

# 1 Quantifying wind and pressure effects on trace gas fluxes 2 across the soil-atmosphere interface

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## 9 10 **Abstract**

11 Large uncertainties persist in estimates of soil-atmosphere exchange of important trace gases.  
12 One significant source of uncertainty is the combined effect of wind and pressure on these  
13 fluxes. Wind and pressure effects are mediated by surface topography: few surfaces are uniform  
14 and over scales of tenths of a meter to tens of meters, air pressure and wind speed at the ground  
15 surface may be very variable. In this paper we consider how such spatial variability in air  
16 pressure and wind speed affects fluxes of trace gases. We used a novel nested wind tunnel  
17 design, comprising a toroidal wind tunnel in which wind speed and pressure may be controlled,  
18 set within a larger, linear wind tunnel. The effects of both wind speed and pressure differentials  
19 on fluxes of CO<sub>2</sub> and CH<sub>4</sub> within three different ecosystems (forest, grassland, peat bog) were  
20 quantified. We find that trace gas fluxes are positively correlated with both wind speed and  
21 pressure differential near the surface boundary. We argue that wind speed is the better proxy for  
22 trace gas fluxes because of its stronger correlation and because wind speed is more easily  
23 measured and wind speed measurement methodology more easily standardized. Trace gas fluxes,  
24 whether into or out of the soil, increase with wind speed within the toroidal tunnel (+55% flux  
25 per m s<sup>-1</sup>), while faster, localized surface winds that are external to the toroidal wind tunnel  
26 reduce trace gas fluxes (-13% flux per m s<sup>-1</sup>). These results are consistent for both trace gases

27 over all ecosystem soil types studied. Our findings support the need for a revised  
28 conceptualization of soil-atmosphere gas exchange. We propose a conceptual model of the soil  
29 profile that has a 'mixed layer', with fluxes controlled by wind speed, wind duration, porosity,  
30 water table, and gas production and consumption.

31

## 32 **1 Introduction**

33 Soils play a key role in the production, sequestration, consumption and release of all  
34 climatically-important trace gases. Soils contribute greater than 25% of surface fluxes of CO<sub>2</sub> to  
35 the atmosphere, while a substantial fraction of the sources (>30%) and sinks (>5%) of  
36 atmospheric CH<sub>4</sub> are driven by soil microbial processes (Holmen and Jaffe, 2000; Wuebbles and  
37 Hayhoe, 2002).

38 The movement of gases within soils has been reviewed by, inter alios, Hillel (1998), Scanlon et  
39 al. (2000), Rolston and Moldrup (2012) and Monson and Baldocchi (2014). Gas movement may  
40 occur via diffusion and/or advection. Different types of diffusion can occur in a soil, although the  
41 most important is 'ordinary' or molecular diffusion. Ordinary diffusion involves the transport of a  
42 gas along a gas concentration or mole fraction gradient. Ordinary diffusion of a mixture of two  
43 gases is usually modeled using Fick's second law, while, for mixtures of three or more gases, the  
44 Stefan-Maxwell equations may be used (Rolston and Moldrup, 2012). Advective fluxes are  
45 typically modelled with Darcy's law which is usually used in combination with the continuity  
46 equation.

47 Little empirical work has been done on the relative importance of gas diffusion and advection in  
48 soils. Despite the lack of substantial empirical evidence, Rolston and Moldrup (2012) suggest  
49 that diffusive flow is more important than advective flow. Their suggestion is commonly  
50 accepted by scientists measuring trace gas fluxes using closed chambers. Static and dynamic flux  
51 chambers are widely employed to measure soil-atmosphere trace gas exchanges, but are usually  
52 set up such that diffusion-only conditions prevail (no or slow circulation of fan air) or under  
53 unrealistic conditions of within-chamber air flow (constant air flow generated by a single fan or  
54 set of fans) (cf., Denmead, 2008; Rochette, 2011) which give an undefined combination of

55 diffusion and advection. Gradient flux measurements also rely upon this basic assumption  
56 (Myklebust et al., 2008).

