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Impacts of passive experimental warming on daytime and night-time respiration in a semi-natural grassland

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Abstract

Soil respiration (SR) is the largest source of CO_2 released from the terrestrial ecosystem. It is greatly influenced by soil carbon pool, climate warming and daily fluxes i.e., daytime (DT) and night-time (NT) temperatures. However, there are hardly any studies relating to the effects of passive experimental warming on Ecosystem respiration (ER) and SR during DT and NT. We conducted a simulated warming experiment using passive Open Top Chamber (OTC) in a semi-natural grassland of Doon Valley, in the state of Uttarakhand, India. OTCs showed an increase in DT and NT soil temperatures. SR and ER were measured within OTC as well as outside using LI-8100A Automated Soil CO_2 Flux System. We found that SR and ER increased under passive experimental warming by 38.66% and 20.35% during DT, and 38.8% and 12.41% during NT respectively. SR/ER ratio increased under passive warming treatment during DT and NT, indicating SR as the major contributor to ER. Temperature-respiration showed a positive relationship under ambient and warming conditions. Q10 analyses revealed that respiration rates are sensitive to passive warming, especially during the NT. This study addresses the crucial gap of monitoring NT respiration in addition to DT respiration to estimate the CO_2 efflux and its response to passive experimental warming.

Keywords: Soil respiration (SR), Ecosystem respiration (ER), Open Top Chamber (OTC), passive experimental warming, Temperature sensitivity, Night-time respiration, Daytime respiration

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1. Introduction

Soil Respiration (SR) is the major source of carbon dioxide (CO_2) emitted from the terrestrial ecosystem (Raich and Schlesinger, 1992; Zhao et al., 2017). The global CO_2 efflux accounts for approximately 50-95 Pg C yr^{-1} (Houghton and Woodwell, 1989; Hashimoto et al., 2015). The emissions from anthropogenic sources are estimated to be approximately ten times lower than that of natural sources (Schaefer et al., 2009; Hashimoto et al., 2015). Alterations in the SR can have a significant impact on atmospheric CO_2 concentrations, resulting in either positive (Lu et al., 2013) or negative (Schlesinger, 1995; Wang et al., 2014) feedback to the climate warming.

SR, a component of ecosystem respiration (ER), is a combination of both heterotrophic and autotrophic respiration. It may respond differently to alterations in temperatures and environmental conditions (Fang et al., 2018). It is observed that the rates of soil respiration (SR) and ecosystem respiration (ER) are more susceptible to fluctuations due to environmental factors, as compared to photosynthesis (Valentini et al., 2000). Despite its importance, respiration is less studied. Furthermore, studies primarily concentrate on DT respiration rates specifically during the growing season. The study of NT respiration rate is infrequently conducted as a result of challenges in its measuring during the night (Hu et al., 2016). DT and NT respiration rates are variable, explained by various microclimatic parameters including soil temperature (Atkin et al., 2003, Xia et al., 2009) and soil water content (SWC) (Xia et al., 2009; Balogh et al., 2011). ST and SWC influence respiration rates by affecting functioning of soil microorganisms, as well as the respiratory enzymes present in microflora and fauna (Fang and Moncrieff, 2001; Atkin et al., 2003; Moyano et al., 2007). To evaluate the effect of experimental warming on respiration rates, many studies have determined the temperature sensitivity of SR and/or ER by calculating Q10 (Raich and Schlesinger, 1992; Wan et al., 2007; Fang et al., 2017; Fang et al., 2018). The Q10 function is considered a better choice for estimating the respiration rates as it includes all the processes and factors that may impact the respiration rates (Vesterdal et al., 2012).

