Assessing the environmental controls on Scots pine transpiration and the implications for water partitioning in a boreal headwater catchment

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Abstract: Climate change projections indicate reduced summer precipitation and increased air temperature for the northern high latitudes. These climate changes are likely to alter forest water budgets of which plant transpiration (*T*) forms a significant component. Plant transpiration is regulated by stomata behavior of particular species, which is constrained by ambient air and soil conditions. Here, we measured sap flow in a Scots pine (*Pinus Sylvestris*) plantation in a low energy Scottish headwater catchment during the main summer growth period. Effects of rainfall on forest transpiration, as well as the response of *T* to four environmental variables were investigated at a daily scale. In this boreal environment, transpiration was mainly restricted by radiation and vapor pressure deficit. Air temperature was the least important controlling factor. Soil water became an important factor when rainfall was limited. Frequent but small rain events dictated that precipitation met short-term transpiration demand most of the time. The trees needed supplementary water from antecedent soil water stores when weekly rainfall was below ~8 mm, but such periods were rare. Water exchange mainly occurred in the canopy or upper 10 cm of the soil, with 47% of rainfall transpired, 45% intercepted and <8% evaporated from the soil surface. Understanding interactions between forests and their hydroclimate, as well as the role of forests in water partitioning is crucial to assist a sustainable land and water management in a changing climate. Whilst such studies are common in semi-arid regions, they are limited in boreal zones, therefore, our findings are a valuable contribution to understanding plant-water relations in a changing environment.

Key words: sap flow; evapotranspiration; climate; hydrology; water partition; Scots pine

1. Introduction

Plant transpiration (*T*) plays an important role in forest water budgets, as it affects the water partitioning in soils, aquifers and streams (Le Maitre et al., 1999; Vivoni et al., 2008; Deutscher et al., 2016). Precipitation has increased in the Northern Hemisphere over the last two to three decades (Easterling et al., 2000; Dore, 2005; IPCC, 2013) which can impact northern ecosystem composition and productivity (Lindner et al., 2008; Ruckstuhl et al., 2008; Chertov et al., 2010). While annual precipitation is predicted to further increase in the future (IPCC, 2013; Krasting et al., 2013), summer rain is projected to decrease in many northern areas possibly falling in fewer higher intensity events (Lindner et al., 2008; IPCC, 2013). In such circumstances, plants may face severe challenges to maintain productivity with foreseeable more frequent occurrence of water stress strongly associated with the precipitation and soil moisture dynamics (Porporato et al., 2001; Lisar et al., 2012). Therefore, a comprehensive understanding of the precipitation effects and soil water controls on plant water use is necessary and holds the key to adapting water and land use management to the future climate change.

T is regulated by stomata behavior constrained by both atmospheric conditions and soil water availability (Whitehead, 1998; Buckley et al., 2003; Wang et al., 2014). The mechanisms have been extensively explored at multiple scales from stomata and leaf to whole tree and ecosystem levels (Jarvis and McNaughton, 1986; Schulze et al., 1994; Bovard et al., 2005). Among the constraining variables, atmospheric vapor pressure deficit (*VPD*) and solar radiation (*Rs*) are the two major dominant controlling factors (Bovard et al., 2005). However, secondary controlling factors (such as temperature, *Ta*, soil water content, θ) vary with climates and species (Guo et al., 2010; Chen et al., 2014). In addition, rainfall can also affect *T* by altering atmospheric demand (or potential evapotranspiration, *ETp*) and soil water content (Findell and Eltahir, 1997). For example, rainless days usually create more favorable conditions for transpiration (higher *Rs* and *VPD*) than rainy days. In arid/semi-arid areas, where vegetation growth is usually water-limited, plant water use highly relies on rainwater, and rainfall pulses stimulate *T* after a certain rainfall threshold is reached, because increased water storage in the root zone increases soil water availability (Ogle and Reynolds, 2004; Potts et al., 2006; Raz-Yaseef et al., 2012).

In contrast to semi-arid regions, in the low-energy northern high latitudes (>45˚N) vegetation growth is usually limited by radiation and not water availability. The studies in this region put a stronger focus on climate-driven vegetation greening attributed mainly to warming temperatures (Buitenwerf et al., 2015; Garonna et al., 2016). Precipitation, soil moisture, and snow accumulation and melt also contribute to enhanced vegetation growth (Luus et al., 2013), and this contribution can be highly variable in space and time (Barichivich et al., 2014). As the treeline has progressed poleward (Beringer et al., 2005; Pearson et al., 2013), investigations of tree water use and environmental controls are important for understanding ecosystem response to climate change, but such work in this critical region has so far been limited. Several studies have shown that tree water use in the high latitudes is often closely linked to permafrost thaw since soil water from thawed permafrost can be comparable to soil water from summer rains (Kropp et al., 2017). Light intensity and humidity also closely restrict tree water use and productivity (Arneth et al., 1996; Gao et al., 2016; Zha et al., 2013). There is a lack of understanding on direct rainfall effects.

