Is above- and belowground phenology of *Eriophorum vaginatum* in sync in a peatland underlain by permafrost?

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Abstract

The phenology of plants in northern ecosystems is currently changing. Roots have a key role in these ecosystems, though the phenology of roots is still poorly understood. The aim of this report was to investigate if above- and belowground phenology of the circumpolar sedge *Eriophorum vaginatum* was synchronized in a subarctic peatland underlain by permafrost, and to investigate which abiotic factors are limiting root growth. Additionally, the length of the belowground growing season was examined. The study was performed with a non-destructive in situ method (minirhizotrons and NDVI measurements) in the northernmost part of Sweden. Both above- and belowground phenology was measured biweekly during the whole growing season in 2016. The depth of the active layer, air temperature, soil temperature and soil moisture were measured to investigate the determinants of root growth. Root growth and aboveground activity was asynchronous, as peak in root growth occurred on average 21 days before maximum NDVI was reached. Soil temperature and thaw depth seem to be important factors regulating root growth in this peatland. The result highlight that solely studying the aboveground parts of plants can give a misleading interpretation about the phenology of the entire plant and thus during which time periods important ecosystem processes take place. Hence, to more accurate forecast ecosystem responses to global warming, both aboveground and belowground phenology should be considered.

Key Words: phenology, root growth, NDVI, permafrost, northern ecosystem
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1 Introduction

1.1 Background

Arctic environments are characterized by cold temperatures and short growing seasons. Plants growing in these regions are in many areas restricted to the thin active layer (annually thawing, upper part of the soil) above the year-round frozen ground (permafrost) (Borden et al. 2010; Iversen et al. 2015). Climate change is leading to an increasing mean annual temperature at a rapid pace globally and the arctic is predicted to be more strongly affected than other biomes (ACIA 2004; IPCC 2013). When temperatures increase in the arctic, areas with permafrost are inevitable thawing. Henceforth, depth of active layers has indeed increased during the last decades in many northern areas (IPCC 2013; Schuur et al. 2015). Furthermore, these northern terrestrial ecosystems, especially peatlands, have an important role in the global carbon cycle as a large amount of organic carbon is stored in the soil (McGuire et al. 2009). When the permafrost thaws, large amount of stored carbon can be released and contribute to a faster warming in the future (Schuur et al. 2015). Nitrogen is also stored in the permafrost soil, with a high proportion of nitrogen accumulated near the thaw front, which when it thaws will be available for plants and potentially benefit deeply rooting species (Keuper et al. 2012). This could on the other hand contribute to an increased plant growth, which would turn the systems into stronger carbon sinks (Natali, Schuur and Rubin 2011).

A large amount of the total plant biomass is located belowground, primarily as roots (Mokany et al. 2006). Roots are important for nutrient and water uptake by plants as well as carbon availability in the soil (Reece et al. 2011). The distribution of roots in the soil profile differs between biomes, and plants in tundra regions have in general very shallow roots, with >90% of the total biomass existing in the upper 30 cm of the soil profile (Jackson et al. 1996). Plants in these regions are adapted to maintain high root growth and root respiration rate even though the temperature is low (Shaver and Billings 1975). The growth of fine roots is, however, limited to the thawed soil (Borden et al. 2010; Iversen et al. 2015), though some plants e.g. in the genus *Eriophorum*, are able to follow the thaw front by rapidly growing deeper during the growing season, when the permafrost is thawing and the active layer is increasing (Shaver and Billings 1975, 1977; Blume-Werry et al. 2016 b). Deep rooting species can thus utilize resources unavailable to other species (Chapin et al. 1988). Also, by producing new roots annually, some species (e.g. *E. vaginatum*) are able to exploit the soil in the active layer from the beginning of the growing season, even though it is very shallow and last years’ roots are still frozen in the deeper soil layer (Shaver and Billings 1975). Other factors, besides the active layer, that potentially determine root growth in permafrost regions are light availability (Shaver and Billings 1977), soil temperature (Shaver and Billings 1977; Blume-Werry et al. 2016 a), snow accumulation (Johanson et al. 2013; Blume-Werry et al. 2016 b), and nutrient availability (Sullivan et al. 2015).

