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Post-Disturbance Dynamics of Soil Respiration in the High Tatra Mts. (Slovakia)

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Abstract: In recent decades, large-scale forest disturbances such as windthrow and bark beetle infestations have significantly impacted the carbon balance of Earth and forest ecosystems, mainly by altering soil respiration (SR) in addition to decreased gross primary productivity. SR is considered the second highest flux on Earth, emitting 78-98 Gt C yr^{-1} to the atmosphere, thus contributing to global warming. Post-disturbance development is marked by changes in the size of SR. To investigate the impact of bark beetle (*Ips typographus*) infestations in mountain spruce forests on SR, we measured SR at infested sites by bark beetles and adjacent undisturbed stands in the High Tatra Mountains (Slovakia). The measurements were conducted during the vegetation period (May-September) in 2016 and 2017, five to six years after the initial attack by bark beetles, at an altitudinal gradient (1100-1400 m a.s.l.). SR varied throughout different months and altitudes, and we observed that SR at infested sites reached higher values (in most cases) than at uninfested stands. Average monthly and altitude SR rates during both vegetation periods showed higher values at infested sites, but not all of them were statistically significant. We observed an insignificant change in SR rate between 2016 and 2017 at both infested and uninfested sites. The highest rates of SR were observed in 2016 from July to August at both infested and undisturbed sites. On the other hand, in 2017 the highest SR rates were observed in June and July at undisturbed sites and from June to August at infested sites. However, yearly SR from May-September at infested sites showed significantly higher rates than uninfested ones in both years. SR showed a decreasing pattern with elevation gain in 2016 at infested sites. However, this pattern was not observed in 2017. Based on our observation and results we postulate that SR rates at infested sites are boosted by needle fall and debris from dead and dying trees, which increases heterotrophic SR and compensates the decrease of autotrophic SR from tree roots. This study provides important insights into the impact of bark beetle infestations on SR and highlights the need for further research on the long-term effects of forest disturbances on carbon cycling.

Keywords: soil respiration; post-disturbance development; bark beetle infestations; infested sites; mountain spruce forest

1. Introduction

Global soil carbon stock represents ~ 1700 Gt C [1], and the contribution of forest ecosystems [2] equals ~ 861 Gt C from which 44%, 42%, 8%, and 5% are found in top meter soil, live biomass, deadwood, and litter, respectively. It creates an enormous carbon pool with the potential to highly increase atmospheric CO_2 concentration [3] after large-scale disturbances to accelerate currently significant climate change.

Global soil respiration is considered the second largest carbon flux with 78 - 98 Gt C yr^{-1} in total [4,5]. Carbon fluxes from forest soils are important contributors to global soil respiration as forests cover 26% of the Earth's total land area [6].

With recent climate change primarily induced by rising CO_2 atmospheric concentration [7], forests in Europe have experienced extreme heat and drought [8]. Consequently, bark beetles as poikilothermic organisms have altered their phenology behavior towards having a bigger population size, extra generations per year [9] and their shift to higher latitudes [10] and altitudes [11] has been observed. As a result, large-scale forest diebacks throughout the northern hemisphere have been caused by the European spruce bark beetle (*Ips typographus*) [12–14] recently. Initially, after host tree death, the biogeochemical and biogeophysical processes (leaf area index, evapotranspiration, productivity, land surface temperature) of forest stands are altered [15,16]. Carbon uptake decreases as a result of tree mortality [17], similarly, GPP sharp decline of infested stands after beetle infestation [18], and reduction of leaf area index corresponds to a contraction of gross primary productivity [15]. Soil pH increases after conifer trees dieback [19]. Swift nitrogen and carbon reduction in upper mineral soils, but an accumulation of soil anorganic N occur as a result of the diminished contribution of roots, mycorrhizae and rhizodeposition [19]. Fine root density decline increases with the level of tree mortality [20]. Root biomass decomposition is accompanied by mycorrhizal fungi decomposition [21]. However, soil respiration decreases after a disturbance event mainly due to reduced input of autotrophic soil respiration [22] and nutrient losses [23].

After some time, infested trees shed their needles [16] and subsequently increased solar radiation input [24,25] accelerates the decomposition rate of the litter as a consequence of higher temperatures [26].

