under severe trampling at 1.375 times the control value, while in the third round, F0 was highest under light trampling ($P<0.01$), reaching 2.003 times the control [Figure 2a: see original paper]. Yellow-green morphotype F0 under light and moderate trampling remained higher than control and severe trampling, with differences increasing across rounds. In round two, severe trampling F0 was significantly lower than other intensities ($P<0.01$), but recovered to control levels by round three [Figure 2b: see original paper].

Red morphotype Fv/Fm in round one was significantly lower than in rounds two and three ($P<0.01$). Light trampling Fv/Fm in round three was significantly lower than control ($P<0.01$) at 97.9% of control value [Figure 2c: see original paper]. Yellow-green morphotype control and light trampling Fv/Fm stabilized in round two, while moderate and severe trampling showed initial increase followed by decrease [Figure 2d: see original paper].

2.3 Effects of Trampling Stress on Y(II), Y(NPQ), and Y(NO) of *Sphagnum magellanicum*

Red morphotype Y(II) gradually decreased under light trampling ($P<0.01$). During round two, Y(II) decreased with increasing trampling intensity. In round three, differences between trampled and control groups became more pronounced ($P<0.01$) [Figure 3a: see original paper]. Yellow-green morphotype Y(II) continuously decreased under severe trampling. In round two, Y(II) under severe trampling was significantly higher than other treatments. In round three, Y(II) reached its lowest value under light trampling [Figure 3b: see original paper].

Red morphotype Y(NPQ) showed no significant differences among intensities in round one, increased with intensity in round two, and was significantly higher in treatment groups than control in round three ($P<0.01$) [Figure 3c: see original paper]. Yellow-green morphotype Y(NPQ) showed similar trends to red morphotype in rounds one and three, but opposite trend in round two, decreasing with intensity [Figure 3d: see original paper].

Both morphotypes showed Y(NO) trends higher than control in round one. By round three, red morphotype showed no significant differences among treatments, while yellow-green trampled groups were significantly lower than control ($P<0.01$) [FIGURE:3e,f] at 95.2%, 92.6%, and 93.1% of control values.

2.4 Effects of Trampling Stress on ETR and NPQ of *Sphagnum magellanicum*

Red morphotype ETR showed little difference among treatments in round one, but decreased with intensity in round two, with moderate and severe trampling significantly different from control ($P<0.01$) at 84.8% and 71.7% of control values. In round three, all trampled groups were significantly lower than control ($P<0.01$) at 70.5%, 79.2%, and 76.1% of control [Figure 4a: see original paper]. Yellow-green morphotype ETR was lower in all trampled groups than control in round one, significantly higher under severe trampling in round two ($P<0.01$), and showed no significant differences among treatments except light trampling in round three [Figure 4b: see original paper].

Both morphotypes showed no NPQ differences in round one, with trampled groups higher than control in round three. Red morphotype NPQ increased with intensity in round two, while yellow-green morphotype decreased, with severe trampling significantly lower than other intensities ($P<0.01$) [FIGURE:4c,d].

3.1 Relationship Between Trampling Stress and Chlorophyll Fluorescence

Initial fluorescence (F0) serves as an indicator of plant damage status (Honorato Júnior et al., 2015). F0 fluctuations in control groups during the first two rounds were associated with winter sampling timing and low-temperature stress (Brüggemann, 1992). Despite indoor recovery, the severe Changbai Mountain winter caused some damage to photosynthetic organs. In round one, F0 under light trampling showed no significant difference from control for either morphotype, but was significantly higher than control by experiment end, indicating cumulative stress effects that damaged thylakoid membranes or photosynthetic pigments (Liu et al., 2004) and limited photosynthesis. This aligns with our hypothesis that trampling stress increases F0. After trampling, light trampling F0 was significantly higher than severe trampling in both morphotypes, possibly because certain stress intensity thresholds induce stronger protective enzyme activity, reducing plant damage.

PSII actual quantum yield [Y(II)], regulated energy dissipation quantum yield [Y(NPQ)], and non-regulated energy dissipation quantum yield [Y(NO)] represent primary pathways for PSII reaction center light quantum consumption (Gao et al., 2018). Xiang et al. (2014) found that when *Sinosenecio jishouensis* experienced stress causing Y(II) reduction, Y(NPQ) increased correspondingly, and when regulatory protection mechanisms were overwhelmed, plants activated non-regulatory self-protection mechanisms. Our results show that Y(NPQ) and Y(II) changes in both *S. magellanicum* morphotypes under trampling stress followed this pattern. At experiment end, Y(NO) differences between trampled and control groups were minimal, indicating trampling stress caused no irreversible damage. This may be because inter-round recovery periods provided buffer time for plants to activate self-regulatory repair mechanisms (Ma & Xie, 2008).

