Title: Short term changes in moisture content drive strong changes in Normalized Difference Vegetation Index and gross primary productivity in four Arctic moss communities

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Abstract

Climate change is currently altering temperature and precipitation totals and timing in Arctic regions. Moss communities constitute much of the understory in Arctic vegetation, and as poikilohydric plants moss are highly sensitive to timing and duration of moisture levels. Here we investigate the role of moisture content on NDVI, red and near-infrared reflectance, and gross primary productivity (GPP) of two sphagnum and two pleurocarpus moss community types during two separate drying experiments. For both experiments, blocks of moss were collected near Imnavait Creek, Alaska, saturated to full water capacity, and then allowed to air dry before being re-saturated. Drying of blocks was conducted in a translucent outdoor tent during the first experiment and under indoor climate-controlled conditions during the second. Community NDVI (experiment 1 and 2), and GPP (experiment 2) were measured at regular intervals during the dry-down and after rewetting. In both experiments, moss NDVI sharply declined between 80% and 70% moisture content for sphagnum moss communities (NDVI change = -0.17 to -0.2), but less so for pleurocarpus moss communities (NDVI change = -0.06 to -0.12). Changes in NDVI were largely the result of increases in reflectance in red wavelengths. Peak GPP for all community types in the second experiment (1.31 to 2.08 µmol m^{-2} s^{-1}) occurred at 80% moisture content and declined significantly as moisture content decreased. Rates of GPP continued to decline below 80% moisture content until near zero as moss reached a steady weight (air dry) over a period of 84 hours, while NDVI values declined slowly between 70% hydration and fully air dry. Re-saturation caused NDVI to increase in both sphagnum (NDVI change = +0.18 to +0.23) and pleurocarpus (NDVI change = +0.10 to +0.17) communities. Only sphagnum communities showed GPP resuming (0.824 µmol m^{-2} s^{-1}) after 24 hours. The strong

changes in NDVI and mismatch of moss NDVI values and GPP with moisture content fluctuations indicate that using NDVI as a proxy for productivity in Arctic vegetation communities may be problematic and underscores the need for quantification of moss community coverage, composition, and moisture content.

Introduction

Arctic regions have experienced significant warming over the past several decades (Overland 2002, Chapin et al. 2005, IPCC 2013) with substantial ecosystem consequences (Hinzman et al. 2005). In some regions of the Arctic, changes in precipitation patterns, increased evapotranspiration, and falling water tables associated with climate change have reduced pond size and number (Riordan et al. 2006, Andreson and Lougheed 2015) and affected soil moisture available to tundra plants (Roulet et al. 1992, IPCC 2013). While precipitation models for the Arctic generally suggest an increase in precipitation, most of this increase is distributed over winter and fall (as snow), while summer would remain relatively unchanged (Kattsov et al. 2007). Arctic plant communities are shifting to vegetation types and resulting carbon dynamics that reflect drier conditions (Oechel et al. 1992, Chapin et al. 1995, Mack et al. 2011). Mosses constitute an important component of Arctic vegetation communities, particularly in the understory, and may contribute substantially to ecosystem carbon fluxes (Shaver and Chapin 1991, Douma et al. 2007, Campioli et al. 2009, Turestky et al. 2010, Olivas et al. 2011, Zona et al. 2011). As a result of warming, recent vegetation measurements in the Arctic have shown a decrease in moss cover (Chapin et al. 1995, Molau and Alattalo 1998, Elmendorf et al. 2012, Hollister et al. 2015, Hobbie et al. 2017).

Decreases in available water have a particularly marked effect on the carbon balance in moss-dominated communities (Titus et al. 1983, Rydin and McDonald 1985, Alm et al. 1999, Komulainen et al. 1999). As poikilohydric plants, mosses do not have the ability to actively control water loss and therefore are highly susceptible to changes in water availability (Van Breemen 1995, Proctor and Tuba 2002). Consequently the moisture content of mosses varies widely and rapidly compared to that of tundra vascular plants, and most mosses are more resilient to periodic drying, or even complete desiccation, than vascular plants (Levitt 1956, Proctor and Tuba 2002). Mosses have an optimal water content for peak photosynthetic rates that does not necessarily occur at full saturation (Ueno and Kanda 2006, Van Gaalen et al. 2007, Harris 2008). Photosynthetic rates of moss are particularly sensitive to drying because cellular water content is a crucial limiting factor in the light reactions (Skre and Oechel 1981). As water loss becomes more severe, photosynthesis declines significantly (Schipperges and Rydin 1998). Even after re-saturation there can be a substantial lag before activity resumes (Oliver and Bewley 1984, Green and Lange 1995, Charron and Quatrano 2009, de Carvalho et al. 2012). Multiple drying and wetting cycles have a negative effect on the photosynthesis of moss due to lengthy recovery times (McNeil and Waddington 2003). As a result, prolonged periods of warmer, drier conditions have the potential to adversely affect moss growth and photosynthesis (Potter et al. 1995, Dorrepaal et al. 2004, Proctor et al. 2007) and therefore ecosystem productivity (Turetsky et al. 2012).