Temperature is considered as the most important factor influencing global soil respiration [5,27,28]. Soil respiration positively correlates to ambient temperature [29]. As the temperature changes within different altitudinal zones [30,31]), consequently, soil respiration declines with increasing elevation [32,33]. Similarly, a higher solar radiation intake on infested sites is observed and therefore soil and air temperature are rising on the plots with bark beetle infested trees [24]. Soil respiration copies seasonal dynamics of soil temperature with water surplus throughout the year [34].

In this study, we measured total SR for 2 consecutive years and examined if there is a significant difference in SR between infested sites (dry) and uninfested sites (green) with living trees within different elevational zones during the vegetation period. Then, if SR varies between seasons and altitudes. And if there is a change in SR between the annual SR rates.

First, we hypothesize that SR under dead trees would be lower than under uninfested trees due to a decrease in autotrophic SR (tree roots). Secondly, the SR will not significantly change within different altitudes, because of only a small microclimatic variation within the measured mountain slope. Thirdly, we expect the highest SR during summer (June to August).

2. Materials and Methods

2.1. Study area

Our study was conducted in the High Tatra Mountains, Slovakia. The studied site is dominated by Norway spruce (*Picea abies* (L.) Karst.) with the contribution of a few coniferous tree species described in [35] and was affected by European spruce bark beetle (*Ips typographus* L.) attack since 2011. The research area was established on the boundary between undisturbed and bark beetle infested areas (standing dead trees) and encompasses an elevation gradient from 1100 to 1400 m a.s.l. between Tatranska Lomnica (820 m a.s.l.) and Skalnate pleso (1754 m a.s.l.). Control undisturbed forest along vertical gradient was 100-165 years old. Stocking density varied from 0.4 to 0.8. Low stocking density was caused by a windthrow in 2014 at the zone of 1200 m a.s.l. which damaged the control plot and decreased stocking density up to 0.4 [35]. Annual precipitation at Tatranska Lomnica during 2016 and 2017 was 922 and 934 mm and the mean annual temperatures were 6.7 and 6.6 °C. in 2016 and 2017, respectively. Two years of experiment were wetter and warmer than the long-term average during vegetation season (1911-1960), where mean annual precipitation is 833 mm and mean annual air temperature is 4.7 °C. Acidic Distric Cambysol is the main soil type of the studied area [36].

2.2. Soil respiration measurements

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Measurements were conducted for two consecutive years in 2016 and 2017 during the vegetation period (May - September). At each elevation zone (1100, 1200, 1300, 1400 m. a.s.l.) 15 points for the undisturbed control plot (green) and 15 points for bark beetle infested plot (dry) were established by plastic collars. These collars 3 to 5cm high with the same diameter as the chamber were inserted into the soil to ensure that the next measurement would be conducted at the same point. Collar tops were at the same level as the soil surface to minimise their influence on microclimatic conditions.

Measurements took place on a biweekly basis. We used manual portable PP Systems, model EGM-4 (PP Systems, MA, USA) for measuring soil CO_2 fluxes. In total 4 x 2 x 15 = 120 measurements were conducted during one sampling day. Soil temperature at the depth of 2 cm, soil moisture and H_2O flux (evaporation) were measured simultaneously as well.

2.3. Statistical analysis

Recorded data were analyzed using three-way repeated measures analysis of variance (ANOVA). Factors were vegetation, year, month and altitude. However, one factor had to be fixed. Statistical analysis was performed by statistical software R [37]. We used the Shapiro-Wilk test to test data normality. As we used three-way repeated measures analysis of variance and at least some of the data were not normal according to the Shapiro-Wilk test and Q-Q plots, we used the aligned rank transform (ART) tool for nonparametric repeated measure factorial ANOVA with Holm method adjustment to perform *post-hoc* pairwise comparisons because we needed to conduct multiple comparisons [38].