The natural vegetation over much of the Scottish Highlands would have been forest dominated by Scots pine (*Pinus sylvestris*), but a long history of clearance, burning and overgrazing by deer and sheep resulted in limited forest cover across Scotland. With the presence of frequent rainfall, low radiation and high humidity, plants are usually not under water stress during most of the year (Haria and Price, 2000). However, future projections of decreased rainfall and increased intensity during growing seasons (Gosling, 2012; Capell et al., 2013) may result in a decreased water availability increasing the probability that vegetation would suffer from more frequent and prolonged water stress (Zhang et al., 2008; Trahan and Schubert, 2016). The role of soil water in regulating plant transpiration may become more important (Geris et al., 2015b) but it is not yet fully understood; neither is the role of plant transpiration on canopy water partitioning relative to interception and soil evaporation losses. Therefore, in this study, we measured sap flow in a Scots pine plantation in a Scottish headwater catchment, aiming to: (1) investigate the dynamics of transpiration in Scots pine in this low energy boreal environment in the summer season which may be more water-limited than other seasons; (2) examine the interactive environmental controls on transpiration; and (3) understand the implications for water partitioning in the forest in terms of likely effects of future climatic conditions.

2. Materials and methods

2.1. Study site

This study was conducted in the Bruntland Burn catchment (3.2 km^2, 57.04ºN, 3.13ºW) in the Scottish Highlands (Figure 1). It is described in detail elsewhere (Birkel et al., 2011; Tetzlaff et al., 2014; Soulsby et al., 2015; Blumstock et al., 2016). The climate is boreal oceanic; the recent decadal mean annual maximum temperature is 19.4±1.3ºC in July, and mean annual minimum temperature is -1.0±1.6ºC in January. Mean annual precipitation (*P*) is around 1000 mm; it is relatively evenly distributed but lowest (mean ~65 mm/month) in April-July and highest (~105 mm/month) in October-February. Throughout the year, it most commonly falls as low-intensity rain; snow is generally <5% of annual *P* and tends to lie for short periods (a few days to a few weeks) in January and February and melts quickly. Annual potential evapotranspiration (*ETp*) calculated using the Penman-Monteith method (Allen et al., 1998) is around 400 mm and annual runoff at the catchment outlet is around 700 mm (Soulsby et al., 2015).

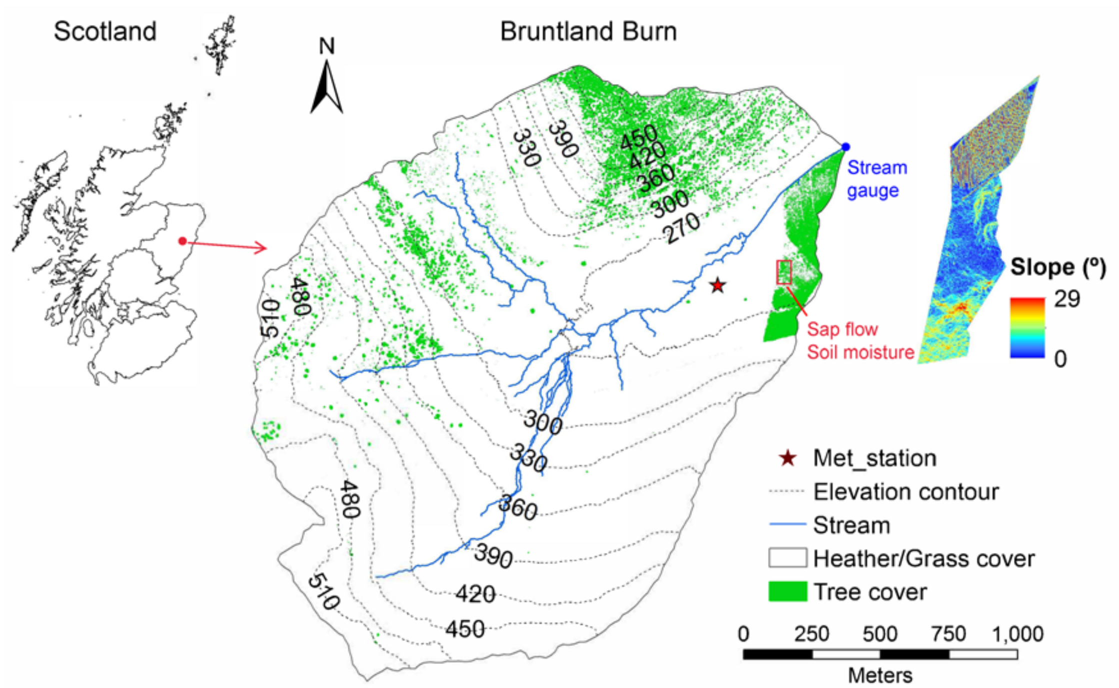

Figure 1 Location of the Bruntland Burn catchment on the map of Scotland, and vegetation cover and instrumentation in the catchment. The forest plot is enclosed by the red rectangle. Numbers on contour lines are elevation in meters above sea level. Vegetation cover and slope data were obtained from 1 m resolution LiDAR data. Slopes at the lower part of the plantation are affected by the furrows.