Carbon and nutrient cycles in tundra regions are driven by complex interactions between plant communities, soil processes, and other environmental variables (Wookey et al. 2009). These areas are expected to be strongly influenced by global warming (ACIA 2004), and complicated responses of vegetation and soil properties to the increased temperature are therefore expected (Wookey et al. 2009). The phenology of plants (the timing of biological events, e.g. bud break or flowering driven by biotic and abiotic factors) could act as a sensitive indicator of a warmer climate (Wolkowich et al. 2012; Radville et al. 2016). The phenology of plants is, however, often measured by solely studying the aboveground parts of plants (Iversen et al. 2015), and ecological models often neglect root phenology (e.g. timing of root production) or assume it to be equal with shoot phenology (Smithwick et al. 2014; Iversen et al. 2015). This can give a misleading interpretation about the phenology of the entire plant, as recent studies show that root and shoot phenology is asynchronous in several occasions.
cases in the Arctic (Blume-Werry et al. 2016 a; Radville, Post and Eisenstat 2016; Sloan, Fletcher and Phoenix 2016) and in other biomes (Du and Fang 2014; Abramoff and Finzi 2015). Recent studies further demonstrate that the most pronounced difference between root and shoot phenology might be that the growing season extends much longer into the autumn belowground than aboveground (Blume-Werry et al. 2016 a; Sloan, Fletcher and Phoenix 2016).

The knowledge about root dynamics in tundra regions is limited (but see Iversen et al. 2015). There is thus a need to obtain more knowledge about fine roots in arctic ecosystems, since they are likely to be strongly affected by global warming, with consequences for the functioning of the entire ecosystem.

1.2 Aim and Research questions

The aim of this study is to determine if there is a difference between above- and belowground phenology of *Eriophorum vaginatum* in a peatland underlain by permafrost and to further investigate the determinants of root growth. The following questions will be addressed:

1. Is shoot- and root phenology synchronous?
2. How long is the growing season for roots?
3. What drives root phenology?

To answer these question, I studied the graminoid *Eriophorum vaginatum* during the whole growing season in 2016 in a peatland underlain by permafrost, situated close to Abisko Scientific Research Station in northernmost Sweden. Non-destructive, in situ methods were used to monitor the above- and belowground phenology of the study species and, additionally, abiotic factors such as air temperature, soil temperature, and soil moisture were measured for investigating the determinants of root growth.

2 Materials and methods

2.1 Study area and study species

The study was carried out 6 kilometres east of Abisko scientific research station, Kiruna municipality, Sweden. The area at which the root and shoot measurements took place was a subarctic peat plateau underlain by permafrost (“Storflaket”, 68°20’48’’N 18°58’16’’E). The soil characteristics of the peatland is a silty lacustrine sediment of glacial origin, which is covered with a ca. 50 cm layer of peat (Klaminder et al. 2008). The mire is located within the sporadic permafrost region and the active layer is ca. 60 cm thick (1978-2012, Johansson et al. 2013). The vegetation on the mire is mainly dominated by *Betula nana, Empetrum nigrum, Vaccinium uliginosum*, some mosses such as *Dicranum scoparium, Sphagnum fuscum* and *Sphagnum balticum*, and some lichens such as *Cladonia spp. and Cetraria cucullate* (Johansson et al. 2013). Additionally, the graminoid *Eriophorum vaginatum* is present, which is the study species in this study. For more detailed information about the area see Johansson et al. (2013).

2.2 Experimental design

The experimental setup in the peatland is originally from a long-term snow fence experiment established in 2005 (Johanson et al. 2013) and the measurements in this study were done in the control plots of the long-term experiment. The experiment consists of six different plots with a size of 10×20 m and because of a possible spatial variation amongst roots, the above- and belowground measurements was done in three different “sub-plots” within each 10×20
The above- and belowground measurements were done on the same dates, biweekly, in 2016, starting 19th of May and ending 10th of October.

