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Effects of sink removal on transpiration at the treeline: Implications for the growth limitation hypothesis

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Abstract

In this paper, we tested if sink removal in treeline trees induces downscaling of the stomatal conductance in treeline trees. Körner [Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia115, 445–459.] hypothesized that treeline trees are particularly sink limited due to low temperatures during the growing season. This implies that they would have lower sapflow rates and their sapflow rates would be less sensitive to variations in temperature than the sapflow rates of control trees. We removed about 75% per year or all buds during 2 subsequent years. We did not find any differences in sapflow rates and their sensitivity to daily mean temperatures in our data. Therefore, our data indicate that the photosynthesis of trees at the treeline might not be sink limited. Furthermore, trees increased their branch extension growth in response to debudding and it seems probable that trees can compensate for a sink removal by increasing the growth rates of remaining meristems.

Keywords: Sink limitation; Treeline; Sapflow; Transpiration

1. Introduction

Global change will probably increase tree growth in treeline ecotone, due to increased temperature, increased nitrogen deposition and enhanced carbon acquisition (Grace et al., 2002). However, the mechanisms that induce changes in growth are not clear, as we do not have an exact understanding of the factors that limit growth at the treeline. This understanding is quintessential, when we try to predict how the treeline will respond to future climate change: under changing climate, trees are modifying their growth and resource acquisition to prevailing conditions, and this can alter the sensitivity of tree growth to the environment.

The dominant theory on the reason for treeline formation is presently the so called "sink limitation hypothesis" that has also been called "growth limitation hypothesis" (Körner, 1998). According to sink limitation hypothesis, low temperatures and a short growing season limit cell formation and growth in treeline trees. Therefore, trees would not be able to fulfill the minimum requirements of growth and cell renewal above the treeline (Körner, 1998). Photosynthesis is not as strongly depended on temperature than growth. In fact, during growth season the net photosynthesis rate in treeline trees is not much depressed by cold temperatures, except in situations during early spring or late fall, when night time temperatures fall clearly below 0 °C and damage to the photosynthetic machinery (Grace et al., 2002). Growth, on the other hand, depends strongly on temperature (Häsler et al., 1999; Pietarinen et al., 1982). According to the hypothesis, the low temperatures at treelines would, therefore, reduce the growth of trees more than their photosynthesis. Earlier studies have also revealed that carbohydrate reserves are never seriously depleted in treeline trees (Hoch et al., 2002; Hoch and Körner, 2003), except under heavy defoliation (Li et al., 2002). However, some authors have expressed doubts on the importance of this limitation (Sveinbjörnsson, 2000; Stevens and Fox, 1991) and seem to prefer the so-called resource limitation hypothesis that assumes that trees cannot acquire enough resources to grow larger than a certain size.

We assumed that the imbalance between growth and photosynthesis inflicted by low temperatures could cause an accumulation of carbohydrates in plant tissues. The reason for this is that low temperatures restrict more the rate of biosynthetic processes, where glucose is used, than photosynthesis (Grace et al., 2002). Under sink limitation, photosynthesis will often be down regulated due to the increasing amount of photoassimilates in tissues

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(Moore et al., 1999; Stitt, 1991). Leaf carbohydrate signalling induces thereafter a downscaling of photosynthesis (Moore et al., 1999). Even though it is clear, that the accumulation of photosynthates leads to a downscaling of the photosynthetic system, there exist controversial viewpoints on what factors are inflicting the down scaling. Phosphate in the stroma of chloroplasts is a fundamental element for the production of ATP, which in turn regulates the starch synthesis (Luxmoore, 1991). During sink limitation, stromal phosphate concentrations are stated to be low (Sharkey and Vandeveer, 1989). In Calvin cycle, ATP and NADPH are used for production of G3P molecules that are used for the construction of sugars. Some authors claim, that enzyme Rubisco (Wittenbach, 1983; Stitt, 1991), which catalyses the entry of CO_2 into the photosynthetic metabolism (Stitt, 1991), or the inactivation of the catalysation process (Sawada et al., 1995) is responsible for the depression of photosynthesis, and Rubisco content is usually lower in plants that have decreased their photosynthetic capacity (Moore et al., 1999). Also the direct accumulation of starch in leaves is presented to act as the regulating factor of photosynthesis (Nakano et al., 2000; Iglesias et al., 2002). Nevertheless, the reduction in the photosynthetic capacity in C_3 plants correlates with the size of the sinks in plant (Arp, 1991), even though there might be species specific mechanisms acting as signals for the down regulation of photosynthesis.

