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Short Communication

Repeated waterlogging affects soil conditions and growth and physiology of Scots pine saplings

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ABSTRACT

Soil waterlogging (WL) during the growing season is known to have adverse effects on soil conditions and plant growth. This is the case especially on peatlands, where groundwater tables are high and can vary within the growing season, even on drained peatlands. For assessing the effects of repeated WL periods on soil conditions and root and shoot growth of 4-year-old Scots pine saplings, we conducted a laboratory experiment lasting for 3 simulated growing seasons. During the second growing season, the plants were subjected either to a 2.5 week anoxic period or three repeated WL periods of the same total time of anoxia. We measured concentrations of soil oxygen (O2), carbon dioxide (CO2), methane (CH4) and nitrous oxide (N2O). In addition we assessed shoot and root growth and biomass and foliage carbohydrate status. Waterlogging had immediate and distinctive effects on soil gas conditions: anoxic soil conditions were observed during the WL periods, but O2 concentrations returned immediately to normoxia when WL ceased. Respectively, CO2, CH4 and N2O concentrations increased instantaneously with WL and decreased thereafter. Waterlogging decreased root growth and survival and increased the proportion of dead roots. Waterlogging reduced also shoot growth, especially one growing season later as an after-effect. Starch concentrations in the needles increased during WL, indicating a missing sink as root growth was impaired.

The WL saplings showed increased raffinose and pinitol concentrations in the needles. These sugars act as antioxidants under abiotic stress conditions and their role might be connected with the mitigation of the effects of reactive oxygen species during re-oxygenation after WL ceased. The rather short WL periods in our experiment did not lead to lethal effects on the Scots pine saplings but our results suggest that even short-termed WL periods can have significant consequences on soil conditions and plant growth.

Introduction:

Winter precipitation has been predicted to increase in northern latitudes in the future. This will crucially affect boreal forest ecosystems, depending on whether it will take place as snow or rain. Together with more frequent snow melt due to increasing winter temperatures, increased precipitation will decrease insulating snow cover in the areas where it is deep in the current climate. Consequently, soils may not freeze in regions where there is deep frost in the current climate. However, low freezing temperatures in winter will probably not disappear in northern latitudes. Due to the change in snow cover, the range of soil frost occurrence will probably move to new areas. Soil freeze–thaw events may become more frequent, and soil, water-saturated or not, may freeze more deeply than in the current climate depending on site. Because soil temperature and moisture are the key exogenous drivers of fine root dynamics, it is important to understand the mechanisms by which changes in boreal winter conditions affect soil–plant–climate interactions and the growth and survival of trees accordingly.

Silver birch has a wide distribution, ranging from Mediterranean mountains near to latitude 70° in the north and to central Siberia in the east. It is a pioneer species and typically grows on well-drained soils, as opposed to downy birch, which is more common on poorly drained sites. Due to its wide distribution, silver birch is potentially exposed to a broad range of conditions including soil freezing, the strength and duration of which depends on snow cover and location. If freeze–thaw events become more common in the future, soils even on well-drained sites may be temporarily both water-saturated and frozen. Because the annual cycle of trees is an entity, the environmental conditions and events in one phase of the cycle may affect the development in the subsequent phase. Therefore, the stress projected on roots in winter may induce long-term lagged changes in leaf and needle morphology and growth of above- and belowground organs, but these linkages are not known well.

Waterlogging is harmful for tree roots, because water replaces air in soil, leading to hypoxic or even anoxic conditions. Survival strategies for WL stress are different during the growing season than during dormancy. Escape mechanisms tend to prevail during the growing season, whereas in winter, survival depends on tolerance by the down-regulation of metabolism. Roots are typically less susceptible during dormancy than in the growing season because of low oxygen consumption of cells for energy production in cold soil, as found in above zero temperatures for Norway spruce and silver birch seedlings in growth chamber experiments. In the boreal zone, the most susceptible phase of the roots of Scots pine and Norway spruce seedlings to WL was found to be in the latter part of the growing season, when the roots were still growing. In the middle of the growing season, the first symptoms in the roots and shoots of Scots pine saplings were observed after 1–2 weeks of WL but more clearly after 3 weeks of WL.