Accompanying variation in moss moisture content are changes in apparent coloration of some mosses. For example, some sphagnum species exhibit a markedly lighter appearance as a result of moisture loss (Van Breeman 1995), suggesting the possibility that desiccation may have implications for plant reflectance and remote sensing indices. Remote sensing has provided an effective method for determination of important environmental parameters on large spatial and temporal scales that, using conventional methods, would be otherwise cost and time prohibitive (Kerr and Ostrovsky, 2003). These resource limitations are exacerbated in Arctic regions as a result of the remoteness and scale of study areas. One metric commonly used is the Normalized Difference Vegetation Index (NDVI) that takes advantage of the strong absorbance of the red and strong reflectance in the near-infrared region of the electromagnetic spectrum by green plants (Kriegler et al. 1969). Changes in growing season length and available moisture associated with climate change have been shown to alter remotely sensed NDVI, a measure strongly correlated with green biomass (Jia et al. 2003, Reidel et al., 2005, Gamon et al. 2013), shrub cover (Stow et al. 2007, Walker et al. 2012), and community productivity (Harris 2008). Increases in Arctic vegetation cover have been associated with increases in peak season NDVI measurements (Laidler et al. 2008, Chen et al. 2009, Kushida et al. 2009), particularly when moisture is high (Riedel et al. 2005, Huemmrich et al. 2010). However, if short-term changes in water content result in significant changes in reflectance of such an important ecosystem component as mosses, considerable uncertainty will be introduced into remote sensing-derived estimates of green biomass and productivity. The role of moisture content on photosynthesis and spectral reflectance has been investigated for a few moss species (Potter et al. 1995, Van Breeman 1995, Dorrepaal et al. 2003, Proctor et al. 2007); however no studies have addressed the role of water content on both of these properties simultaneously for different Arctic bryophyte communities

Here, we investigate how variation in plant water content affects NDVI, red and near-infrared reflectance, and gross primary productivity (GPP) of four moss communities through a full cycle from saturation, dry down, and re-saturation. We hypothesize that NDVI will be greatest at high but not fully saturated water contents and decrease with drying at rates specific to each community type. Re-saturation will quickly re-establish initial NDVI values. Gross Primary Productivity will peak at levels below full saturation, similar to those reported in previous studies (Ueno and Kanda 2006, Van Gaalen et al. 2007, Harris 2008), and decrease strongly with drying. We also expect that air drying of moss to constant weight will cause a delay in re-establishment of initial GPP values after re-saturation.

Methods

Sample handling

In two separate drying experiments, conducted in July (Exp 1) and August (Exp 2) 2016, monoliths of four moss communities were collected from the low Arctic tundra near Toolik Field Station (TFS) at Imnavait Creek, Alaska, USA (68.635˚ N, -149.349˚ W). The four communities included two sphagnum communities, >95% *Sphagnum angustifolium* (green in color), >95% *Sphagnum capilliofolium* (red in color), and two pleurocarpous communities, >95% *Hylocomium splendens* and a mixed community (~50% *Aulocomnium* spp., ~30% *Hylcomnium splendens*, and ~10% *Polytrichum* spp.). Four replicate 20x20x8 cm (length x width x depth) blocks of each community were collected (16 total) for both experiments. Each replicate was prepared by removing vascular plants and soil prior to placing them in a tray of distilled water (3 cm depth) to hydrate. Moss blocks were soaked for two hours until they reached full saturation and then allowed to drain for one hour to remove excess water. The vertical faces of each moss block were wrapped in cellophane and then placed in a Styrofoam tray to prevent uneven drying from the sides.

During Exp1, blocks were allowed to dry gradually in a translucent white outdoor tent to allow temperatures (range 3-29˚C) to track daily temperature changes. During Exp2, blocks were allowed to dry gradually in the TFS Incubation Facility maintained at 23˚C to minimize temperature variability during the drying process. This temperature was determined to be a suitable analog of natural peak season conditions (TFS Environmental Data Center, 2016). Drying in the incubation facility took place under constant lighting using Hydrofarm® 1000 watt lamps at a height of 1.5 m and 400 µmol m^{-2} s^{-1} (Hydrofarm, Inc., Petaluma, California, USA). For both experiments, moss blocks reached ecologically dry status (air dry) after 84 (Exp2) and 96 (Exp1) hours and then were re-saturated with distilled water to determine drying resilience.

Measurements

All measurements during the drying process were taken at approximately 12 h intervals. After rehydration, measurements were conducted at 4, 12 and 24 h intervals. Blocks were then dried further at 50˚C for 48 hours to achieve 0% water content allowing for calculation of percent saturation at each measurement. To monitor water loss, block weight was measured to 1 mg using an electronic balance (Ohaus Corporation, Parsippany, New Jersey, USA) throughout the study period of both drying experiments. During Exp1, community reflectance (350 – 1100 nm) was measured in ambient light conditions using a single channel Unispec® (PP Systems, Amesbury Massachusetts, USA) at a height of 10 cm with NDVI calculated afterward (see below). During the second experiment, NDVI was measured using a Trimble self-illuminated, handheld GreenSeeker® crop sensing system (Trimble Navigation, Ltd., Sunnyvale, California, USA) at a height of 15 cm, the minimum recommended distance. The GreenSeeker® system with an internal light source was ideal for these measurements by providing accurate NDVI values despite being under artificial light conditions. NDVI for both experiments was calculated using the reflectance of near-infrared light (R_{774}) and red light (R_{656}) as (R_{774} - R_{656})/(R_{774} + R_{656}). Community CO_2 exchange for Exp2 was measured using a custom-made transparent acrylic chamber (32 x 32 x 32 cm) with the moss block positioned on a hard flat surface that formed a gas-tight seal with the chamber using weather stripping. One 12V fan fixed inside the chamber insured full mixing of chamber air. The chamber was attached to a LI-6400XT Portable Photosynthesis System (LI-COR Inc., Lincoln, Nebraska, USA) in closed system mode. Gas exchange measurements were conducted under the Hydrofarm® 1000 watt lighting systems at 900 µmol m^{-2} s^{-1}. A good seal between the chamber and the flat surface was determined if gas concentrations showed a steady rate of change with no fluctuations for 20 s. Following the methods of Shaver et al. (2007), when a stable change in CO_2 concentrations was observed, CO_2 concentration, chamber air temperature and PAR were logged every 2 s for 40 s. Flux (µmol CO_2 s^{-1}) was calculated as a linear change in CO_2 concentration over time multiplied by the air density (mol m^{-3}). Flux was expressed on an ecosystem area basis using the moss surface area (0.04 m^{-2}). For each moss block, measurements were taken in the light (Net Primary Production (NPP)) and in the dark under an opaque tarpaulin (Ecosystem Respiration (ER)). Gross Primary Production (GPP) was calculated as the difference between NPP and ER, assigning positive values to GPP and negative values to ER.