2.3 Below- and aboveground measurements

Root growth was studied with the minirhizotron method, which are transparent tubes permanently installed into the soil and a fitting camera system, making it possible to take pictures of roots at fixed positions repeatedly. Minirhizotrons have been shown to be a good method for measuring root dynamics as it, with the indexing handle, makes it possible to take pictures at the exactly same spot during every measurement, thus the same roots can be traced throughout the whole sampling period in a non-destructive way (Johnson et al. 2001) (Bartz Technology Corporation, Carpinteria, CA, USA). The minirhizotron tubes were installed at a 45° angle from the soil surface in the autumn of 2012 (September, October; 1 tube per plot) and spring 2013 (April, May; all remaining tubes) (Blume-Werry et al. 2016 b). The minirhizotron pictures were analysed with the program Rootfly 2.0.2 (Birchfeld & Wells, Clemson University, Clemson, SC, USA) and all pictures from every tube were processed and the length and width of the roots of *E. vaginatum* were marked (identifiable by their bright white colour, Fig. 1). The total amount of accumulating roots will further be referred to as root length and the newly appearing roots plus the elongation of existing roots, between the sampling occasions, will be referred to as root growth. To determine the timing of root growth during the growing season, the time when 10% and 90% of total root growth had occurred was calculated.

The plots for the aboveground measurements were 20×20 cm and positioned above the minirhizotron tubes, making it possible to trace the above- and belowground phenology of the same area in every sub-plot. A camera that was reprogrammed to measure the normalized difference vegetation index (NDVI), a measure of how much light plants take up in the photosynthetic active spectra, was used to take pictures at every sampling occasion. Each picture was captured from a height of ca. 1 m directly above the plot with the NDVI-programmed Canon EOS Digital Rebel XSi camera with a Canon Ultrasonic 20–35mm lens. The pictures were processed with WinCAM 2011a (Regent instruments Inc.) and the NDVI value for the whole 20×20 cm square was estimated.

![Figure 1. The bright white root of *E. vaginatum* growth during three sampling times a) 7th of June, b) 2nd of August, c) 15th of August. For each date the elongation of existing roots and the appearance of new roots was marked and calculated as root growth.](image)
2.4 Abiotic factors

The thaw depth was measured in six different spots on the peatland, at every sampling occasion, and the mean thaw depth of the mire was calculated. The soil temperature and soil moisture was measured hourly with EC-5 sensors and recorded on Em50 loggers (Decagon Devices, Pullman, WA, USA) and the measurements were done at the depth of 0, 5, 15, 25 and 35 cm. Additionally, air temperature was measured with the same type of sensor and the min, max and mean temperature was estimated for every day of the whole season. As the experiment setup was originally designed for another experiment, the measurements of the abiotic factors were not performed at the exact same spots as the minirhizotron and NDVI measurements in this study. Thus, the mean soil temperature, soil moisture and active layer were calculated for the peatland. For the analysis including soil temperature and soil moisture, the depths of 5 and 25 cm were chosen as they represent a shallow layer and a deeper layer in the soil profile (the 35 cm depth was excluded due to errors in the sampling leading to only one measurement of that layer).

2.5 Statistical analyses

To investigate the synchrony of below- and aboveground phenology, the day when peak in root length (maximum accumulation of roots) had occurred was compared with the day when peak in NDVI (maximum estimated NDVI value) had occurred. Further, peak in root growth (the day when maximum root growth had occurred between two sampling occasions) and peak in NDVI were compared. Finally, peak in root growth was compared with peak in NDVI increase (the day when maximum NDVI increase had occurred between two sampling occasions). All the above tests were performed with paired t-tests. Root growth was further tested for correlations between the abiotic factors air temperature, soil temperature at depth 5 cm and 25 cm, soil moisture at depth 5 cm and 25 cm. Also, the active layer was correlated with root length and the increase in active layer over the season was correlated with root growth. The hypothesised correlation between air temperature and an increase in active layer was also tested. All correlations were performed with Pearson’s product-moment correlation, except for correlations with soil moisture, which was performed with Spearman’s rank correlation coefficient, due to non-normally distributed data. As the response of root growth could be delayed to abiotic changes, cross-correlations were performed. To further investigate the determinants of root growth, a multiple linear regression was carried out with root growth as the response variable and increase in active layer depth, air temperature and soil temperature at depth 5 cm as the explanatory variables. Before any analyses were carried out, all data were visually analysed for assumptions for normality with qqplots and tested with Shapiro-Wilk normality test, respectively. All statistical analyses were performed with R 3.3.2 (R Core Team 2016, Vienna, Austria).