57 In general there is considerable uncertainty about the degree to which chambers provide reliable  
58 measurements, and problems with chamber use are discussed in the reviews by Denmead (2008)  
59 and Rochette (2011). The use of fans provides a good example of this uncertainty. Some authors,  
60 such as Davidson et al. (2002), suggest that chambers fitted with fans give unreliable readings. In  
61 contrast, Christiansen et al. (2011) found that, only in chambers in which the air was mixed by a  
62 fan, was the measured flux similar to reference fluxes (they introduced CH<sub>4</sub> at controlled rates  
63 through the base of various laboratory sand beds – some dry and some wet – and used chambers  
64 to record the fluxes above the sand). Furthermore, Denmead (2008) notes that chambers without  
65 fans or with fixed wind speeds may give unrealistic flux estimates, especially during windy  
66 conditions in the environment outside of the chambers. To illustrate the problem, he cites  
67 Denmead and Reicosky (2003) who, in a study of a tilled soil, found that, while CO<sub>2</sub> fluxes  
68 within a chamber with a fixed-speed fan stayed steady, those in the area around the chamber (as  
69 measured using a micrometeorological dispersion method) increased with ambient wind speed.

70 Even if we assume that diffusive fluxes are an important form of gaseous movement in soils,  
71 such fluxes are highly sensitive to gradients in local soil gas concentrations. Spatial variation in  
72 soil trace gas profiles are determined by a complex set of biological, chemical and physical  
73 processes (Holmen and Jaffe, 2000; Montzka et al., 2010). For instance, CO<sub>2</sub> is produced  
74 biologically in soils by respiration, contingent upon the vertical distribution of roots, hyphae and  
75 labile organic C, temperature, moisture, redox state and CO<sub>2</sub> concentration. Other trace gases,  
76 including CH<sub>4</sub>, are both produced and consumed by separate groups of microbes that reside in  
77 different locations (at different depths or different locations at the same depth) within soils.  
78 Local gas concentrations are also dependent upon the residence time of the trace gas in the soil  
79 profile, since first order chemical and biological consumption rates are time and concentration  
80 dependent. Sufficiently high local concentrations can either lead to negative feedbacks (reduced  
81 root respiration rates; Qi et al., 1994) or greater consumption of the gas of interest (CH<sub>4</sub>;  
82 Wuebbles and Hayhoe, 2002). Gas residence time will depend on the processes transporting  
83 gases through and within soils.

84 Advection may significantly affect local gas residence time. Advection of soil gases occurs when  
85 there is a pressure gradient between the air in the soil and that in the overlying atmosphere.  
86 Horizontal pressure gradients and horizontal advection may also occur. Pressure gradients form  
87 under a range of circumstances. Variations in wind speed at the soil surface, both over time and  
88 spatially, can lead to variations in pressure within the soil profile. Percolation of water through  
89 the soil profile and spatial variations in soil temperature may also be the cause of within-soil  
90 pressure variations.

91 Empirical and modeling studies have shown that, through their effect on advection, soil-  
92 atmosphere pressure differentials can alter the direction and magnitude of gas fluxes  
93 substantially ( $\pm \leq 1000\%$ ) (Yonemura et al., 2000; Takle et al., 2004; Xu et al., 2006; Flechard et  
94 al., 2007; Reicosky et al., 2008; Bowling and Massman, 2011; Maier et al., 2012; Rey et al.,  
95 2012). The suggested mechanism for this process is that localized pressure differentials, driven  
96 by spatially and temporally variable winds, create a push-pull mechanism by which soil pore  
97 spaces are mixed with neighboring pores and overlying air (Webster and Taylor, 1992,  
98 Massman, 2006). This mechanism has been shown to be significantly more effective than  
99 diffusion alone in driving soil-atmosphere fluxes (Massman and Frank, 2006; Bowling and  
100 Massman, 2011; Maier et al., 2012) and is particularly affected by abrupt boundary transitions,  
101 examples including a stone or a fence in a field and the edges of denser vegetation patches.