The geology of the catchment is mainly granite and associated metamorphic rocks (Tetzlaff et al., 2014; Dick et al., 2015). Elevation ranges from around 250 m.a.s.l at the flat valley bottom, to about 550 m on the steeper slopes (Figure 1). Organic-rich soils dominate the catchment, with large areas of deep (>1 m) peats in valley bottoms and shallow (<0.5 m) peats on the lower hillslopes. The steeper slopes with the studied plantation are characterized by podzols which have a 0.1-0.2 m deep O horizon overlying a freely draining mineral sub-soil.

The dominant vegetation in the catchment is heather (*Calluna vulgaris* and *Erica tetralix*) shrubs with a canopy height ~0.3-0.6 m, distributed throughout the valley and hillslopes. Trees, mostly Scots pine, cover about 10% of the catchment, mainly in plantations near the outlet and as natural forest on the south-facing steeper slopes. The tree height ranges from 5 m in the natural forest to 15 m in the plantation. The understory is sparsely vegetated in the plantation where canopies are dense and light penetration is low. The majority of tree roots are present in the upper 0.3 m of the soils (Geris et al., 2015a) but extend a few meters horizontally. Trees are ~30 years old without any cutting/thinning history. Tree density is lower in the middle part of the forest (960 trees/ha) than the upper and lower parts (>2000 trees/ha).

2.2. Measurements

This study covers July to September 2015, a period in the year that is usually the warmest and driest. In total, 32 sets of Granier-type (Granier, 1987) thermal dissipation sap flow probes (TDP probes, *Dynamax Inc. Huston*, USA) were installed on 10 trees at 1.3 m high above ground with a range of stem sizes (10-32 cm in diameter at breast height, *DBH*). Each set of sensors comprises 1 heater probe and 1 thermocouple probe 4 cm below it. Four sensors were installed on trees with *DBH* over 20 cm in four cardinal directions; two or three sensors on trees with *DBH* of 15-20 cm on the south-north (and west when applying) sides; and one sensor on 1 tree with *DBH* below 15 cm. Data were collected using a CR1000 data logger (*Campbell Scientific*, USA) at an hourly interval. Incremental wood cores were taken from 51 trees in 3 plots in the plantation at the end of study period to establish the relationship between sapwood area (*As*) and *DBH* at 1.3 m above ground ($As = 0.0049 \times DBH^{2.0048}$, R^2=0.95). The average ratio of sapwood area to forest area (25 m^2/ha) obtained from surveys in the three plots was used to estimate forest transpiration.

An automatic weather station (*Environmental Measurement Limited, North Shields, UK*) was established near the forest site in an open area (Figure 1), giving continuous measurements of air temperature (*Ta*), relative humidity (*RH*), net radiation (*Rn*), soil heat flux (*G*), precipitation (*P*), wind speed/direction, and atmospheric pressure. Volumetric soil water content (θ) was measured near the sample trees using time domain reflectometry (TDR) soil moisture probes (model CS616, *Campbell Scientific, Inc. USA*). Sensors were calibrated against gravimetric soil water content and bulk density in the lab with a range of water content. Two replicate TDR probes were inserted at depths of 0.1, 0.2 and 0.4 m prior to the sap flow measurements commencing, allowing soil stabilization after refilling of the pits. The slopes derived from a 1 m resolution LiDAR elevation map (Figure 1) show that most of the plantation is relatively flat. Measurement of soil moisture at one location will not capture the spatial heterogeneity within the plantation, but comparison to measurements elsewhere in the catchment showed that the sensors at this site captured the general soil water dynamics in response to rainfall and evapotranspiration. Meteorological parameters and soil water content measurements were recorded by CR800 data loggers (*Campbell Scientific, Inc. USA*) at 15-minute intervals.