Grasslands, one of the world's major ecosystems, occur in a wide range of eco-climatic conditions and are governed by anthropogenic as well as climatic factors (Hall and Scurlock, 1991). The tropical and sub-tropical grasslands in India are mostly anthropogenic in origin derived from clear-felling, livestock grazing and burning. More actively managed grasslands are often referred to as semi-natural grasslands. Such grasslands are known to be seral in nature and are rapidly colonized by shrubs and trees in the absence of management (Queiroz et al., 2014). Soil carbon stock in such grasslands corresponds to at least 10% of the world's total (Eswaran et al., 1993; Zhao et al., 2017). However, several studies suggest that the estimation could be as high as 30% of the world's soil carbon (Scurlock and Hall, 1998). The exploration of interactions between climate change and grasslands has been relatively limited compared to forests (Hall and Scurlock, 1991). This highlights the significance of understanding the phenomenon taking place within this particular ecosystem. In the present study, we simulated passive experimental warming in a semi-natural grassland using an Open Top Chamber (OTC) to study the impacts of passive warming on SR and ER. The objectives of the study were to (1) examine the impacts of passive experimental warming on microclimatic parameters, (2) assess the impacts of passive experimental warming on DT and NT respiration, and their temperature sensitivities, (3) evaluate SR/ER ratio during DT and NT, and (4) understand temperature-respiration and moisture-respiration relationships.

2. Materials and Methods

2.1. Study site

The study was conducted in a semi-natural grassland patch in Doon Valley, within Wildlife Institute of India, Dehradun, Uttarakhand, India (30°17’02” N; 77°58’23” E, 598 m asl). The area experiences a typical sub-tropical climate with an annual mean air temperature of 21.8 ± 0.1 °C (from January 2020 to January 2021) and precipitation of about 2073.3 mm (India Meteorological Department, 2015). The study site is a maintained grassland with dominant plant species, including *Dicanthium annulatum*, *Medicago polymorpha*, and *Alternanthera sessilis*, surrounded by trees such as *Butea monosperma*, *Shorea robusta*, and *Bombax ceiba*. Soil pH, bulk density, electrical conductivity and organic carbon are 7.12 ± 0.16, 0.96 ± 0.08 g cm-3, 36.48 ± 4.43 dS m-1 and 25.26 ± 1.35 g Kg-1, respectively.

2.2. Experimental Design

A 2×2 m plot was selected for the study based on uniform vegetation, even terrain, and an equal proportion of sunlight reaching the ground, with careful avoidance of shade from trees. The plot was divided into two halves and assigned to control and experimental warming. To achieve passive warming, hexagonal Open Top Chamber was installed (Fig. 1) during the first week of January 2019. The chamber was made up of transparent polycarbonate sheets of 3 mm thickness with base, height and upper diameter of 175 cm, 70 cm, and 110 cm respectively. An adjacent paired hexagonal control plot was marked and fenced to avoid disturbances. In each plot, six cylindrical opaque soil collars (diameter 20 cm and height 11 cm) made of polyvinyl chloride were randomly inserted 2 cm in the soil. Among the six soil collars in each plot, we allocated three for SR measurements and the remaining three for ER measurements. These collars were left at the site for the entire duration of the experiment to minimize disturbance.

Figure 1: Hexagonal Open Top Chamber and adjacent control plot

2.3. ER, SR, and CO_2 measurements

Aboveground vegetation was clipped from three collars 24 hours prior to the measurements for SR measurement. ER and SR were measured on a clear day using LI-8100A Automated Soil CO_2 Flux System equipped with the LI-8100-103 opaque chamber (LICOR Inc., Lincoln, NE, USA). Respiration readings were taken by gently mounting the LI-chamber on each collar and observing for 120 seconds with a dead band of 15 seconds. Two types of measurements were taken (i) 2 times during 0600-1800 hours, twice a week, depending upon the temperature peak and environmental feasibility and (ii) continuous hourly measurements for 24 hrs, twice a month. The measurement period was from January 2020 to March 2020. Data between 0600-1800 hours and 1800-0600 were pooled into DT and NT, respectively. The LI-8100 instrument recorded surface CO_2 concentration before mounting the chamber for respiration measurements.

2.4. Microclimatic Parameters

Air temperature (AT) at 30 cm height and ST at 5 cm depth were monitored hourly using HOBO U23 Pro v2 data loggers (Onset Computer Corporation, Pocasset, MA, USA) installed in the middle of each treatment plot. Instantaneous ST and SWC at 5 cm depth were also recorded during respiration measurements using a 6000-09TC soil thermocouple probe (LICOR Inc., Lincoln, NE, USA) and GS1 soil moisture sensor (Decagon Devices, Inc., Pullman, WA), respectively connected to the LI-8100 system. The LI-8100 system recorded relative humidity during the measurement cycle.