3 Results

3.1 Phenology

Root length increased constantly during the growing season (Fig. 2 a) and there was an observed root growth throughout the season until the middle of September with a rather large variation among the plots (Fig. 2 b). The NDVI measurement showed a constant increase in the beginning of the season and a slight decrease in the end (Fig. 2 c). However, the increase and decrease in the NDVI value, i.e. the NDVI change, were very inconsistent during the growing season (Fig. 2 d). The timing of root growth, when 10% and 90% of total root growth had occurred, was on the 17th of June ± 2 days and the 13th of August ± 15 days (mean ± 1 SE), respectively.
Peaks in root length and maximum NDVI were asynchronous (mean ± 1 SE, belowground 29\textsuperscript{th} of September ± 2 days, aboveground 20\textsuperscript{th} of August ± 6 days, df=5, t=6.27, p=0.002) (Fig. 3 a). Peaks in root production and maximum NDVI were also asynchronous (mean ± 1 SE, belowground 28\textsuperscript{th} of July ± 6 days, aboveground 20\textsuperscript{th} of August ± 6 days, df=5, t=−4.26, p=0.008) (Fig. 3 b). Maximum root growth between two samplings and maximum increase in NDVI between two samplings were, however, not asynchronous (mean ± 1 SE, belowground 28\textsuperscript{th} of July ± 6 days, aboveground 2\textsuperscript{nd} of August ± 8 days, df=5, t=−0.92, p=0.400) (Fig. 3 c).

Figure 2. Mean ± 1 SE of a) the total accumulating roots during the growing season (root length), b) the appearance of new roots and elongation of existing roots between samplings (root growth), c) the estimated NDVI and d) the increase and decrease of the NDVI between samplings (NDVI change).
3.2 Abiotic factors

Air temperature fluctuated during the sampling period with a maximum temperature of 27.2°C measured on the 22nd of July. An early peak which reached 23.3°C was also observed on the 30th of May followed by a time with lower temperatures. The lowest measured temperature was -7.9°C observed on the 4th of October, but the air temperature dropped below 0°C on the 21st of June and the 15th of August, leaving July as the only freezing-free month of the summer of 2016 (Appendix 1, Fig. 1). The soil temperature at a shallow depth (5 cm) followed the pattern of the air temperature, with a rather large daily variation. Maximum soil temperature at that depth was measured on the 23rd of July and was on average 17°C (Appendix 1, Fig. 2). In the deeper layer (25 cm) the maximum temperature was reached a few days later, on the 27th of July (Appendix 1, Fig. 3). Root growth was positively correlated with air temperature (Pearson’s r=0.711, p=0.014) and soil temperature (Pearson’s at 5 cm depth, r=0.758, p=0.007 and at 25 cm depth r=0.595, p=0.053). In the middle of the growing season, the 2nd of August, the average soil moisture of the area was 0.477 m^3 m^-3 volumetric water content (VWC) and 0.549 m^3 m^-3 VWC at a depth of 5 cm and 25 cm, respectively (Appendix 1, Fig. 4 and 5). Water availability was probably not a limiting factor for root growth in this study site as no correlation between root growth and soil moisture was detected (Spearman’s at depth 5 cm rho=-0.082, p=0.818 and at depth 25 cm rho=-0.237, p=0.483).

During the first measurement, on 19th of May, the mean depth of the active layer of the peatland was 14 cm, and on the last sampling, 10th of October, it was 62.3 cm (Fig. 4 a). The rate of increase in active layer depth peaked in the middle of the growing season (Fig. 4 b) and was positively correlated with air temperature (Pearson’s r=0.709, p=0.014). A weak positive correlation between rate of increase in active layer and root growth during the growing season was observed, but it was not statistically significant (Pearson’s r=0.516, p = 0.104). No time lags were detected because the best correlation was always with the direct temperature estimates, rather than a delayed response. Further, a strong positive correlation between the depth of the active layer and the root length during the growing season was determined (Pearson’s r=0.99, p<0.001). In addition, the abiotic factor that most strongly affected root growth was soil temperature at depth 5 cm (p=0.007).
4 Discussion