2.3. Methods

Forest transpiration was estimated using the average sap flux density per unit sapwood area multiplied by the sapwood area index (Granier et al., 1996). Measurements of forest transpiration and hydroclimatic variables, including *Ta*, vapor pressure deficit (*VPD*, calculated from mean *Ta* and *RH*, Allen et al., 1998), *Rn* and θ, were aggregated to daily values for comparison of temporal dynamics. We used two measures to investigate the potential effects of rainfall on transpiration. First, we calculated the mean diel *T* rates (mm/h) on days before rain and after rain. Second, we grouped rainfall data into different amount classes (mm/d), and then calculated the increases in *T* on days after rain in comparison to prior to rain for each rainfall class, in order to examine the effects of different rainfall amounts on tree water use. “Before rain” refers to the day before one or several rain days; “after rain” refers to the day when *T* peaked after the same rainy day(s) (Zeppel et al., 2008; Zhao and Liu, 2010). Daily rainfall <0.2 mm was considered as rain free. There were 13 pairs of before-rain and after-rain days for the calculations.

Relationships between *T* and environmental variables (*Ta*, *VPD*, *Rn*, θ) were analyzed using linear regression to investigate the major influencing factors on transpiration. Despite various functions published to capture the effects of these environmental variables (Whitley et al., 2013; Wang et al., 2016), here, we used a linear regression as the data ranges of all examined variables at this site were much smaller than those found in other studies (McLaren et al., 2008). Since *T* can be estimated as the multiplication of canopy conductance and leaf-air vapor pressure deficit (Jarvis and McNaughton, 1986; Whitehead, 1998), the ratio *T/VPD* can be considered as a proxy of canopy conductance. In this sense, we analyzed the relationships between *T* and the environmental variables at different ranges of *T/VPD* to differentiate the interactive controls of atmospheric and soil water on *T*.

3. Results

3.1. Hydroclimatic measurements

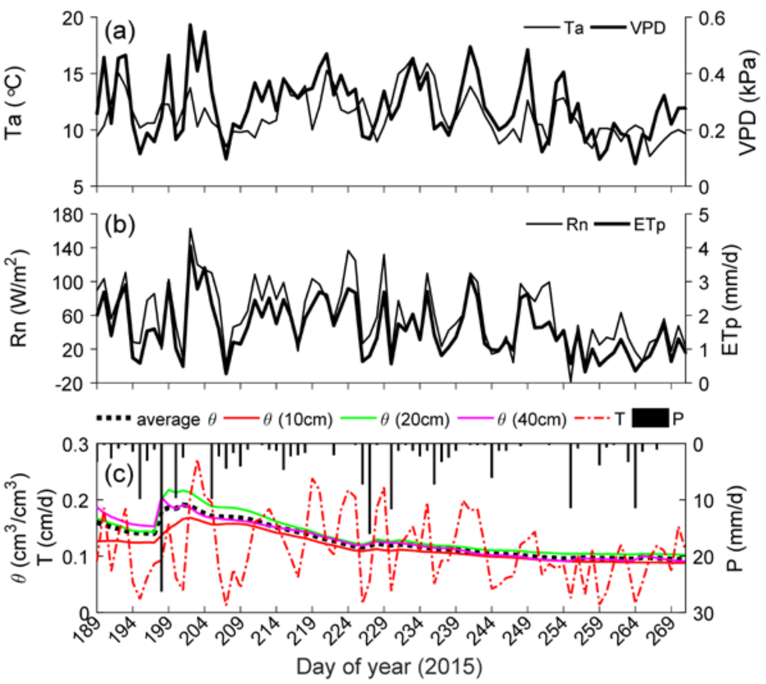

Figure 2 Daily dynamics of hydroclimatic variables during the study period 8/7-28/9/2015. (a) mean air temperature (*Ta*) and vapor pressure deficit (*VPD*); (b) net radiation (*Rn*) and potential evapotranspiration (*ETp*); (c) Rainfall (*P*), transpiration (*T*) and soil water content (θ) at three depths (10, 20 and 40 cm) and depth-mean.

During the study period, variability in daily mean *Ta* was small with an average of 11.3°C (Figure 2a). Low temperature and high humidity resulted in a small range of *VPD* (0.1-0.6 kPa). Similarly, daily *Rn* values were small with the maximum only ~180 W/m^2 (Figure 2b), showing a general decreasing trend over time. *Ta*, *VPD* and *Rn* were lower on rainy days (usually cloudy, cool and humid) than rain-free days (warm and less humid). Atmospheric demand (or *ETp*) corresponding to low radiation, temperature and high humidity only totaled 118.6 mm during the study period (83 days). There were frequent rainfall inputs, with most rain days characterized by small low-intensity events (<5.0 mm/d, Figure 2c). The podzolic soil was dry with a mean θ ~0.13 cm^3/cm^3. There was only one increase to about 0.2 cm^3/cm^3 on day of the year 198 (July 17) with rain >20 mm/d, followed by a gradual drying. Water content at 0.1 m depth was consistently the lowest, whereas it was highest at 0.2 m depth, however, the differences were small. Soil water content generally decreased over summer; despite continued rainfall inputs only a few events caused small increase in soil moisture, though to some extent this likely reflects the location of the soil moisture sensors under a dense part of the forest canopy. Corresponding to the hydrometric conditions, transpiration rates were relatively low, usually <2 mm/d (Figure 2c) with more water transpired during rain-free days than rainy days. Transpiration showed a general decreasing trend over time, consistent with the decrease in *Rn* and *θ*. Transpiration increased rapidly after rainy days, e.g., days 213-218, which was coincident with increasing *Rn* and *VPD*.