Data Analysis

Replicates of moss GPP and NDVI measurements were grouped by measurement time and separately by 10% moisture content increments for statistical analysis. Time and moisture content groupings were compared using a repeated measures analysis of variance with Tukey's post-hoc analysis. In the second experiment, resilience of each moss community to re-hydration after drying was determined using a drying response index (DRI) calculated as the proportion of

NDVI or GPP measured after re-saturation ($V_{re\text{-}sat}$) compared with the initial saturation values ($V_{initial}$), DRI=-($V_{re\text{-}sat}$/$V_{initial}$). All statistical tests were performed using the R statistical environment (R Core Team, Vienna, Austria).

Results

During Exp1, all moss communities were fully air dried after 96 h with the largest changes in NDVI occurring between 12 and 24 h of drying (Figure 1). Values of NDVI began to decline with drying between 80 and 70% water content for all communities, but communities differed in the magnitude of NDVI change. The sphagnum communities, *S. capilliofolium* and *S. angustifolium*, showed the largest decline in NDVI with drying (-0.190, $p<0.001$ and -0.230, $p<0.001$ respectively). Mixed pleurocarpus and *H. splendens* communities decreased in NDVI to a lesser extent compared to the sphagnum communities but were still significant (-0.112, $p=0.021$ and -0.140, $p<0.001$ respectively). All community NDVI values rebounded to near initial saturation levels upon re-saturation.

Decreases in NDVI were largely driven by increases in reflectance of red light (Figure 1), with the largest increases in the two sphagnum communities (*S. capilliofolium* +0.058 $p=0.025$ and *S. angustifolium* +0.067 $p=0.017$) compared with *H. splendens* (+0.039 $p=0.231$) and the mixed pleurocarpus (+0.038 $p=0.234$). Near-infrared reflectance for all communities was mixed with drying; some communities increased and some decreased, but no changes were significant (0.009-0.045). Red and near-infrared reflectance returned to near initial saturation levels upon re-saturation after only a few minutes.

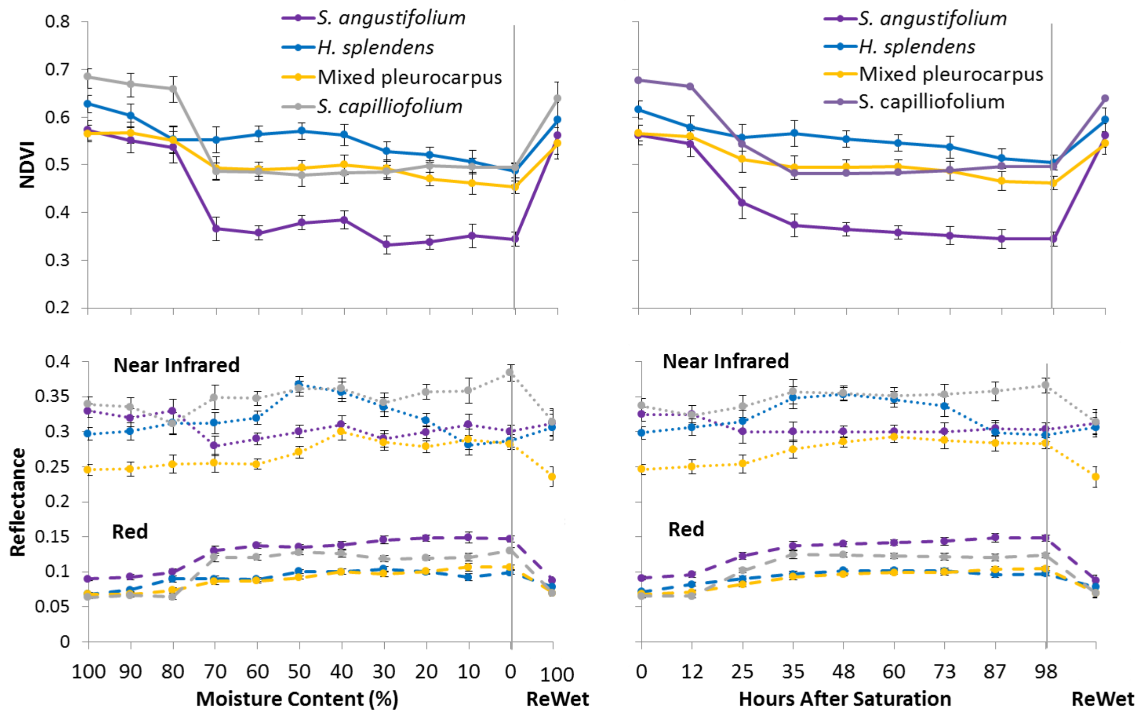

Figure 1: NDVI (solid line), near-infrared (dotted line), and red (dashed line) of four communities by percent moisture content (left panels) and hours after initial saturation (right panels) during drying and after re-saturation during experiment 1.