Mechanical damage not only reduces PSII actual quantum yield [Y(II)] but also disrupts electron transport pathways, causing excess electrons to leak and form reactive oxygen species (ROS) (Bown & Macgregor, 2002), exacerbating photosynthetic apparatus damage. Under light trampling, red morphotype ETR continuously decreased with trampling rounds, indicating inhibitory effects on electron transport rate. Zeaxanthin-mediated energy quenching represents a self-protection measure (Golan et al., 2010). When trampling stress adversely affects plants and reduces ETR, NPQ values increase correspondingly, enhancing thermal dissipation to maintain photosynthetic electron regulation stability (Mamat et al., 2014). Our study indicates both red and yellow-green *S. magellanicum* can process harmful ROS harmlessly through energy quenching systems composed of PSII carotenoids, superoxide dismutase, and ascorbic acid (Proctor & Bates, 2018; Ralph et al., 2005), thereby reducing self-damage.

3.2 Differences in Chlorophyll Fluorescence Between Different Ecotypes of *Sphagnum*

Yellow-green *S. magellanicum* primarily inhabits shaded habitats, while red morphotype grows mainly in open areas. Bonnett et al. (2010) found that shaded mosses often have greater chlorophyll concentrations than open-area species. Chlorophyll concentration is an important indicator of photosynthetic capacity and regulates biomass accumulation (Du et al., 2019). Although we did not directly measure chlorophyll content, initial fluorescence (F0) serves as a good indicator of chlorophyll content (Honorato Júnior et al., 2015). We found that under identical trampling conditions, yellow-green morphotype F0 was consistently higher than red morphotype, indicating higher chlorophyll concentration. This aligns with Bonnett et al. (2010).

After trampling, yellow-green morphotype Fv/Fm in trampled groups showed no significant difference from control, while red morphotype decreased slightly. Trampled red morphotype Y(II) was significantly lower than control, whereas yellow-green morphotype only decreased slightly under light trampling. These results indicate yellow-green *S. magellanicum* possesses higher trampling tolerance than red morphotype, possibly because more intact chlorophyll under trampling stress enables yellow-green morphotype to maintain normal photosynthesis.

Carotenoids (lutein plus carotene) are photosynthetic pigments that primarily absorb excess light energy and quench ROS, thereby preventing membrane lipid peroxidation (Yin & Tian, 2013). At experiment end, red morphotype Y(NPQ) and NPQ in trampled groups were significantly higher relative to their controls compared to yellow-green morphotype, indicating open-area red morphotype has higher carotenoid proportions for better dissipation of excess light energy. This is consistent with Marschall & Proctor (2004). Evidence shows that NPQ photoprotection in open-area mosses not only exceeds that of shaded mosses but also far surpasses most vascular plants (Proctor & Smirnoff, 2011).

These findings suggest that open-area plants represented by red *S. magellanicum* may prioritize photoprotection over energy capture, while shaded plants represented by yellow-green morphotype possess stronger trampling tolerance due to more intact chloroplasts. Furthermore, Laine et al. (2011) found that red morphotype *Sphagnum* in open areas, suffering long-term high-light inhibition, often has lower photosynthetic efficiency than shaded green morphotypes. Manninen et al. (2011) found yellow-green *S. capillifolium* had stronger nitrogen stress tolerance than red morphotype. We infer that when facing environmental stress, yellow-green morphotype with higher chlorophyll concentration generally exhibits stronger stress tolerance than open-area red morphotype.

Although short-term trampling primarily reduces photosynthetic efficiency in red *S. magellanicum*, long-term trampling stress can reduce surrounding vascular plant biomass (Takala et al., 2012). Even for relatively trampling-tolerant yellow-green *S. magellanicum*, this can lead to water loss from sun exposure and photosynthesis inhibition (Laing, 2014). Gerdol et al. (1994) found chlorophyll decomposition accelerates in late autumn growing seasons, reducing plant photosynthesis. Therefore, controlling wetland visitor flow, especially during dry periods or after autumn, is particularly important for protecting wetland *Sphagnum* ground cover.

Although indoor simulation differs somewhat from actual field trampling, it effectively avoids climate-related interference and still reflects *Sphagnum* stress tolerance differences. Our findings demonstrate that: (1) Despite self-regulatory mechanisms, plant photosynthesis suffers damage as trampling rounds increase, with even light trampling causing cumulative stress effects; (2) Yellow-green morphotype *S. magellanicum* from forest margin habitats with higher chlorophyll concentration exhibits stronger trampling stress tolerance than red morphotype from open areas. Wetland protection and management should reduce visitor trampling disturbance, particularly by strictly controlling access to open habitats.

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Note: Figure translations are in progress. See original paper for figures.