3. Results

3.1. Spatial dynamics of SR

SR varied throughout the vegetation period (from May to September) at different altitudes in 2016 and 2017 (Figure 1). Infested sites showed higher mean SR than uninfested sites at each elevation indicating a high contribution of heterotrophic respiration (decomposition of organic matter by microorganisms) to total SR at these sites. However, the mean SR rate in 2016 at the elevation zone of 1400 and in 2017 at the elevation of 1300, showed insignificant difference (Table 1, Figure 2). In 2016, the mean highest SR was observed at the elevation of 1200 m a.s.l. at both forest status sites. Similarly, in 2017, the highest rates of SR were observed at the same elevation zone at undisturbed sites. Nevertheless, the highest SR rates were observed at the elevation of 1100 m at infested sites.

We observed that SR reached its peak in the summer (July or August) at each elevation zone except in 2017 at the elevation of 1400, where the highest SR was measured in May (Figure 1). In almost every month and at each elevation zone infested sites emitted more CO_2 than uninfested ones, but in many cases insignificantly higher. The exception was elevation of 1200 m, in 2017, where uninfested forest site was damaged by windthrow (previously mentioned in the description of study area) and where measured SR at uninfested site showed significantly higher rates in July than at infested site.

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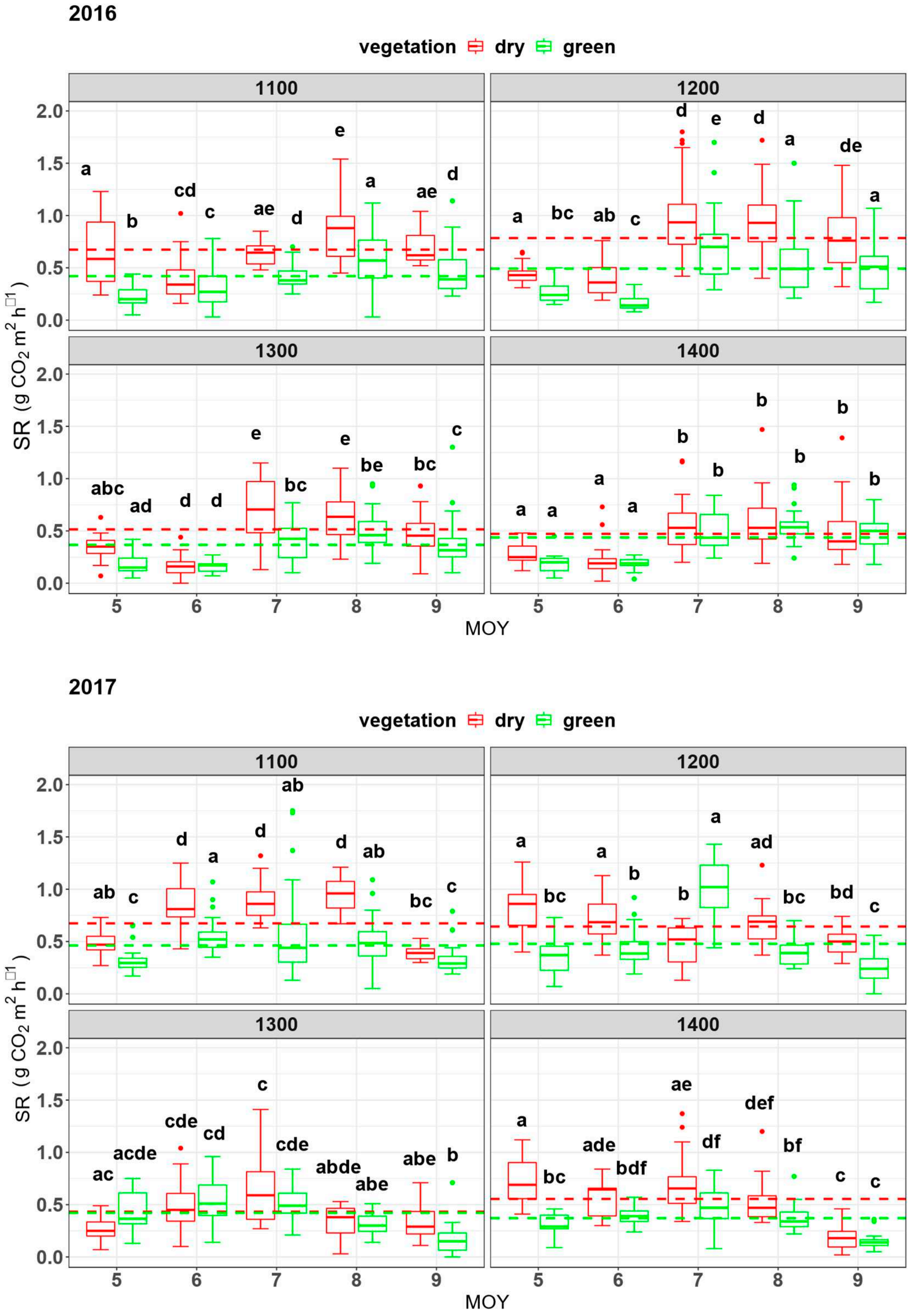