In Exp2, all communities took approximately 84 hours to reach air dry and the lowest NDVI values (0.29 to 0.47, Figure 2). The largest decrease in NDVI observed as water contents declined occurred between 12 and 36 h post-saturation for all communities. *Sphagnum capilliofolium* and *H. splendens* communities had the highest NDVI measurements (0.70 and 0.64 respectively) at initial full saturation, while the *S. angustifolium* and mixed pleurocarpus were lower (0.55 and 0.57, Figure 2, Table 1). The NDVI of all community types was generally stable from 100% to 80% saturation, followed by an abrupt decline between 80 and 70%, after which there was steady but slow decline in NDVI to fully air dry. The largest decreases in NDVI between 80% and 70% saturation were found for the two sphagnum communities (*S.*

capilliofolium -0.19, *P* < 0.001 and *S. angustifolium* -0.16, *P* < 0.001), while the decreases for the mixed pleurocarpus and *H. splendens* communities were less, albeit still significant (-0.06, *P* = 0.038 and -0.09, *P* = 0.014 respectively). NDVI of all communities increased strongly upon re-saturation (+0.17 to +0.23, all p<0.001).

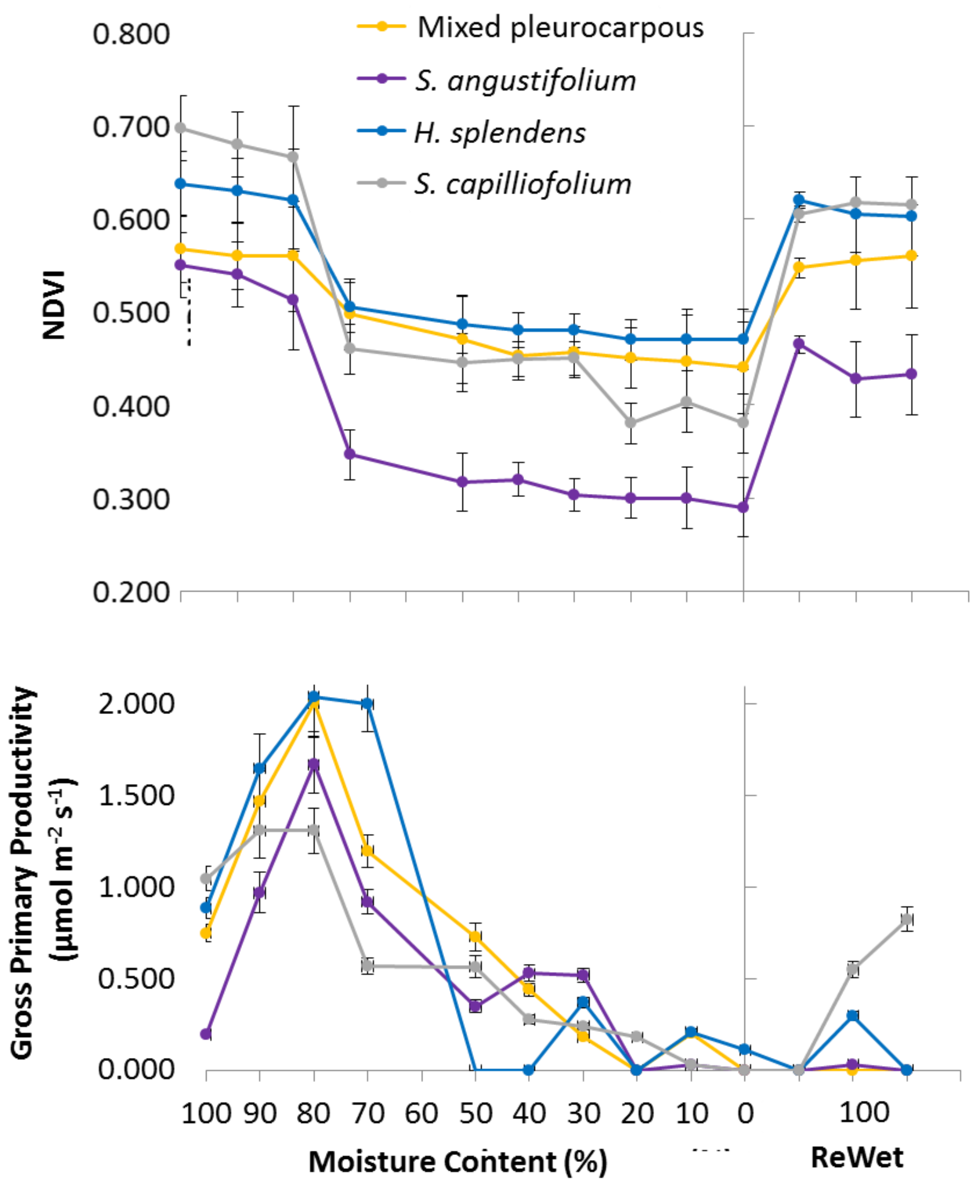

Figure 2: Gross primary productivity and NDVI of four communities by percent moisture content during drying and three measurement times after re-saturation during experiment 2.