102 While these published studies note the importance of advective transport in surface-atmosphere  
103 fluxes, they have not systematically quantified its importance over a broad range of  
104 environments, soil types or wind states. Likewise, the majority of these studies have only  
105 observed one trace gas at a time, reducing our ability to generate broadly applicable rules for  
106 surface-atmosphere trace gas fluxes. Here we close this knowledge gap by using a novel nested  
107 wind tunnel (Fig. 1, Fig. S1) to investigate the role of advection in regulating soil-atmosphere  
108 gas exchange for two different trace gases, each of which is controlled by very different  
109 processes at different depths within the soil. CO<sub>2</sub>, under dark conditions, is predominantly  
110 produced through plant, fungal and bacterial respiration and will have high soil concentrations  
111 (relative to the atmosphere) close to the soil surface. In contrast CH<sub>4</sub>, whose biological response  
112 in soils is broadly insensitive to sunlight, is often consumed by aerobic soils and therefore has

113 lower than atmospheric concentrations within the soil column. At greater depths within the soil  
114 profile, in anaerobic regions, CH<sub>4</sub> can be produced by methanogenic archaea but much of this  
115 CH<sub>4</sub> is consumed by methylotrophic bacteria in the regions directly above the production zone.

116 Using four sites, we investigated three different ecosystem types: peat bog (two sites), evergreen  
117 coniferous forest, and managed grassland. We use the empirical data that we collected to build  
118 upon the model proposed by Massman (2006) in which diffusive flow is enhanced by pressure-  
119 based mixing. Based on our measured flux data we propose two modifications: (i) a 'mixed layer'  
120 of soil pore spaces near the soil surface that, depending on wind speed, has a similar gas  
121 composition to the atmosphere immediately above the surface, and (ii) an inherent likelihood of  
122 horizontal gas flow through advective/diffusive mechanisms, which can affect observed trace gas  
123 fluxes.

124

## 125 **2 Methods**

### 126 **2.1 The nested wind tunnel**

127 In order to quantify the impact of local ( $\leq 1$  m) and microscale (in the meteorological sense; 1 m  
128 to 1 km) winds on trace gas fluxes from various ecosystem surfaces, we required an experimental  
129 design that allowed us to vary local wind speeds and atmospheric pressures concurrently. We  
130 resolved this difficulty by nesting a toroidal wind tunnel within a larger, straight-line wind  
131 tunnel. By increasing wind speeds in both wind tunnels we were able to maintain similar  
132 pressures in the local space of the toroidal wind tunnel ( $\sim 1$  m<sup>2</sup>), relative to zero-wind speed  
133 conditions, under higher wind speeds (up to 4 m s<sup>-1</sup>) (Figures 1, S1). Gas fluxes were estimated  
134 for the inner wind tunnel (the toroid) by measuring changes in gas concentration in the enclosed  
135 air space over time (see section 2.3).

136 Current flux measurement methodology relies, in many cases, on the assumption that diffusive  
137 flux is dominant within the system. The nested wind tunnels allowed us to test a number of  
138 different real-world scenarios in which this assumption may not be valid. For instance, with high  
139 winds both within the toroidal tunnel and externally, within the straight-line wind tunnel (similar  
140 to an entire region experiencing a windy day) we can examine whether faster winds drive more

141 rapid mixing of air within soil pores. Alternately, if we keep the air flow within the toroid at zero  
142 and increase the wind speeds externally, within the straight-line wind tunnel (similar to a  
143 sheltered forest/field edge near open land), we can examine the influence of greater mixing  
144 within the soils external to the toroid and the impact of horizontal mixing within the soil column.

### 145 **2.1.1 The inner, toroidal wind tunnel**

146 The inner toroidal wind tunnel was equipped with internal fans, which can generate wind speeds  
147 up to  $6 \text{ m s}^{-1}$ . The toroid was constructed from acrylic and was 40 cm high, 120 cm in diameter,  
148 with an internal ring 30 cm in diameter (Figs. 1, S1). These dimensions created a tunnel footprint  
149 of  $1.06 \text{ m}^2$ , with an internal volume of 424 L. If the toroid is considered within a compass  
150 ordinate system there were two sets of three high-speed computer fans (5214 NH, EBM-Papst,  
151 Mulfingen, Germany) placed at North and South, 20 cm above the soil surface as well as two  
152 digital anemometers (ATP Instrumentation; Leicestershire, UK) placed at West and East, 22 cm  
153 above the soil surface. Anemometers were tested in various locations within the toroid, from near  
154 the inner, bottom edge to near the outer, top edge and were found to record similar wind speeds  
155 in all locations; therefore, the anemometers were ultimately placed for ease of access.