Figure 1. Variation of SR (y-axis) in g CO$_2$ m^2 h^{-1} within the same altitude in different months of the year (MOY) from May (5) to September (9) in both years. Letters display a significant difference with $P < 0.05$. Comparison is conducted within one box (elevation is in m a.s.l.). Horizontal dashed lines show the mean SR of the uninfested (green line) and infested forest sites (red line) for each elevation zone.

The average fluxes from soil surface under infested sites are in both years higher, but not always significantly (Figure 2, Table 1). Average SR at undisturbed sites showed the same amount of carbon, in terms of significance, emitted throughout the vegetation period at each elevation zone (Figure 2).

Higher variation of SR was observed under infested plots, then we suggest that these sun-exposed sites without any stand canopy causes an increase in soil temperature [39], which is the most influencing factor of SR, and its variance.

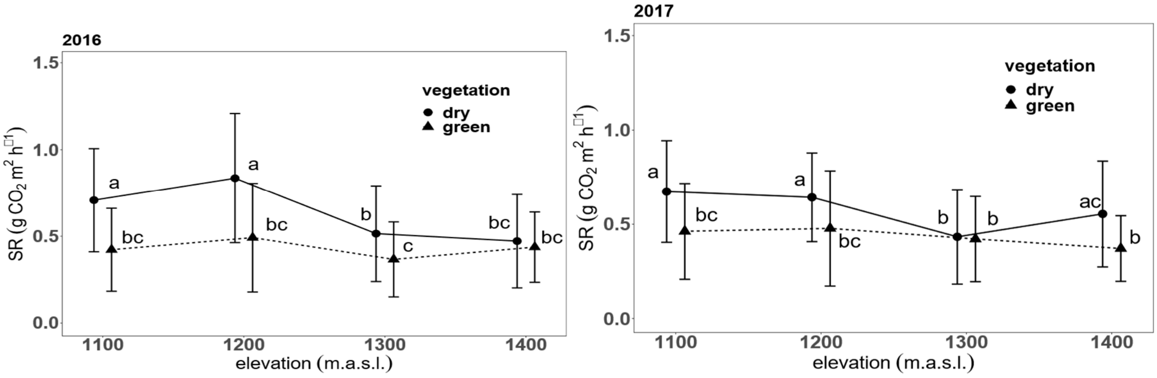

Figure 2. Average SR rate in 2016 and 2017 at different altitudes and forest statuses. Dry means infested, green means uninfested spruce forest. Letters display a significant difference with P < 0.05.

A decline of SR with elevation has only been observed in 2016 at infested sites, however, an unambiguous pattern (decrease or increase) in soil efflux was observed within the elevation gradient in 2017 at infested sites in agreement with [40] (Figure 2).

Table 1. Comparison of SR between dry (infested) and green (uninfested, control) spruce forest at different altitudes. Critical p-value is ($\alpha = 0.05$). Mean and standard deviation (sd) is in g CO_2 m^2 h^{-1}. *** = P close to 0, ** = P ~ 0.001, ns = non-significant.