Table 1: Gross primary productivity and NDVI of four communities by percent moisture content during drying and three measurement times after re-saturation compared using repeated measures analysis of variance with Tukey's post-hoc analysis, along with the initial saturated and final oven dry weight for each of the four community types during experiment 2. Letters denote statistically significant differences (p<0.05) between moisture content measurements.

	Moisture Content %										ReWet (100% Moisture) Hours After			Initial Saturated Weight (g)	Dry Weight (g)
	100	99-90	89-80	79-70	59-50	49-40	39-30	29-20	19-10	9-0	4	12	24		
NDVI															
Mixed Pleurocarpus	0.57 a	0.56 a	0.56 a	0.50 ab	0.47 b	0.45 b	0.46 b	0.45 b	0.45 b	0.44 b	0.55 a	0.56 a	0.56 a	578.5	113.8
S. angustifolium	0.55 a	0.54 a	0.51 a	0.35 b	0.32 b	0.32 b	0.30 b	0.30 b	0.30 b	0.29 b	0.47 a	0.43 a	0.43 a	584.0	101.5
H. splendens	0.64 a	0.63 a	0.62 a	0.51 b	0.49 b	0.48 b	0.48 b	0.47 b	0.47 b	0.47 b	0.62 a	0.61 a	0.60 a	403.3	116.2
S. capilliofolium	0.70 a	0.68 a	0.67 a	0.46 b	0.45 b	0.45 b	0.45 b	0.38 c	0.40 bc	0.38 c	0.61 a	0.62 a	0.62 a	753.3	144.6
Gross Primary Productivity (µmol m^{-2} s^{-1})															
Mixed Pleurocarpus	0.749 a	1.472 b	2.081 c	1.207 b	0.727 a	0.443 d	0.175 e	0.000 f	0.202 e	0.000 f	0.000 f	0.000 f	0.000 f		
S. angustifolium	0.195 a	0.970 b	1.671 c	0.913 b	0.352 ad	0.526 d	0.521 d	0.000 e	0.033 e	0.000 e	0.000 e	0.034 e	0.000 e		
H. splendens	0.883 a	1.652 b	2.042 c	1.608 b	0.002 d	0.000 d	0.374 e	0.000 d	0.206 e	0.111 d	0.000 d	0.296 e	0.000 d		
S. capilliofolium	1.046 a	1.320 b	1.311 b	0.571 c	0.565 c	0.277 d	0.235 d	0.184 de	0.031 e	0.000 e	0.000 e	0.552 c	0.824 f		

All moss communities were photosynthesizing at full water saturation (0.195 to 1.046 µmol m^{-2} s^{-1}) and initially increased as drying began (Figure 2, Table 1). *Sphagnum capilliofolium* community GPP peaked at approximately 90% saturation (1.320 µmol m^{-2} s^{-1}) while all other communities peaked at 80% saturation (mixed pleurocarpus 1.332 µmol m^{-2} s^{-1}, *S. angustifolium* 1.476 µmol m^{-2} s^{-1}, *H. splendens* 1.159 µmol m^{-2} s^{-1}). Rates of GPP for all communities decreased precipitously below 80% saturation with little or no GPP occurring at fully air dry (0 to 0.111 µmol m^{-2} s^{-1}). Rates of GPP peaked for all communities after 12 hours of drying following the initial saturation and then continued to decline until a total of 84 hours of drying. Twelve hours after re-saturation, *S. angustifolium* (0.034 µmol m^{-2} s^{-1}), *H. splendens* (0.296 µmol m^{-2} s^{-1}), and *S. capilliofolium* (0.552 µmol m^{-2} s^{-1}) had regained some GPP (Figure 3). Twenty four hours post saturation only the *S. capilliofolium* community showed any GPP (0.824 µmol m^{-2} s^{-1}).