4.1 Phenology

In this study, I compared the aboveground and belowground phenology of the sedge *Eriophorum vaginatum* which is an important circumpolar species. Different methods were used to measure above- and belowground phenology (minirhizotrons as a measure of root growth in mm and NDVI as a measure of plant activity), which could complicate a comparison between the two. The NDVI measurement is a measure of how much light plants take up in the photosynthetically active spectra and is thus more related to plant chlorophyll content and gross photosynthesis (Street et al. 2007) than shoot production. It is, however, often used as a proxy for plant biomass and has been used in other studies comparing above- and belowground phenology (e.g. Radville, Post and Eissenstat 2016). The calculated NDVI increase and decrease (NDVI change) should therefore reflect a change in the aboveground biomass. Potential factors that might influence the NDVI value are the levels of incoming light as well as the wetness of the vegetation. The measure of aboveground activity in this study was rather fluctuating, and other studies in subarctic regions have reported peaks earlier in the growing season (Blume-Werry et al. 2016 a, Sloan, Fletcher and Phoenix 2016, Radville, Post and Eissenstat 2016). On the other hand, the root growth pattern (Fig. 2 b) is similar to patterns observed in other studies, i.e. observed growth late in the season (Blume-Werry et al. 2016 a; Sloan, Fletcher and Phoenix 2016; Radville, Post and Eissenstat 2016).

Hence, when further interpreting the results, it should be emphasized that above- and belowground production is not directly compared, but rather, the aboveground phenology measured by NDVI is compared with belowground phenology measured by root growth. Three analyses were performed to investigate the synchrony of below- and aboveground phenology; i) peak in root length against peak in NDVI (the day when mean maximum NDVI value was estimated), ii) peak in root growth against peak in NDVI and iii) peak in root growth against peak in NDVI increase.

The later peak in root length than in NDVI (Fig. 3 a), and lack of root mortality, indicates that roots are active later than shoots. However, total accumulation of roots will increase with every new measurement; thus, root length does not give much insight of when roots are
active. Therefore, root growth might be a better option for estimating activity, when comparing phenology below- and aboveground. In this study, the later peak in NDVI than in root growth (Fig. 3 b) shows asynchrony between above- and belowground phenology. Several earlier studies have also shown that root and shoot phenology is asynchronous in arctic environments (Blume-Werry et al. 2016; Radville, Post and Eissenstat 2016; Sloan, Fletcher and Phoenix 2016) and in other biomes (Du and Fang 2014; Abramoff and Finzi 2015). Though, in studies performed in arctic or subarctic regions, root growth often peaked later than shoot (Blume-Werry et al 2016 a; Sloan, Fletcher and Phoenix 2016). However, in a study by Radville, Post and Eissenstat (2016), where NDVI was used as an estimation of leaf cover, belowground peak occurred 18 days earlier than leaf cover peak, which is in line with my result. Furthermore, the lack of difference between peak in root growth and peak in NDVI increase (Fig. 2 c) indicates that the most favourable growing conditions, for both above- and belowground plant production, was in the middle of the summer when e.g. both air and soil temperature was beneficial.

This study was carried out from the 19th of May until the 10th of October and on the last sampling occasion the ground was covered in frost; hence, the major part of the growing season was included in the sampling interval. To estimate the growing season length belowground, start and end was calculated as the time when 10% and 90% of total root growth had been reached. It occurred on average on the 17th of June ± 2 days and on the 13th of August ± 15 days, respectively. In another study performed in the region of Abisko, in three different habitats (high alpine tundra, low alpine tundra and subalpine birch forest), 90% of fine root growth was exceeded in the beginning of September in the years 2011 and 2012 (Blume-Werry et al. 2016 a). Hence, the growing season length belowground may differ depending on the ecosystem type. Furthermore, the end of the belowground growing season varied much more between plots than the onset of the season. Thus, the questions are what the drivers of root growth are and if they differ depending on season?

4.2 Abiotic factors

It is known that temperature and water availability are important drivers of root growth (Pregitzer et al. 2000; Abramoff and Finzi 2015; Radville, Post and Eissenstat et al. 2016). This study was performed in a peatland, which in general is an environment with high water content. Thus, root growth was probably not restricted by water availability, and in favour of this assumption, no correlation between soil water content and root growth was detected. Soil temperature, on the other hand, might be a more important driver in this type of ecosystem, as I found a strong positive correlation between root growth and soil temperature. Soil temperature may be one explanation of the difference in variation between when start and end of root growth was initiated. It is shown that root growth of cold-adapted species, such as E. vaginatum, is possible at very low temperatures (just above 0°C) (Shaver and Billings 1977). Thus, when the temperature starts to increase above 0°C in the spring root growth can be initiated (Radville et al. 2016). In the autumn, the soil temperature responds slower to the annual decreasing air temperature, and when aboveground plant parts risk freezing the roots can continue to grow for a longer time as the soil temperature remains above freezing point in the autumn. Temperature may thus be an important factor for the initiation of root growth in the spring, though, other factors such as carbon availability may also be important (Radville et al. 2016).