Missing snow cover and the formation of an ice layer in the soil or on the soil surface by freeze–thaw events have consequences for both plant roots and soil microbes. Although short-term subzero temperatures may not be harmful for cold-acclimated roots long-term Fr may worsen the situation, especially in water-saturated soil. In snow removal experiments in field conditions, prolonged soil Fr was harmful for several conifer species. In a laboratory experiment, root damage by artificial frosts caused a reduction of growth and survival, but roots recovered, depending on the proportion of root damage and species, white spruce being more sensitive to frost than black spruce and jack pine. In an experiment using Scots pine saplings with Fr and WL for 6 weeks during dormancy, chlorophyll fluorescence and the water potential of needles were lower, and the apoplastic electrical resistance of needles was higher in Fr than in NoFr (soil not frozen) already during dormancy. In the same study, shoot elongation started earlier if exposed to Fr than NoFr conditions, but the onset of fine root growth was delayed by 20 days when Fr was combined with WL. It is not known whether a deciduous species, like silver birch, responds to Fr and WL during dormancy similarly to evergreen Scots pine. Although a missing snow cover and the formation of an ice layer on the soil surface were more harmful for young seedlings of Scots pine than downy birch, it is unknown whether the responses of older plants would be similar.

The winter dynamics of greenhouse gases, i.e., carbon dioxide, nitrous oxide and methane, are particularly interesting in terms of the ongoing climate change. This is due to a predicted change in soil Fr by altered snow cover and in soil water table by increased precipitation. In addition, draining of managed forests to decrease the water table, aiming to increase tree growth, affects GHG fluxes between the soil and atmosphere. Much of the annual N_2O emission, depending on the ecosystem, has been observed during winter and during the transition from winter to spring, when freeze–thaw events are common, but the influx of CH_4 decreased with soil Fr. On the other hand, winter fluxes of CO_2 were less important to the annual flux than those of N_2O, respectively. This pattern is probably because one primary process of soil CO_2 production, i.e., root respiration, is likely small during winter. Nevertheless, short- and long-term bursts of CO_2 are caused by different processes during soil thawing in the spring. Greenhouse gases fluxes are linked to the soil water table such that CH_4 emissions decrease but N_2O emissions increase with the lowering of the water table. However, the interactive effects of WL and Fr on GHG fluxes between the soil and atmosphere and possible counter effects on physiological processes and the growth of roots and shoots are unknown.

The aim of this study was to obtain an integrated view of the changes in the root zone environment and the mechanisms of the root and shoot responses of silver birch saplings, as affected by WL and soil Fr during dormancy. We hypothesized that although roots are physiologically not very active during dormancy, WL and soil Fr, with accompanying changes in soil gas concentrations, induce lagged changes in the physiology and growth of the roots and aboveground organs during the following growing season.

Conclusion:

A whole-tree approach was used to study the reactions of silver birch saplings to WL and soil Fr during dormancy and the changes in the soil gas concentrations by the treatments. In our experiment in controlled conditions, more consistent changes in roots and shoots were observed by soil Fr than by WL. The activation of physiological processes and growth in the aboveground organs took place earlier if the roots were exposed to soil Fr than without Fr. Fine root mortality increased by soil Fr at the beginning of the post-treatment growing season, followed by compensatory growth of fine roots in the later part of the growing season. However, the fine root function did not completely recover by the end of the growing season, when another winter would follow in field conditions. As the frost effects on roots are not well known even in the present climatic conditions, also basic studies into repeated Fr are required. In contrast, no effects or only temporary effects of WL were observed, which corroborates earlier findings on stronger effects of WL in the growing season under than dormancy conditions. The soil gas concentrations support the observations of increased root damage by soil Fr. The changes in gas concentrations most probably are a result of increased decomposer activity and nutrient leaching into soil due to increased root damage. According to the climate scenarios for winter precipitation in the boreal zone, soil conditions are in transition and will change within the coming decades. Whether the precipitation falls as snow or rain, winter floods may become more common, and soil Fr may increase or decrease. According to the present study, the increasing variability in soil Fr and thawing deserves further attention, while winter-time WL effects on boreal trees are less severe than those of growing season WL.