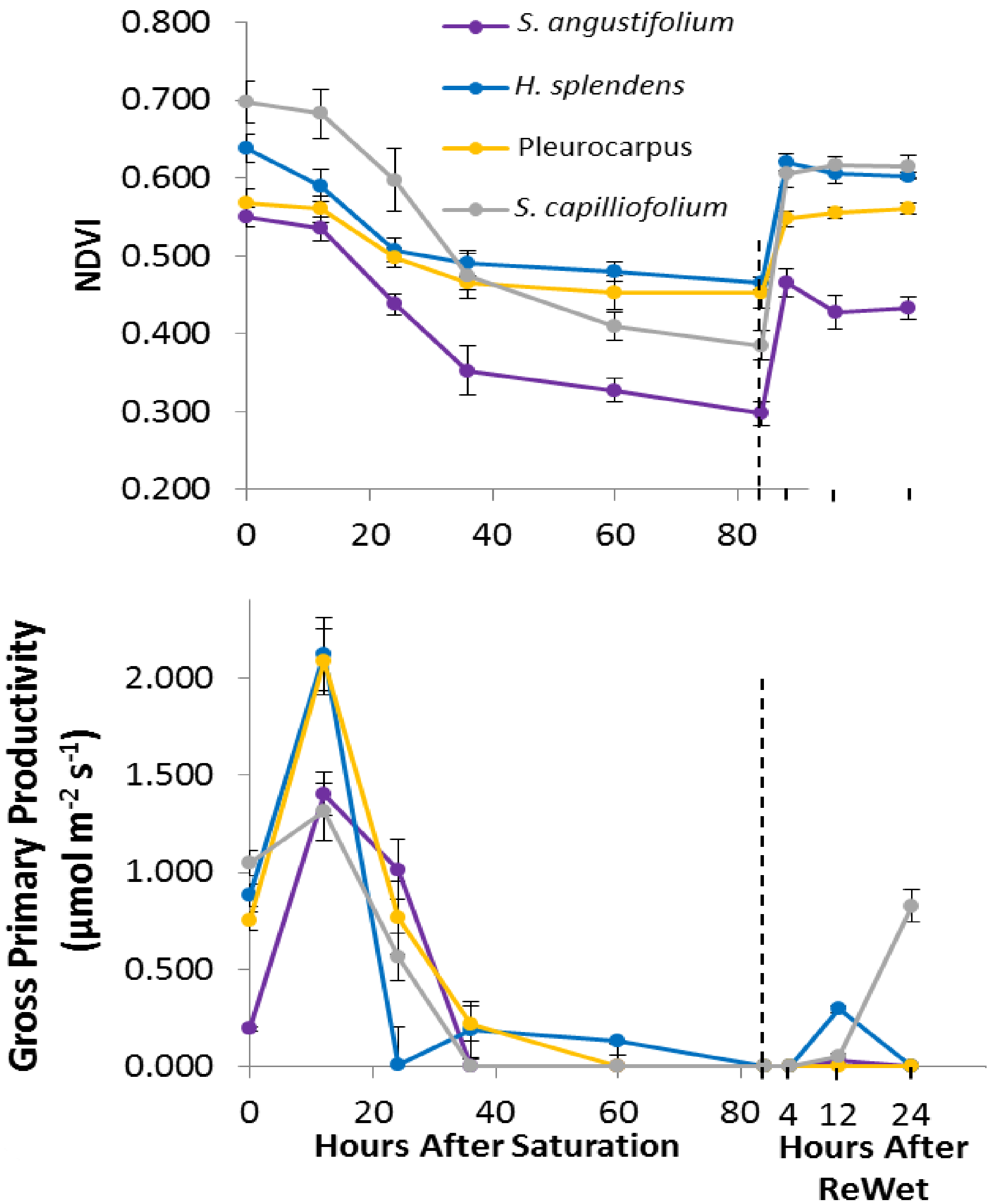

Figure 3: Gross primary productivity and NDVI of four communities by hours of drying and three measurement times after re-saturation during experiment 2.

Measuring drying resilience by means of the DRI showed that NDVI and GPP decreased in all community types after re-saturation compared with the initial comparison (Figure 4). Drying response index for NDVI of the mixed pleurocarpus and *H. splendens* communities decreased only slightly (-0.023, *P* = 0.101 and -0.044, *P* = 0.081 respectively), returning to near original saturation values. The DRI for NDVI for both sphagnum communities had significant declines in response to full drying (*S. angustifolium* -0.197, *P* = 0.013 and *S. capilliofolium* -0.122, *P* = 0.042). The DRI for GPP of all communities decreased after drying with mixed pleurocarpus (-1.000, *P* < 0.001), *S. angustifolium* (-0.942, *P* < 0.001), and *H. splendens* (-0.888, *P* < 0.001) declining the most and the *S. capilliofolium* community being the most resilient to drying (-0.562, *P* = 0.013).