3.2. Rainfall effects on transpiration

To investigate the effects of rainfall on forest transpiration in more details, we calculated the average diel transpiration rates on days before and after rain (Figure 3). Results were based on 13 eligible data pairs. Across all dates, tree water uptake began at 08:00-09:00 in the morning and peaked around 14:00-15:00 in the afternoon. The largest difference in transpiration rate before and after rain occurred in the afternoon. On average, trees transpired 18.4% more water on days after rain than they did on days before rain.

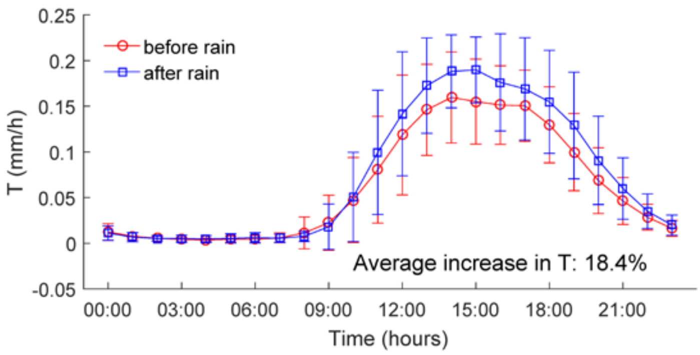

Figure 3 Comparison of mean diurnal transpiration (*T*) on days before rain and after rain events. Before rain refers to the day before one or several consecutive rainy days; after rain means the day when *T* peaked after the same rainy days.

The frequency of different rainfall amount classes and the increase in transpiration linked to each class are given in Figure 4. Most rain fell in small intensity events: almost half of the rainfall events had a rain amount less than 2.0 mm/d, one third of the events had rainfall of 2.0-5.0 mm/d, and only ~22% of the events had rainfall over 5.0 mm/d. In Figure 4(b), the largest increase in transpiration occurred when rainfall was below 2.0 mm/d (~240%), followed by 2.0-5.0 mm/d. As rainfall amount increased, the relative increase in forest transpiration decreased. This means, frequent small rain events appear to have a more positive effect on transpiration than large rain events.

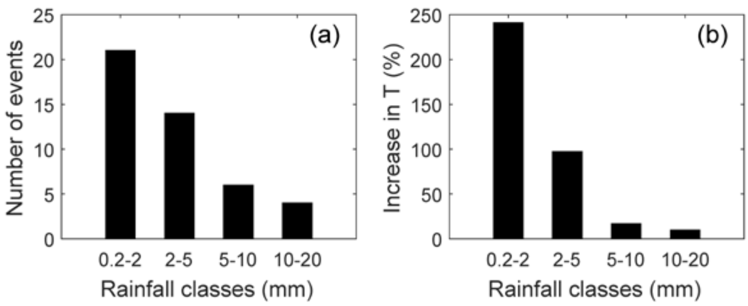

Figure 4 (a) Frequency of different rainfall amount classes; (b) Increase in transpiration (*T*) between the days before rain and the days after rain when *T* peaked. There was only one day with >20 mm rain and is not shown in the figure. Rain ≤0.2 mm/d was considered as rain free.

3.3. Responses of transpiration to environmental variables

Relationships between *T* and four environmental variables are shown in Figure 5. At the daily scale, *Rn* and *VPD* were, unsurprisingly, the two major factors influencing *T* (R^2>0.50). Higher amount of *T* corresponded to higher amount of *Rn* and *VPD*. In contrast, the effects of *Ta* and

θ were not significant (R^2=0.05) as there was barely a clear linear relationship between *T* and the two variables (bottom panels in Figure 5).

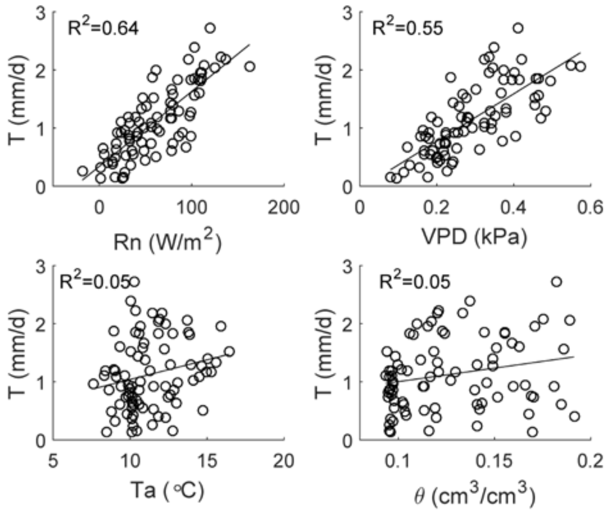

Figure 5 Relationships between transpiration (*T*) and environmental variables: net radiation (*Rn*), vapor pressure deficit (*VPD*), air temperature (*Ta*), and depth-average (0-40 cm) volumetric soil water content (θ). Solid lines are linear regressions between *T* and the relevant variables.