2.5. Statistical analyses

Data from the LI-8100 instrument and HOBO loggers were extracted using SoilFluxPro 4.2.1 (LICOR Inc., Lincoln, NE, USA, https://www.licor.com/env/support/SoilFluxPro/software.html) and HOBOware 3.7.22 (Onset Computer Corporation, Pocasset, MA, USA, https://www.onsetcomp.com/products/software/hoboware/) software, respectively. SR/ER ratio was evaluated from respiration data of similar time points. The normal distribution and homogeneity of variance of the data were tested using Shapiro-Wilk and Levene's test, respectively. The data was not distributed normally even after transformations; hence non-parametric tests were performed. Mann Whitney U test was conducted to assess the effect of passive experimental warming on DT and NT environmental parameters.

Temperature-respiration and moisture-respiration relationships were assessed by carrying out the respective exponential (Eq. (1)) and linear regression models (Eq. (2))

$$(R= \alpha e \beta t) \qquad (1)$$

$$(R=\alpha M+\beta) \qquad (2)$$

where α and β are coefficients, and R, t, M represents respiration (SR or ER), soil temperature, and soil moisture, respectively. To assess the temperature sensitivities of SR and ER, Q10 of respiration was calculated based on the coefficient β as (Eq. (3)):

$$Q10 = e10\beta \qquad (3)$$

Mean values were reported as mean ± standard error of mean and significant differences were evaluated at the level $p < 0.05$ and $p<0.001$. All statistical analyses were performed in SPSS 23.0 (IBM, Chicago, IL, USA).

3. Results

3.1. Microclimate under passive experimental warming

OTC increased only DT AT by 2.78 °C ($p < 0.001$), while increased both DT and NT ST by 0.53 °C ($p < 0.05$) and 0.79 °C ($p < 0.05$), respectively (Fig. 2). We observed higher SWC under passive experimental warming by 32.39% (0.046 m^3 m^{-3}, $p < 0.001$) during DT and 49.46% (0.056 m^3 m^{-3}, $p < 0.001$) during NT. Relative humidity (RH) increased during DT by 3.42% ($p < 0.001$) and reduced during NT by 1.72% ($p < 0.001$) under warming.

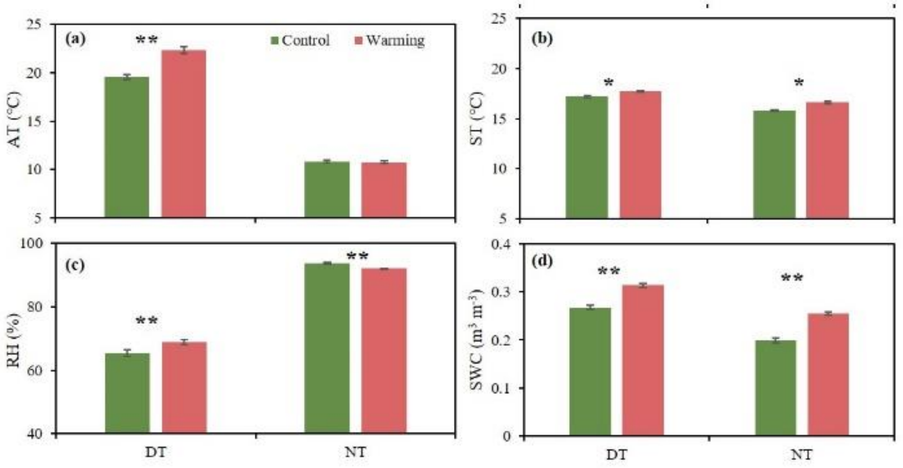

Figure 2. Daytime (DT), night-time (NT) mean (a) air temperature (AT), (b) soil temperature (ST), (c) relative humidity (RH), and (d) volumetric soil water content (SWC), under control and warming condition, significant at *<0.05 and **<0.001

3.2. Impacts of passive experimental warming on Respiration rates and SR/ER ratio

SR and ER ranged from 0.53-3.29 µmol m^{-2} s^{-1} and 1.58-7.13 µmol m^{-2} s^{-1} during DT and from 0.71-2.03 µmol m^{-2} s^{-1} and 1.49-3.85 µmol m^{-2} s^{-1} during NT respectively. Passive experimental warming increased both SR and ER by 38.66% and 20.35% during DT and by 38.8% and 12.41% during NT, respectively (Fig. 3). SR/ER ratio also increased under passive experimental warming from 0.58 to 0.66 and from 0.53 to 0.67 during DT and NT.