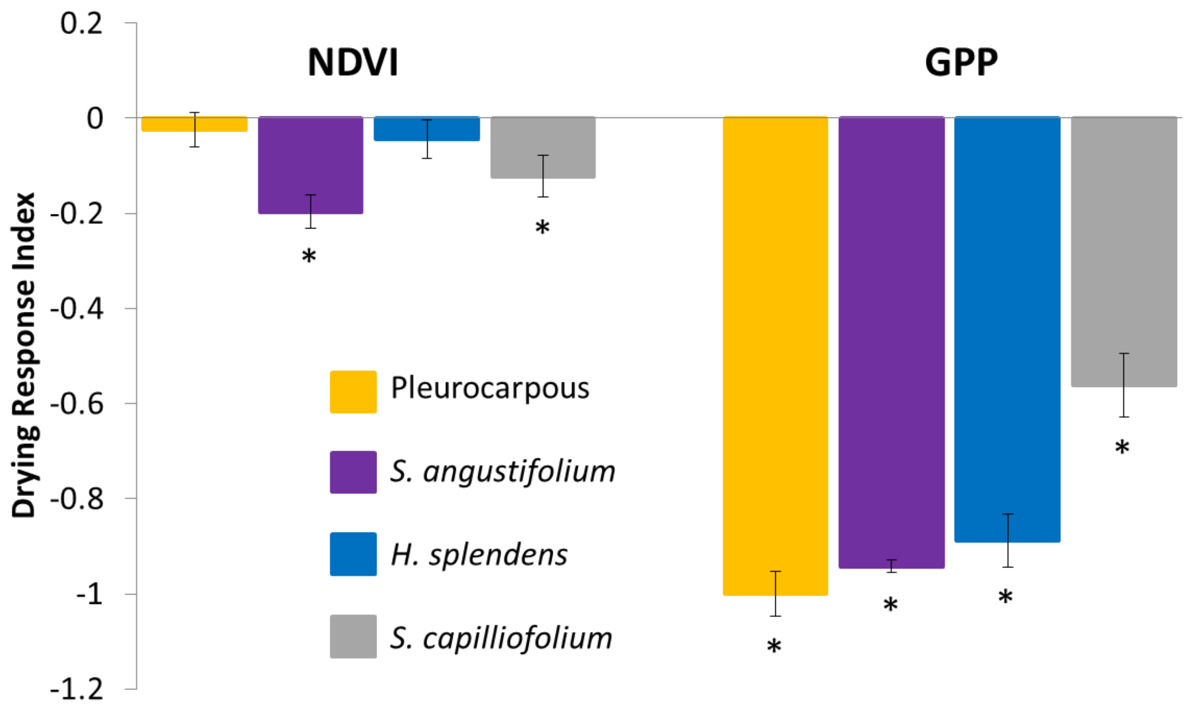

Figure 4: Drying response indexes of four communities for GPP and NDVI during experiment 2 compared using a one-way analysis of variance. Statistical significance denoted with *.

Discussion

Previous studies have shown that drying alters spectral reflectance (Riedel et al. 2005, Huemmrich et al. 2012) and moss productivity (Skre and Oechel 1981, Ueno and Kanda 2006, Harris 2008). Here we show that the reflectance index, NDVI, and GPP decline strongly with moss desiccation, but they do not occur at the same rate and magnitude, resulting in a mismatch between NDVI levels and productivity. Reductions in NDVI of the moss communities with desiccation were very large, approaching 50% of maximum values and driven mostly by increases in red light reflectance during drying. With rewetting after the strong dry down, NDVI values were near peak levels while GPP was near zero.

Moss water content effect on NDVI values

In recent decades, measured NDVI values have been increasing in the Arctic as temperatures warm and ecosystem productivity increases (Jia et al. 2003). These changes in peak season NDVI values, however, have not been increasing uniformly across spatial and temporal time scales, with evidence of a slowing of the rate of increase (Bhatt et al. 2013). The heterogeneity of changes in peak season NDVI values may be a result of the non-uniformity of the well-documented community dominance and moss decline in the Arctic (Shaver and Chapin 1991, Douma et al. 2007, Campioli et al. 2009, Elmendorf et al. 2012, Hollister et al. 2015). Moss communities are often an important component of Arctic understories and have been shown to play a large role in community production (Duoma et al. 2007, Campioli et al. 2009) and remotely-sensed spectral measurements (Walker et al 2003). Our results show that even small changes in the water content of the moss understory may play a role in the slowing of changes in landscape scale NDVI. Warmer, drier conditions during peak growing season may artificially decrease estimates of peak season landscape scale NDVI estimates.

These results have important implications for remote sensing of plant biomass and productivity in regions where mosses are important components of the vegetation. A general assumption in the use of NDVI to estimate green biomass of plants is that NDVI is not strongly affected by short-term changes in leaf water content. While this assumption is generally the case for vascular plants, our results show that changes in moss water content can induce rapid and large changes in NDVI with no change in biomass. Furthermore, the relationship between NDVI and water content is markedly nonlinear. Variation in the water content of moss may be an important source of error in models using NDVI to estimate green biomass or leaf area (Oechel et al. 2000, Vourlitis et al. 2000, Shaver et al. 2007) that is then used in ecosystem photosynthesis models.

All of the moss communities in this study followed similar patterns of NDVI reductions with drying, although the magnitude of NDVI change in response to drying was community-specific. As predicted, all communities had the highest NDVI values at full, initial saturation (80-100% moisture content) with marked NDVI declines with drying. NDVI of all communities declined sharply over a relatively narrow range of water content from 80-70% moisture content, with the most substantial declines found for the two sphagnum communities. The lower NDVI values and higher levels of red reflectance at lower moisture content levels may act as a mechanism to minimize absorption of irradiance to prevent further evaporative water loss or cellular damage (Charron and Quatrano 2009, de Carvalho et al. 2012). The *H. splendens*-dominated and pleurocarpus mixed communities showed moderate increases in NDVI upon re-saturation. In contrast, both sphagnum communities had abrupt (<2 minutes), significant increases in NDVI values upon re-saturation. The rapidity of NDVI increases upon re-saturation of sphagnum communities suggests that changes in NDVI with drying and rehydration are in part a physical rather than biological response. Despite the rapid recovery of NDVI values of sphagnum communities upon rewetting, values did not attain those of initial saturation, unlike the pleurocarpus mixed and *H. splendens* dominated communities that recovered fully. This lack of full rebound in sphagnum communities may be a result of, at least temporary, physiological damage occurring in response to desiccation to fully air dry (Oliver et al. 2005; Hájek and Beckett, 2008).