It is known that E. vaginatum has the potential to grow deep and that the root growth can follow the thaw front as the active layer deepens during the growing season (Shaver and Billings 1975, 1977; Blume-Werry et al. 2016 b). Although I did not test if the root growth followed the thaw front, I found a strong correlation between total accumulation of roots (root length) and active layer depth, and a tendency for root growth to increase with increasing depth of active layer. The active layer depth increases throughout the season when the warmer temperature thaws the frozen soil. The total accumulation of roots also increases.
throughout the season as the roots grow. Thus, the relationship between root length and active layer might not be surprising as they could both be explained by an ongoing growing season. The relationship between root growth and increasing active layer might be more complicated and, again, the determinants of root growth need to be considered.

As established, root growth and soil temperature are probably linked, and so is soil temperature and the depth of active layer. However, it is not just the amount of thawed soil that is important for root growth, but rather what unfrozen soil provides, such as nutrients. Plants in arctic regions may be more restricted to nutrient availability than temperature (Sullivan et al. 2015). Species dominance in arctic region is related to available soil nitrogen and the ability to efficiently utilize the recourse (McKane et al. 2002). Furthermore, a high proportion of nitrogen is accumulated near the thaw front, which could benefit deep rooting species, such as E. vaginatum. Hence, an increase in the active layer depth due to global warming will release more nitrogen, benefit some species more than other, and thus affect species composition in tundra regions (Keuper et al. 2012). It is also shown that removal of shrubs leads to degradation of permafrost and a further increase in graminoid cover (Nauta et al. 2015). Thus, change in species composition and abundance could strongly affect the growing conditions in regions with permafrost. Permafrost regions play a key role in global carbon storage, and when permafrost thaws, large amount of the stored carbon might be released and affect the subarctic wetlands ability to function as a carbon sink (Schuur et al. 2015). But at the same time, productivity is increasing in these areas as more nutrients are being released from the newly thawed soil (Keuper et al. 2012). Thus, a larger accumulation of carbon could be expected in tundra regions and this could potentially offset some respiratory losses (Natali, Schuur and Rubin 2011).

4.3 Conclusions

There is a need for broadening the knowledge about fine root in ecosystems, such as arctic and subarctic environments, that are predicted to be strongly affected by climate change (ACIA 2004; IPCC 2013; Iversen et al. 2015). To predict vegetation responses to global warming, plant phenology could act as a sensitive indicator (Wolkovich et al. 2012; Radville et al. 2016). This study highlights the pattern of root growth and aboveground activity in a habitat expected to be strongly affected by increasing temperatures; a peatland underlain by permafrost in a subalpine region. An asynchrony between above- and belowground phenology was found, suggesting that solely using the aboveground plant parts as a representation for phenology of the whole plant is misleading. Furthermore, soil temperature is probably an important driver of root growth in the studied ecosystem. Though, other factors, such as nutrient availability, could further influence root growth. As the temperature continues to increase, several complicated responses of the vegetation and soil processes is to be expected, and more research, which accounts for effects on both above- and belowground phenology, is needed to further investigate plant responses in a warming world.
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Appendix 1

Figure 1. Max, mean and min daily air temperature on the peatland from 19th of May to the 10th of October, measured 20 cm above the ground (n=1).

Figure 2. Max, mean and min daily soil temperature at a soil depth of 5 cm, measured on the 19 of May to the 12th of October (n=2).

Figure 3. Max, mean and min daily soil temperature at a soil depth of 25 cm, measured on the 19 of May to the 12th of October (n=3).
Figure 4. Max, mean and min daily soil moisture (m$^3$ m$^{-3}$ VWC) at a soil depth of 5 cm, measured on the 19 of May to the 12th of October (n=4).

Figure 5. Max, mean and min daily soil moisture (m$^3$ m$^{-3}$ VWC) at a soil depth of 25 cm, measured on the 19 of May to the 12th of October (n=2).