When *T*, *Ta* and θ were analyzed according to different rainfall thresholds, the R^2 between *T* and *Ta* were consistently low (<0.10, and mostly p>0.05). However, relationships between *T* and θ varied greatly with rainfall amounts (Figure 6). When rainfall was below 2.0 mm the soil water was important to maintain forest transpiration (R^2>0.20, p<0.001). This effect decreased with increasing rainfall thresholds; when rainfall was between 2.0 and 4.0 mm/d the effect was still statistically significant (R^2<0.10, p<0.05) but not as strong as below 2.0 mm/d. When rainfall was over 4.0 mm/d there was no clear relationship between transpiration and soil water any more (R^2<0.10, p>0.05). This indicates that the trees tend to deplete soil water storage when there was little daily rainfall.

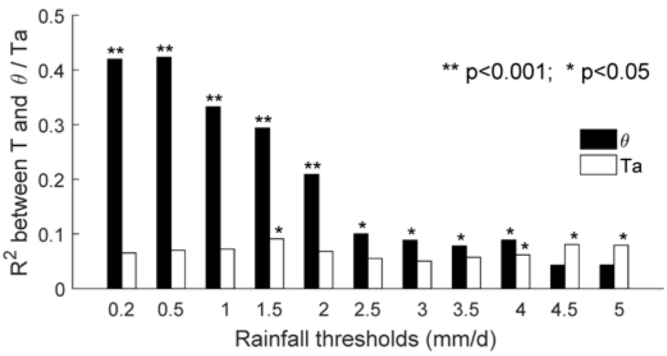

Figure 6 Coefficient of determination (R^2) of linear regression between transpiration (*T*) and soil water content (θ) and air temperature (*Ta*) below different rainfall thresholds. For example, the R^2 for rainfall threshold 1.5 mm/d means R^2 between *T* and θ/*Ta* using data when rainfall is ≤1.5 mm/d.

Plant transpiration is regulated by stomata via stomatal conductance (and hence, canopy conductance). When transpiration was plotted against *T/VPD*, which serves as a proxy of canopy conductance (higher values correspond to higher *T* rates), we observed a rapid increase of *T* before *T/VPD* ~4.0 mm/d/kPa. Above this value, the increase was much less and plateaued. We therefore used this *T/VPD* threshold (4.0 mm/d/kPa) to divide the data into two groups (below and above this threshold), and examined the environmental controls on transpiration again for these two data groups in Figure 7. The scatterplots show the different influences of atmospheric condition and soil water on transpiration with contrasting ranges of *T/VPD*. *Rn* and *VPD* were the two major influencing factors on transpiration on all occasions (Figure 7a, b). When *T/VPD* was below 4.0 mm/d/kPa, *Ta* showed weak influences on *T* (R^2=0.27, p<0.001), and *T* was not related to θ (R^2=0.06, p=0.08). In contrast, when *T/VPD*>4.0 mm/d/kPa, the relationship between *T* and θ on was enhanced (R^2=0.32, p<0.001) while *Ta* effect was minimal.

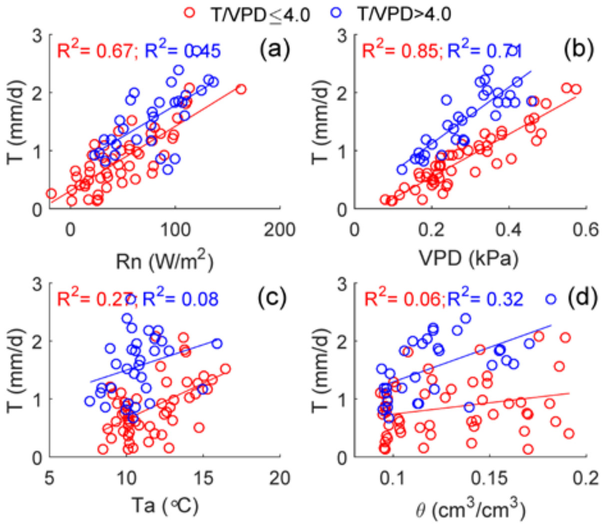

Figure 7 Relationships between transpiration (*T*) and environmental variables with varying *T*/*VPD* (unit: mm/d/kPa). (a) *Rn*-net radiation; (b) *VPD*-vapor pressure deficit; (c) *Ta*-air temperature; and (d) *θ*-volumetric soil water content. Significance test *p* values for *T* and *Ta* relationship with *T*/*VPD*>4.0 and for *T* and *θ* with *T*/*VPD*≤4.0 are 0.11 and 0.08 respectively, for others are <0.001.