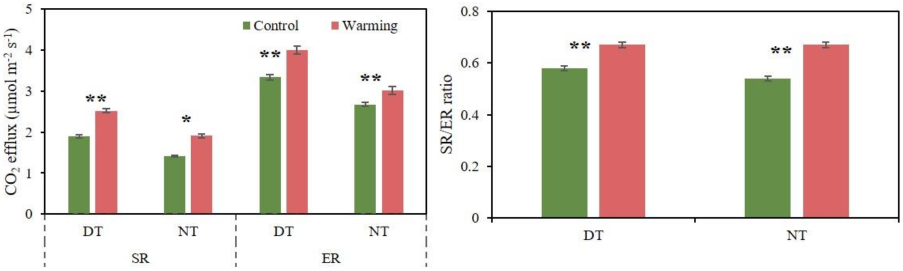

Figure 3. Daytime (DT), night-time (NT) mean Soil respiration (SR), Ecosystem respiration (ER), and SR/ER ratio, under control and warming condition, significant at *<0.05 and **<0.001

3.3. Surface CO_2 levels

Surface CO_2 ranged from 396–531 ppm and 422-594 ppm during DT and NT, respectively, in our study. Passive experimental warming increased the mean surface CO_2 during DT and NT by 12 ppm ($p < 0.001$) and 24 ppm ($p < 0.001$), respectively (Fig. 4.).

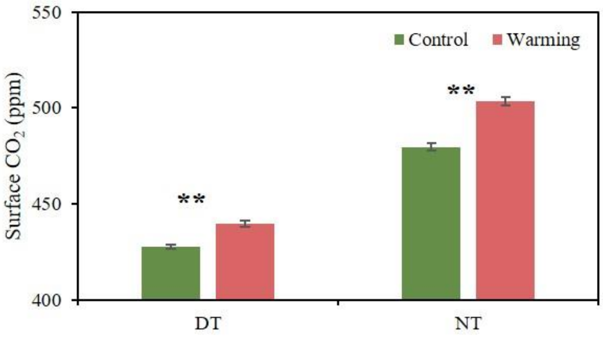

Figure 4. Daytime (DT), night-time (NT) mean surface CO_2 levels, under control and warming condition, significant at **<0.001

3.4. Temperature-respiration and moisture-respiration relationships

In our study, soil temperature and respiration rate were positively correlated. Under passive experimental warming, the exponential relationships between temperature and respiration (both SR and ER) increased (Table 1 & 2). ST explained variability in SR significantly ($p < 0.001$) by 24% and 13% under ambient conditions, which increased to 57% and 78% under passive experimental warming during DT and NT, respectively. Similarly, ST explained variabilities in ER significantly ($p < 0.001$) by 36% and 48% under ambient conditions, which increased to 66% and 87% under passive experimental warming during DT and NT, respectively.

Soil moisture only showed a significant yet weak relationship with SR during NT. It explained 5.6% and 5.3% of its variabilities in control and warming, respectively, while ER related to moisture only during DT in control ($r^2 = 0.056$, $p < 0.01$) (Table 1 & 2).

Table 1. Regression models to show exponential relationships between ST and SR ($R=ae^{bt}$) and linear relationship between SWC and SR ($R = aM+b$). values in the parenthesis represent S.E. of the estimate.

			Soil respiration			
			a	**b**	**r^2**	**p**
$R = ae^{bt}$	**Day-time**	Control	0.776 (0.084)	0.050 (0.006)	0.240	<0.001
		Warming	0.360 (0.042)	0.109 (0.007)	0.571	<0.001
	Night-time	Control	0.915 (0.096)	0.026 (0.006)	0.132	<0.001
		Warming	0.275 (0.027)	0.113 (0.006)	0.779	<0.001
$R = aM+b$	**Day-time**	Control	0.781 (0.397)	1.677 (0.114)	0.019	0.050
		Warming	0.255 (0.767)	2.441 (0.246)	0.001	0.740
	Night-time	Control	0.849 (0.338)	1.244 (0.071)	0.056	0.014
		Warming	2.708 (1.109)	1.218 (0.287)	0.053	0.016

Table 2. Regression models to show exponential relationship between ST and ER ($R=ae^{bt}$) and linear relationship between SWC and ER ($R = aM+b$). values in the parenthesis represent S.E. of the estimate.