		contrast			p.value	sig.
2016	vegetation/altitude	dry,1100	-	green,1100	9.490750e-15	***
	mean/sd	0.708/0.298	-	0.422/0.239		
	vegetation/altitude	dry,1200	-	green,1200	2.471856e-09	***
	mean/sd	0.836/0.374	-	0.492/0.314		
	vegetation/altitude	dry,1300	-	green,1300	0.000040e-05	***
	mean/sd	0.515/0.276	-	0.367/0.216		
	vegetation/altitude	dry,1400	-	green,1400	1.000000e+00	ns
	mean/sd	0.472/0.270	-	0.437/0.203		
2017	vegetation/altitude	dry,1100	-	green,1100	2.135766e-09	***
	mean/sd	0.674/0.27	-	0.462/0.254		
	vegetation/altitude	dry,1200	-	green,1200	8.329859e-09	***
	mean/sd	0.643/0.236	-	0.478/0.306		
	vegetation/altitude	dry,1300	-	green,1300	1.000000e+00	ns
	mean/sd	0.433/0.251	-	0.422/0.227		
	vegetation/altitude	dry,1400	-	green,1400	0.000033e-05	***
	mean/sd	0.555/0.281	-	0.371/0.174		

3.2. Temporal dynamics of SR

SR varied throughout an elevational gradient during vegetation period (from May to September) in 2016 and 2017 (Figure 3). Infested sites showed higher mean SR than uninfested sites in every month which indicates a high contribution of heterotrophic respiration to total SR at these sites as well as at different altitudes (Figure 4). We observed that average monthly SR reached its peak in the summer (July or August) at each elevation zone. In every month and at each elevation zone infested sites emitted more CO_2 than uninfested ones, but in many cases insignificantly higher, except of May and July 2017 at the elevation 1300 m and 1200 m, respectively. The mean lowest values of SR at infested sites were observed in June, on the other hand, the lowest SR rates were observed at uninfested sites in May and June (Figures 3 and 4; Table 2).