3.4. Partitioning of water supply to plant transpiration

To understand the water sources for forest growth, we calculated the water balance between rainfall and transpiration on a weekly basis (Figure 8). Rainfall maintained the water stores in the forest and accounted for 98% of the variation in the *P*-*T* budget. In most of the 12 weeks, total rainfall exceeded the transpiration demand. Rainwater deficit (*P*-*T*) existed only when weekly rainfall was below ~8 mm. It is noticeable that in the three weeks with rainfall deficit, transpiration did not decrease significantly but remained similar to previous weeks with more rainfall (Figure 8).It is also noteworthy that periods of deficits were limited, and the deficits were small. The regression between *P* and *P*-*T* in Figure 8b indicates that the forest used supplementary water supply from soil water storage when weekly rainfall was less than ~8 mm on average. Rainfall here was the total gross rainfall, and although interception accounts for around 45% of summer precipitation (Braun, 2015), the effective rainfall should be sufficient to maintain transpiration in most weeks.

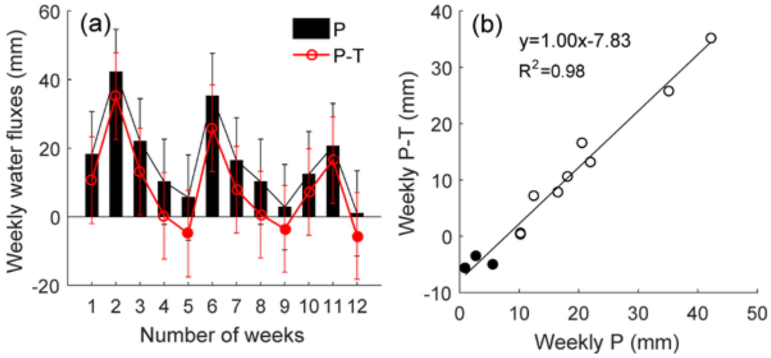

Figure 8 (a) Time series of weekly rainfall (*P*) and water balance between rainfall and transpiration (*T*): *P-T*. (b) Regression between *P-T* and *P*. Filled black circles correspond to the data points in (a). Error bars in (a) are one standard deviation of each data series: 12.4 mm/week for *P* and 12.6 mm/week for *P-T*.

4. Discussion

4.1. Transpiration in Scots pine forest and the environmental controls

Average *T* (1.1 mm/d) was low and coincident with low average atmospheric demand. *T* values were at the low end of regional estimates across Europe (1.2-1.8 mm/d along a latitudinal range of >20ºN) , closest to the estimates at a Finnish site (Berninger, 1997; Meiresonne et al., 2003) and a Scottish site in the central Highlands (Haria and Price, 2000), and slightly lower than in a plot in central Scotland (~1.3 mm/d from mid-May to end of August 1995 in Irvine et al., (1998)). The Scots pine water use in this study was generally within the range reported in studies conducted in wet temperate/boreal conifer forests (Unsworth et al., 2004; Barbour et al., 2005).

Rn and *VPD* were the dominant variables restricting transpiration. The influence of *VPD* on *T* was similar to a temperate coniferous rainforest reported by Barbour et al. (2005) who showed a strong linear relationship between *T* and *VPD* when *VPD*<0.6 kPa. This threshold of *VPD* is lower than other reported values in a temperate hardwood forest and a boreal aspen forest (1.0

kPa) by Bovard et al., (2005) and Hogg and Hurdle, (1997), respectively. Compared to *Rn* and *VPD*, the role of *Ta* in affecting *T* is more ambiguous. *Ta* is often also regarded a major factor influencing forest water use (Jarvis, 1976; Zheng and Wang, 2015), but it is not always a primary controlling factor (Lhomme et al., 1998; Wang et al., 2014). In fact, a number of studies showed a more significant relationship between soil/leaf temperatures and transpiration (Mellander et al., 2004; Pallas et al., 1967; Wieser et al., 2015). Results in this study also demonstrated no direct air temperature effect on transpiration.

The rapid increase in *T* after rainfall probably cannot be simply attributed to rainfall stimulation as reported for semi-arid areas (Zeppel et al., 2008; Huang and Zhang, 2016), where soil wetness clearly increased due to more rainfall and, in turn, increased *T*. Instead, compared to before-rain atmospheric condition, the exposure of canopy to increased solar radiation and reduced humidity was likely to be at least as important as the rainfall itself for an increased *T*. This is similar to Cory et al. (2013) where the increased biological activity indexed by CO_2 release from soil carbon was due to intensified light exposure. This is also partly supported by the observations that *T* increased more during smaller amount rainfall events (Figure 4) and that soil moisture dynamics (Figure 2c) were largely irresponsive to rainfall.