Hoch et al. (2002) provided evidence that treeline trees have usually higher labile carbohydrate concentrations than lower elevation trees. However, Sveinbjörnsson (2000) questioned if such trends could be rather an acclimation to a colder more hazardous environment. Under these extreme climate conditions, trees would require a larger carbohydrate reserves to recover from more frequent and more severe climate induced damages.

In sub-arctic latitude forests, large variations of photosynthetic capacity have been observed during spring, but also during summer (Hari and Mäkelä, 2003), and these changes have been associated with changes in average temperature with delay (Mäkelä et al., 2004). Increase in the day or even night-time temperatures have been found to accelerate photosynthesis. Even more important in the perspective of sink limitation, is the increase in the night-time temperature.

One possibility to increase the sink limitation of tree growth is to debud the trees, since due to the treatment the carbon sinks in growing new shoots and new foliage are suppressed. By extracting the buds the largest sink where photosynthates are used during growing season is removed. According to Körner's hypothesis, removing of buds should not have any effect on the stem growth, but at the same time, as photoassimilates accumulate, the photosynthesis should be down regulated.

In this paper, we test if sink removal in treeline trees has an effect on tree transpiration. We use sapflow as a proxy for photosynthesis. We tested if stomatal conductance acclimates to changes in short-term average temperature (over several days) using the optimal stomatal control modeling approach of Mäkelä et al. (2004). The approach, originally developed and tested for a non-treeline forest situated only a few kilometers away from our study site, assumes that the photosynthetic capacity acclimates to changes in temperature according to a time-delay process. Since Mäkelä et al. (2004) did not find any evidence for changes in the intrinsic water use efficiency with changes in temperature we think that the approach is applicable to transpiration data. Also in a study of Hari et al. (1999), the model was found to produce realistic estimates on both photosynthesis and transpiration.

There are two different scenarios which our trees under experiment might encounter:

1. The growth of treeline trees is sink limited. Trees have adjusted their stomatal control to a level, where they are able to acquire enough resources to fill their carbohydrate reserves and they are able to acclimate according to the prevailing need of resources. According to this scenario:
    1. Mean sapflow will be depressed in debudded trees since debudding increases the sink limitation in trees.
    2. Debudding reduces the temperature sensitivity of photosynthesis, because debudded trees are carbon saturated and variations in sink activity would not affect the sink limitation very much.
    3. Debudded trees will be unable to increase the growth of the remaining apical buds since meristem extension growth is primarily sink limited.
2. Trees are not sink limited:
    1. Sapflow will not be depressed in debudded trees, since trees are using acquired photosynthates for increased growth of remaining buds and branches.
    2. The sensitivity of photosynthesis to temperature will not decrease as carbohydrate concentrations are not accumulated to saturation level.
    3. Biomass growth will be increased, since temperature is not the sole factor controlling growth.

2. Materials and methods

2.1. Study site

The Värriö Naturepark is located in northeast of Finland, near Russian border at the geographical location of 67 48°N, 29 40°S. Annual mean precipitation in the area is about 600 mm and average mean temperature is −1 °C. This study was made in Värriötunturi 1 fjell (altitude 471 m). On the fjelltop there are growing scattered *Pinus sylvestris* (L.) trees, some of them have clear Krummholz growth form, where as other have maintained their normal growth form. Trees used in this study were about 50 years old and the heights of these trees were between 235 and 335 cm. The area is sparsely populated and a strict nature reserve. Direct anthropogenic disturbances at the treeline are therefore not likely, but reindeer densities and deposition of anthropogenic pollutants have changed over the last decades.

2.2. Measurements

During springs 2003 and 2004, we removed 3/4 of buds from total six trees prior to bud break (for each branch we left every fourth bud, excluding the apical dominance buds, which were all left intact). In other words, each tree in the debudding treatment