Moss water content effect on GPP

Rapid changes in NDVI of moss communities with water content are associated with large changes in GPP, albeit nonlinearly. This variability is in addition to the already substantial difference in photosynthesis rates between vascular plants and mosses (Longton 1988). At Barrow, Alaska, production rates of mosses are on the order 10% of that of vascular plants (Oechel and Sveinbjornsson 1978), which means that photosynthesis per unit NDVI are very different for vascular plants compared to those of mosses. Our results show that moss communities may have relatively high NDVI values (0.55- 0.70), that if interpreted as vascular plant biomass would lead to large overestimates in productivity. These mismatches compromise the use of remotely-sensed NDVI data to estimate productivity in communities where mosses are abundant, but information on local moisture content or precipitation are lacking. Models using NDVI as a measure of productivity through estimating productivity by metric such as leaf area index (LAI) are highly effective across a range of spatial scales (Shaver et al. 2007, Loranty et al. 2011, Stoy et al. 2013). As spatial scale and vascular plant cover increases, the proportion of moss contribution to community spectral measurements is likely to decrease.

The magnitudes of changes in moss community GPP rates with drying were also community specific. However, all communities showed moderate rates at initial saturation and increased with drying to around 70-80% moisture content. This pattern of lower productivity at full saturation and increasing productivity after initial drying begins is similar to results found by Van Gaalen et al. (2007). A moderate amount of drying allows for air space within the plant while allowing cells to retain adequate moisture for full function. All communities had a peak GPP at 70-80% moisture content. Drying below 70-80% moisture content caused incremental decreases in GPP dropping to near zero in all of the communities when they reached air dry. Re-saturation had minimal effects on GPP, a finding consistent with previous findings that showed delayed recovery of moss physiological activity with rewetting after drying (Van Breeman 1995). Only the *S. capilliofolium* community showed a recovery of GPP during the 24 hours after re-saturation.

Moss communities such as those in this study are often intermixed at relatively small spatial scales across Arctic terrestrial ecosystems, implying a heterogeneous matrix of drying and recovery responses. While all four communities showed strong reduction in NDVI at the 80% drying threshold, the responses of both sphagnum communities were substantially greater than those in the pleurocarpus moss communities. To use remotely-sensed, reflectance-based productivity monitoring of Arctic ecosystems, further investigation is needed on the effects of intra-seasonal drying and rehydration on productivity and spectral reflectance of different moss communities.

These results in response in moss moisture content highlight the need for repeated remote sensing measurements over the same study regions with monitoring of a region's recent precipitation events. Because of the remoteness and scale of Arctic regions, remotely sensed data are currently the best means to investigate seasonal productivity and vegetation composition shifts associated with climate change (Raynolds et al. 2008, Bhatt et al. 2010, Stow et al. 2007, Walker et al. 2012). This issue is crucial in Arctic regions where mosses comprise a major vegetation component, contribute substantially to ecosystem productivity (Olivas et al 2011), and are often a large component of total community reflectance (Hope et al. 1993). Our results show that periods of little or no precipitation combined with clear skies, high temperature and windy conditions have the potential to rapidly (<24 hours) lower moss water content sufficiently to reduce ecosystem NDVI values that would imply low predictions of ecosystem productivity even though vascular plant productivity may remain high. Remotely-sensed NDVI values measured for the same area shortly before and after a precipitation event may differ simply in response to moss moisture content.

Conditions conducive to moss desiccation are expected to increase with climate warming as temperatures increase, driving greater evapotranspiration. These changes will increase the frequency of moisture-induced changes in NDVI. Mosses grow in many different conditions ranging from on the surface of mineral soil or even on bare rock to areas that remain nearly continually wet or submerged. The frequency at which mosses desiccate is dependent in part on the microtopographic conditions where they are growing as well as weather conditions. Those growing on well-drained mineral soil or rock surfaces and hummocks are likely to desiccate frequently, whereas others may rarely if ever desiccate. Species colonizing conditions subject to frequent desiccation are likely to tolerate desiccation better than species in areas that rarely dry out (Longton 1988). Sites where mosses are continually wet are less likely to show rapid NDVI changes in response to drying, but species from these conditions may be more susceptible to climate change-related drying in the long term.

Conclusion

This study reinforces the importance of understanding the moisture content of moss when using remotely-sensed, reflectance techniques for monitoring productivity in Arctic terrestrial systems. Reflectance measures of different communities of moss revealed species-specific variation in response and resiliency to drying, therefore complicating the aggregation of moss as a uniform understory in Arctic ecosystems. At similar NDVI values, GPP varied depending on moss moisture content, demonstrating that moss NDVI is not an accurate proxy for physiological activity of some important Arctic mosses. This study underscores the need for monitoring and understanding the composition, spatial coverage, and moisture content of mosses for remote sensing-based monitoring of Arctic terrestrial ecosystems. Methodologies for remotely monitoring surface water content (e.g. Normalized Difference Water Index (NDWI) (Gao 1996), Normalized Difference Infrared Index (NDII) (Serrano et al. 2000), among others) are improving and could be useful for addressing these issues

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Figure 1: NDVI (solid line), near-infrared (dotted line), and red (dashed line) of four communities by percent moisture content (left panels) and hours after initial saturation (right panels) during drying and after re-saturation during experiment 1.

Figure 2: Gross primary productivity and NDVI of four communities by percent moisture content during drying and three measurement times after re-saturation during experiment 2.

Figure 3: Gross primary productivity and NDVI of four communities by hours of drying and three measurement times after re-saturation during experiment 2.

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Table 1: Gross primary productivity and NDVI of four communities by percent moisture content during drying and three measurement times after re-saturation compared using repeated measures analysis of variance with Tukey’s post-hoc analysis, along with the initial saturated and final oven dry weight for each of the four community types during experiment 2. Letters denote statistically significant differences ($p<0.05$) between moisture content measurements.