The influence of soil water on *T* varied with rainfall amounts. *T* was most clearly linked to soil water when rainfall was limited. This is consistent with Granier et al, (2007). The dependency declined as rainfall increased, and diminished when daily rain >4 mm/d. This phenomenon could be the explained by the antecedent soil water storage built up in the rainy days (or months) that was depleted by trees later. Plants will adjust stomatal conductance in response to the changing atmospheric and soil water conditions (Buckley et al., 2003). The ratio *T*/*VPD*, a proxy of canopy conductance (Jarvis and McNaughton, 1986; Whitehead, 1998), helped to differentiate atmospheric and soil water controls on transpiration. In this study, soil water started to limit transpiration when *T*/*VPD*>4 mm/d/kPa, but otherwise not. This indicates that when trees transpired water at a higher rate, stomata regulation of *T* in response to soil water limitation was triggered to prevent rapid water loss; while at the lower conductance rate, *T* was more related to atmospheric conditions, near the potential rate, and stomatal regulation was barely involved (Tang et al., 2006; Tognetti et al., 2009). This phenomenon was also reported in Chen et al., (2014) with a different *T*/*VPD* threshold for a poplar plantation in Beijing, China.

4.2. Implications for water partitioning

Throughout the study period, ~47% of rainfall returned to the atmosphere through transpiration in the plantation, ~45% through canopy evaporation (Braun, 2015), and the rest to soil evaporation or deeper infiltration (Sprenger et al., 2017). Whilst the soil moisture sensors indicated little, if any, deeper recharge, their location under an area of denser canopy with likely high interception losses may have shown an extreme case and infiltration was likely higher where the canopy is less dense (Braun, 2015). With the projected future decrease in summer rain and increase in temperature in the area (Capell et al., 2013), the forest may contribute to more rainwater loss through transpiration and interception. Although increased rain intensity may reduce interception loss, with the context of decreased rain and increased transpiration, less groundwater recharge and runoff generation in summer can be expected (Sahin and Hall, 1996; Farley et al., 2005). Thus, the situation of relative summer “dry gets drier” (Feng and Zhang, 2015) could then be enhanced. There are proposals in the area to increase tree cover to maintain low temperatures in river channels for important species (Hrachowitz et al., 2010). Since the catchment is important to sustain local drinking water supplies and maintain important Atlantic salmon fisheries (Tetzlaff et al., 2008), assessing the effects of Scots pine trees on water partitioning and storage is important for water and land management.

The *P-T* budgets indicate that for the study period, water re-cycling by the forest stand was rapid, with new inputs of rainfall quickly contributing to tree water uptake. This would be consistent with Scots pine having most of its roots in the upper 10 cm of the soil (Geris et al., 2015a) and would help explain why the soil moisture measurements at 10 cm showed no response to most rainfall events. However, in the driest weeks, antecedent deep soil water (>0.4 m) might help sustain transpiration (Schwinning et al., 2002; Chen et al., 2014). Moisture deficits in the deeper soil layers can only be relieved by large rain events because of high interception losses at the site (Braun, 2015) and root water uptake in the upper soil horizons limiting deeper percolation. Without enough replenishment from rainfall, the soil water (mainly stored from previous rainfall in the wet spring and early summer) continued to drop attributable mainly to transpiration and little to soil evaporation (Sprenger et al., 2017). There is no evidence showing the trees accessed groundwater in the dry summer (Geris et al., 2015a).

5. Conclusions

We analyzed Scots pine transpiration and its response to rainfall and four other environmental variables in a low-energy boreal Scottish forest. We investigated different rainfall effects on tree water use and the possible mechanism behind. Scots pine in this forest stand was characterized by rapid water recycling. The increase in transpiration was particularly large when daily rainfall was <5 mm, mainly ascribed to enhanced solar radiation on days after rain; while the increase was small to negligible when rainfall was over 5 mm/d implying water stress was not marked. Daily variation of transpiration could be explained by radiation and atmospheric vapor pressure deficit. Air temperature was not a direct controlling factor in this environment. Soil water only became significant when rainfall was limited; and antecedent soil water from deep layers was depleted by the trees when there was a rainwater deficit. In total, the forest transpired 47% and intercepted ~45% of rainfall in the study period, leaving ~8% of rainfall loss through soil evaporation. The water exchange processes mainly occurred at the canopy and in the upper 10 cm soils. Future warmer and drier summer in the area may present more occurrences of rainwater deficit for plant water uptake.

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