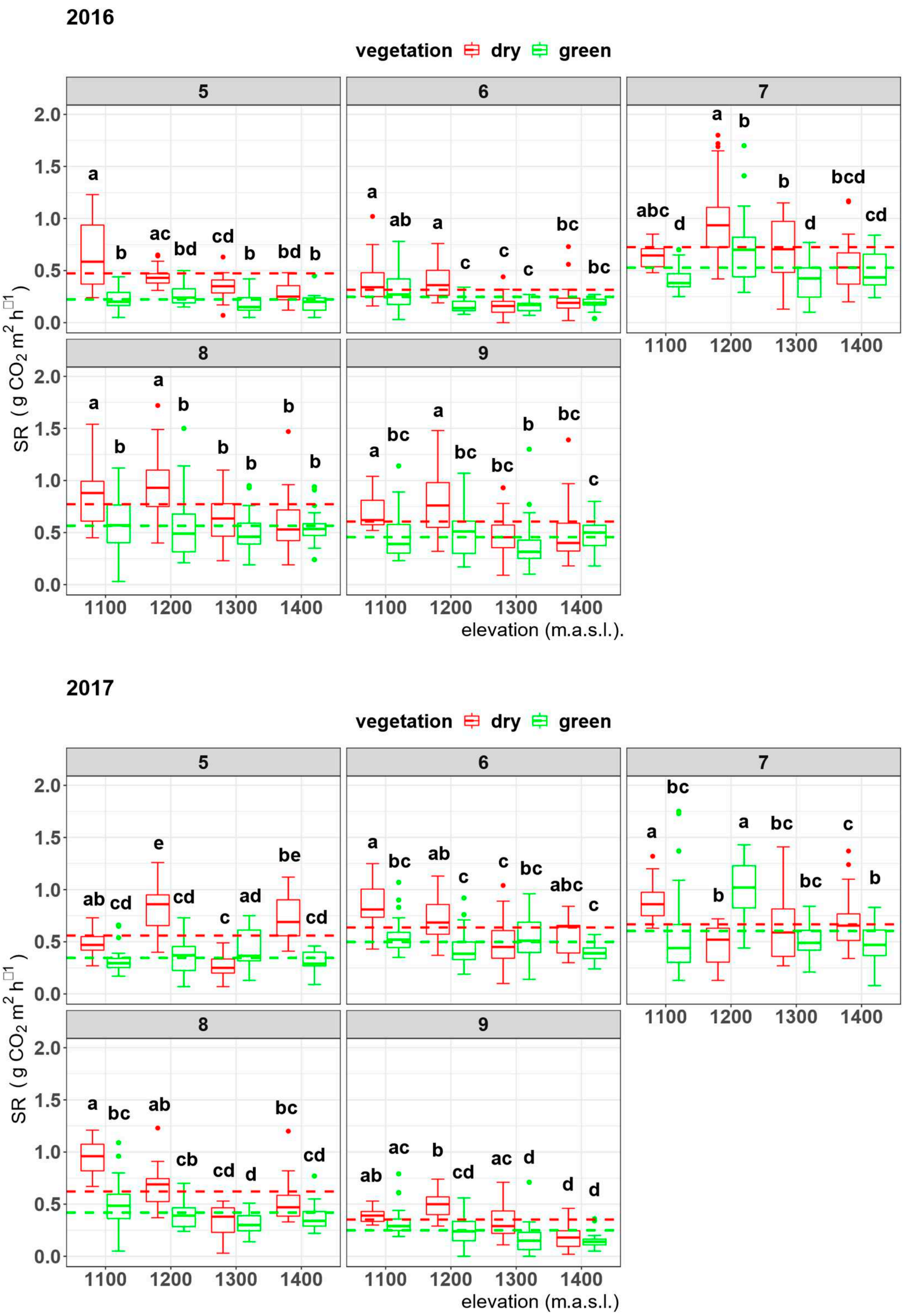

Figure 3. Variation of SR within the same altitude in different months of the year (MOY) from May (5) to September (9) in both years. Letters display a significant difference with $P < 0.05$. Comparison

is conducted within one box (elevation is in m a.s.l.). Horizontal dashed lines show the mean SR of the uninfested (green line) and infested forest sites (red line) for each elevation zone.

In our experiment mean monthly SR were statistically higher at infested sites than at uninfested ones in both vegetation periods, except for June 2016 and July 2017. The highest rates of SR were observed during the summer months (from June to August) in both years. However, in 2016, the highest SR values were measured from July to August at both infested and undisturbed sites. On the other hand, in 2017 the highest SR rates were observed in June and July at undisturbed sites and from June to August at infested sites (Figure 4, Table 2).

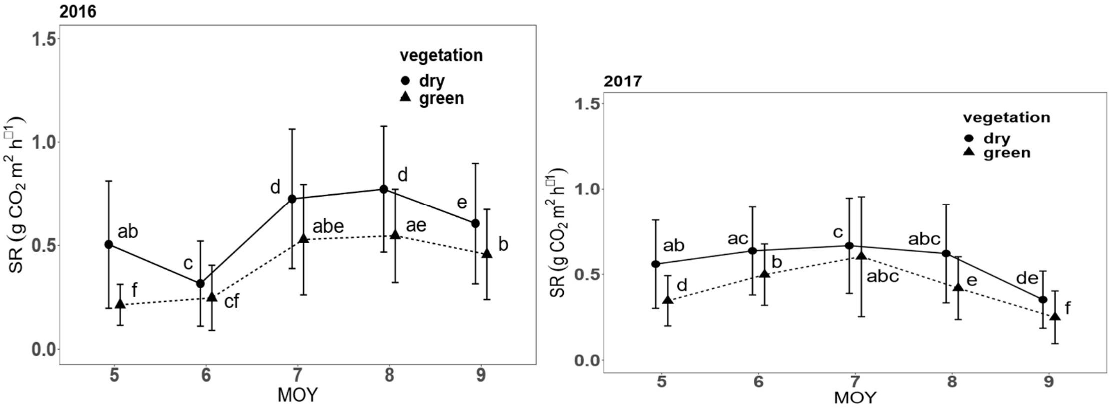

Figure 4. Average SR rate in 2016 and 2017 at different months of the year (MOY) and forest statuses. Dry means infested, green means uninfested spruce forest. Letters display a significant difference with $P < 0.05$. The months of the year are from May (5) to September (9).

The highest values of SR were measured during summer as mentioned before. So, according to [34] soil respiration copies seasonal dynamics of soil temperature with water surplus throughout a year.