			Ecosystem respiration			
			a	**b**	**r^2**	**p**
$R = ae^{bt}$	**Day-time**	Control	1.188 (0.112)	0.059 (0.006)	0.363	<0.001
		Warming	0.312 (0.039)	0.142 (0.007)	0.663	<0.001
	Night-time	Control	1.208 (0.097)	0.048 (0.005)	0.476	<0.001
		Warming	0.165 (0.018)	0.168 (0.006)	0.870	<0.001

R = aM+b	**Day-time**	Control	2.427 (0.707)	2.694 (0.201)	0.056	0.001
		Warming	1.666 (1.363)	3.481 (0.440)	0.007	0.223
	Night-time	Control	0.182 (0.679)	2.633 (0.144)	0.001	0.789
		Warming	3.387 (2.604)	2.149 (0.668)	0.016	0.196

3.5. Temperature sensitivity of SR and ER

Temperature sensitivity of SR and ER was assessed based on the Q10 values of the respiration calculated from the beta value of the temperature-respiration relationship. Q10 values ranged from 0.70-1.61 and 2.95-4.57 under ambient and warming condition respectively, as shown in Fig. 4. We observed that passive experimental warming increased Q10 of both SR and ER by 117% and 139% during DT and 337% and 246% during NT, respectively.

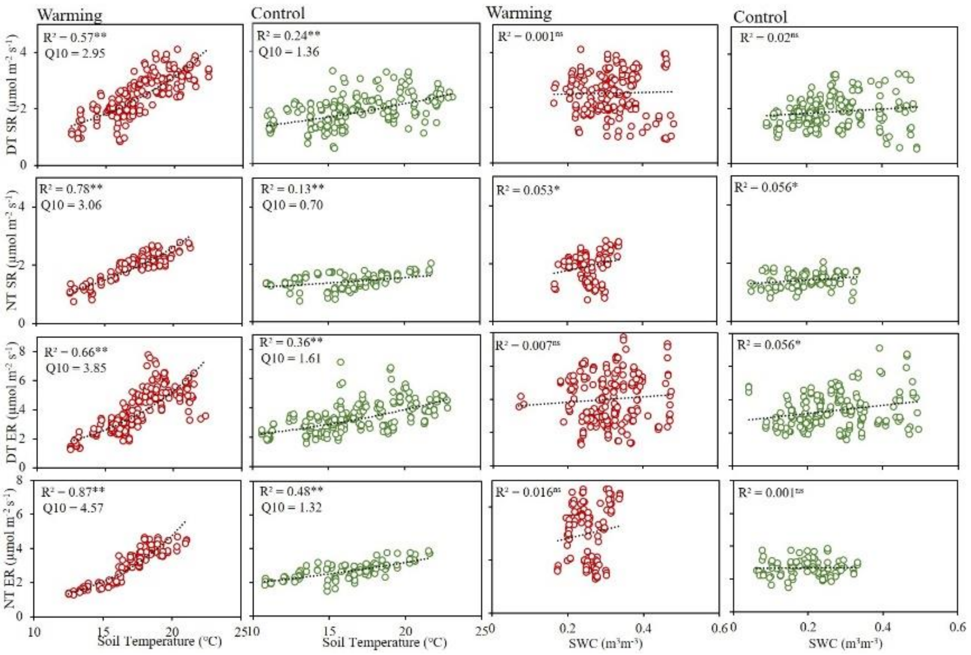

Figure 5. Regression models with Q10 values to show relationships between temperature and respiration (R=aebt) and SWC and respiration (R = aM+b), significant at` *<0.05 and **<0.001, ns represents non-significant, under control and warming conditions.

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4. Discussion

4.1. Effect of passive experimental warming on microclimate

OTC increased DT AT by 2.78°C, consistent with several other studies in the grassland ecosystem (Flanagan et al., 2013; Tiruvaimozhi and Sankaran, 2019). ST at 5 cm depth increased significantly under passive experimental warming both during DT and NT, as found in other studies (Defernne et al., 2010; Fang et al., 2017; Tiruvaimozhi and Sankaran, 2019). The possible reason for this may be the reduction in wind speed inside the OTC and, thus, the reduced diffusion rates (Molau, 1997; Flanagan et al., 2013).