Table 2. Comparison of SR between dry (infested) and green (uninfested) spruce forest in different months of the year (MOY) and years. Critical p-value is ($\alpha = 0.05$). Mean and standard deviation (sd) is in g CO$_2$ m^2 h^{-1}. *** = P close to 0, ns = non-significant.

	contrast				p.value	sig.
2016	vegetation/MOY	dry,5	-	green,5	5.285897e-16	***
	mean/sd	0.473/0.256	-	0.223/0.1		
	vegetation/MOY	dry,6	-	green,6	5.226800e-02	ns
	mean/sd	0.316/0.205	-	0.247/0.157		
	vegetation/MOY	dry,7	-	green,7	4.568729e-07	***
	mean/sd	0.725/0.337	-	0.528/0.267		
	vegetation/MOY	dry,8	-	green,8	1.838438e-09	***
	mean/sd	0.772/0.304	-	0.565/0.231		
	vegetation/MOY	dry,9	-	green,9	9.547313e-06	***
	mean/sd	0.606/0.291	-	0.456/0.217		
2017	vegetation/MOY	dry,5	-	green,5	1.805378e-10	***
	mean/sd	0.56/0.258	-	0.346/0.146		
	vegetation/MOY	dry,6	-	green,6	7.586355e-04	***
	mean/sd	0.637/0.257	-	0.498/0.179		

vegetation/MOY	dry,7	-	green,7	5.109233e-02	ns
mean/sd	0.667/0.278	-	0.604/0.35		
vegetation/MOY	dry,8	-	green,8	1.117026e-06	***
mean/sd	0.622/0.288	-	0.42/0.183		
vegetation/MOY	dry,9	-	green,9	1.727742e-03	**
mean/sd	0.352/0.167	-	0.25/0.154		

3.3. Years and vegetation status comparisons

Rates of SR differed between vegetation statuses, but not between the years. In both years infested sites showed significantly higher values than uninfested ones. In 2016, the mean annual (during vegetation period) SR at infested forest sites reached 0.625 g CO_2 m^2 h^{-1} in comparison with 0.428 g CO_2 m^2 h^{-1} at uninfested ones. And, in 2017, 0.576 CO_2 m^2 h^{-1} and 0.438 g CO_2 m^2 h^{-1} at infested sites and uninfested sites, respectively (Table 3). This confirms the theory that SR is increased by the higher contribution of heterotrophic SR in the post-disturbance forest environment and rejects our initial hypothesis. We observed an insignificant change in the SR rate between 2016 and 2017 at both infested and uninfested sites.

Table 3. Comparison of SR between dry (infested) and green (uninfested) spruce forest in different years. Critical p-value is ($\alpha = 0.05$). Mean and standard deviation (sd) is in g CO_2 m^2 h^{-1}. *** = P close to 0, ns = non-significant.

		contrast		**p.value**	**sig.**
vegetation/year	dry,2016	-	dry,2017	7.938475e-01	ns
mean/sd	0.625/0.335	-	0.576/275		
vegetation/year	dry,2016	-	green,2016	2.101335e-12	***
mean/sd	0.625/0.335	-	0.428/0.248		
vegetation/year	dry,2017	-	green,2017	1.911597e-07	***
mean/sd	0.576/275	-	0.438/0.249		
vegetation/year	green,2016	-	green,2017	7.938475e-01	ns
mean/sd	0.428/0.248	-	0.438/0.249		

4. Discussion

Changes in soil respiration rate after disturbance events are not consistent throughout the published research papers [18,23,41–45]. In the girdling experiment in boreal Scots pine (*Pinus silvestris* L.) forest soil respiration decreases up to approximately 50% relatively to ungirdled sites within one to two months [41] where forest mycorrhizae alone contributes to one-third of dissolved organic matter in forest soils, together with associated roots, to 50% of dissolved organic matter [21]. Notwithstanding, a recent meta-analysis of [46] concluded 57%, 28% and 15% contribution of microbial, root and mycorrhizal respiration to total soil respiration, respectively. Soil fluxes decline as a consequence of altering key factors and nutrients [23] controlling soil respiration rate.