Temperature and RH showed an inverse relationship. Passive experimental warming increased SWC throughout the day, as also reported by Defrenne et al. (2010). This may be due to the condensation of water droplets on the inner side of the polycarbonate sheets.

4.2. Effects of passive experimental warming on SR, ER and SR/ER ratio

Several experimental warming studies have reported either increased (Fang et al, 2017; Flanagan et al., 2013; Tiwari et al., 2021), decreased (Sharkhuu et al., 2016), or no change (Sharkhuu et al., 2013; Wan et al., 2007) in respiration rates. In our study, SR and ER increased under passive experimental warming during DT and NT. This can be due to: (i) enhanced microbial activity due to the direct effect of increased temperatures, contributing more to the respiration rates in the warming plot (Flanagan et al., 2013, Fang et al., 2017) (ii) increase in the amount of carbon substrate available in grassland ecosystem due to the as a result of increased carbon allocation to the roots, microbes and exudates (Shaver et al., 2000; Flanagan et al., 2013).

The mean SR/ER ratio increased under passive experimental warming from 0.58 to 0.66 during DT and from 0.53 to 0.67 during NT, suggesting that SR is the major contributor to total ER in our study area.

4.3. Temperature-respiration relationship and Q10 values

In our study, ST was the best predictor of SR and ER, consistent with other studies (Fang et al., 2017; Wan et al., 2007). We observed an exponential relationship between respiration rates and ST, and a linear relationship between SWC and respiration rates, similar to other studies (Rey et al., 2011; Thomas, 2012; Escolar et al., 2015). Our study showed a positive relationship between ST and respiration rates, indicating that respiration increases with the increase in ST (Fang et al., 2017) in semi-natural grassland. The temperature-respiration relationship became stronger under passive experimental warming, indicating more CO_2 emissions in the future. This was also supported by the increase in the temperature sensitivity of respiration (Q10) under warming in our study (Escolar et al., 2015). An increase in Q10 values was more in the NT than DT, indicating that NT respiration rates are more sensitive to climate warming than DT.

5. Conclusion

In conclusion, passive experimental warming resulted in significant increase in air and soil temperatures. This study indicates that passive warming is likely to enhance the respiration rates in sub-tropical grasslands. Furthermore, NT respiration rates are more sensitive to warming than DT as indicated by increase in Q10 values in our study. This addresses a crucial gap in monitoring NT respiration responses along with DT to estimate the CO_2 efflux and its impact on future climate warming in similar ecosystem.

6. Future works

This novel study has underlined the importance of both daytime and night-time respiration in understanding the respiratory dynamics of an ecosystem. To strengthen the statistical robustness, future research endeavours should incorporate multiple replicates throughout various seasons, thereby contributing to a more comprehensive understanding. The investigation of microclimate impacts remains of utmost importance. Furthermore, an examination of the biotic regulatory factors, including the impact of plant species composition, microbial populations, and nutrient availability on the dynamics of respiration, would contribute to a more thorough understanding of carbon cycling in these ecosystems.

Data availability

Data available upon request from the corresponding author.

Author contributions

1. **Fund acquisition:** GSR & GT (funds for the equipment and conducting the experiments)

2. **OTC design, construction and installation:** GT & PT (designing, manufacturing and ground installation)
3. **Conceptualization:** DB, PT & GT (Daytime and night-time respiration comparison under warming, developing the question and planning the objectives)
4. **Study design:** DB & PT (site selection, no. of plots, collars, readings, time-intervals etc.)
5. **Methodology:** DB & PT (standardization of respiration measurement protocol)
6. **Data collection:** DB (respiration measurements)
7. **Data analysis:** DB & PT (type of statistical tests to be performed and execution)
8. **Preparation of figures & tables:** DB & PT (presenting the data and preparing figures and tables)
9. **Manuscript writing:** DB
10. **Review and comments on manuscript:** PT, GT & GSR

Competing interest

The authors declare that they have no conflict of interest.

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Rahul Tomar (OTC and control plot installation)

Pooja Panthari (respiration measurements)

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