[47] mentioned that up to 3 years since lodgepole pine (*Pinus contorta* Dougl. ex Loud.) infestation by mountain pine beetle most needles remained on the trees. Then no extra needle litter is added from dead pines to increase soil respiration rate during this period since infestation. After a pulse of dead needles soil respiration almost fully recovered lasting for up to 2 years which is similar to our study and then followed by a decline again [18]. We suppose that needlefall and debris input from dying and dead spruce trees in our study sites increased heterotrophic respiration which exceeded the loss of autotrophic respiration at infested sites. As our study was conducted 5 to 6 years after initial infestation by bark beetles results are quite similar to [18,39] with the difference that SR in our study on infested plots not only equaled to control plots but exceeded SR at control plots.

Nonetheless, [43] did not notice any significant soil respiration changes at a stand level from July to September over 5 years between live lodgepole pine sites and bark beetle-infested sites. This phenomenon is supplied by surviving trees, understorey vegetation and [48] nutrient pulse from needlefall. And because the decline in autotrophic respiration is compensated by higher heterotrophic respiration induced by higher soil temperature [26,49]). However, it is suggested that if mortality reaches 100% total soil respiration decreases to one-third of the uninfested site [43]. A similar pattern as [43] has been observed by [44] in fir-spruce forests explained by root-respiring carbohydrates after trees death or a decrease of autotrophic respiration is replaced by heterotrophic respiration from dead roots and foliage. Because dying roots and mycorrhizae respire their stored carbon for 2-3 years after disturbance [50]. In addition, an increase in soil temperature and soil moisture in infested ponderosa pine (*Pinus ponderosa* Laws.) forests [24]. [39] confirmed that up to six years after disturbance SR did not decrease at windthrow disturbed sites due to the suggested substitution of decreased autotrophic SR by increasing heterotrophic SR supported by disturbance induced alteration of soil temperature.

In contrast, [23] concluded that the fast decline of dissolved organic carbon, organic nitrogen and phosphorus is accompanied by a decrease in soil respiration after trees dieback. Then after 4 years, nutrients start to recover as a consequence of litter mineralisation. Then post-disturbance development is an important factor influencing soil respiration rate after bark beetle infestation. These varying results can be supported by different mortality rates, gap size formation and already present understory vegetation.

Temperature is considered the most important factor influencing global soil respiration [5,27,28] and according to [29] soil respiration positively correlates to ambient temperature. As the temperature decreases within different altitudinal zones [30,31], consequently, soil respiration declines with increasing elevation [32,33] which is consistent with our study in 2016 at infested sites. On the other hand, infested sites in 2017 did not show consistency with the mentioned studies, which was similar to [40]. Steady SR rates were measured with increasing elevation at uninfested sites in both years.

5. Conclusions

The highest average SR was observed during the summer of 2016 from July to August at both infested and undisturbed sites. However, in 2017 the highest SR rates were observed in June and July at undisturbed sites and from June to August at infested sites. We observed an insignificant change in the SR rate between 2016 and 2017 at both infested and uninfested sites. The decrease in SR with altitude was only observed in 2016 at infested sites, however, an unambiguous pattern (decrease or increase) in soil efflux was observed within the elevation gradient in 2017 at infested sites in agreement with [40]. Steady SR rates were measured with increasing elevation at uninfested sites in both years. A mean monthly SR were statistically higher at infested sites than at control ones in both vegetation periods, except of June 2016 and July 2017 (Figure 4, Table 2). The highest rates of SR were observed during the summer months (from June to August) in both years, however in 2016 from July to August at both infested and undisturbed sites. On the other hand, in 2017 the highest SR rates were observed in June and July at undisturbed sites and from June to August at infested sites.

Statistically higher annual SR has been observed under infested sites than control ones. So, we rejected our hypothesis that under an infested stand SR will be lower than under an uninfested one. Then, we suppose that needlefall and debris input from dying and dead spruce trees in our study sites increased heterotrophic respiration which exceeded the loss of autotrophic respiration at infested sites. During vegetation season SR under infested sites did not differ from uninfested plots in some months.

This study provides important insights into the impact of bark beetle infestations on SR. As our study was conducted five to six years after infestation during 2 consecutive years, we propose long-term research after bark beetle infestations to fully capture soil respiration dynamics and the carbon cycle.

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