156 Four separate 30 cm diameter removable vents were located at each compass ordinate, although  
157 in practice only those located over the anemometers were covered (during measurements) or  
158 uncovered (during equilibration periods) (Figs. 1, S1). During gas flux measurements each vent  
159 was covered and pressure sealed with silicone gaskets. Internal air temperature probes (DT-612,  
160 Thermosense, Manchester, UK) and pressure differential gauges (264, Setra Systems Inc.,  
161 Boxborough, MA, USA) were located at the top of the apparatus above the anemometers and  
162 penetrated 15 cm and 2 cm respectively into the toroidal tunnel.

163 The installation of the toroid at each site occurred at least 24 hours before tests were run. At our  
164 forest site, one of the two bog sites (Forsinard – see below) and the managed grassland it was  
165 sealed at the soil surface using wet sand, while at the second bog site (Cors Fochno – see below)  
166 its weight caused it to sink slightly into the peat so that its lower edge was below the water table.  
167 Sealing of the toroid was required to maintain/isolate its air mass over the course of each  
168 experiment.

169 **2.1.2 The outer wind tunnel**

170 The straight-line wind tunnel enclosing the toroid comprised a standard aluminium and wooden  
171 agricultural tunnel (FirstTunnels, Lancashire, UK) (3.5 m long × 2 m wide × 1.5 m high) with  
172 the option to be covered by PAR (photosynthetically active radiation) transparent or opaque  
173 plastic sheeting. This option meant the combined wind tunnel system was capable of examining  
174 the soil-plant-atmosphere system under either respiration- or photosynthesis-dominant conditions  
175 (Fig. 1). Only 'dark' results are shown here. In terms of soil-atmosphere CO<sub>2</sub> exchanges,  
176 diffusion will almost always occur from soil to atmosphere because soil CO<sub>2</sub> concentrations are  
177 higher than those in the atmosphere above due to ongoing respiration by plants, fungi, bacteria,  
178 and archaea. By using dark conditions, we were able to remove photosynthetic uptake of CO<sub>2</sub>  
179 and its assimilation into plant tissue as a confounding factor. That is, we were able to interpret a  
180 decrease in chamber CO<sub>2</sub> concentrations as due to advective transport processes without having  
181 to adjust our data for CO<sub>2</sub> fixation by plants which can vary greatly with small changes in  
182 incident irradiance.

183 Three high-volume drum fans (DF24S, Prem-I-Air, Manchester, UK) were placed at one end of  
184 the wind tunnel, each capable of moving 235 m<sup>3</sup> of air per minute at the highest speed setting  
185 (for a maximum calculated wind speed of ~10 m s<sup>-1</sup>).

186 Between measurements, which typically took less than 10 minutes, the toroid was unshrouded  
187 (the available sunlight between measurements was similar to that of a regionally cloudy day) and  
188 its vents opened. Therefore, the effects of the apparatus on the soil being studied were kept to a  
189 minimum; i.e., gas concentrations in the air above the soil were not allowed to build over long  
190 time periods which would have affected gas concentrations in the soil and soil biochemical  
191 processes.

192 **2.2 Field sites**

193 To investigate wind and pressure effects on air flow into and out of soils, we selected four sites  
194 offering a broad range of soil porosities, pore water contents, and organic matter contents. The  
195 sites also differed in the processes affecting CO<sub>2</sub> and CH<sub>4</sub> production and consumption.

### 196 **2.2.1 Wheldrake Forest**

197 Investigations at Wheldrake Forest (53° 54' 36" N, 0° 59' 55" W) occurred on April 20<sup>th</sup> and  
198 from 4<sup>th</sup>-6<sup>th</sup> December, 2011. The site was within a lodgepole pine (*Pinus contorta* Douglas)  
199 plantation with a small, scattered population of silver birch (*Betula pendula* Roth) with little or  
200 no understory. The soil is a well-drained, fine, sandy podzol. CO<sub>2</sub> fluxes from the soil are likely  
201 to be dominated by tree roots and heterotrophic respiration (Heinemeyer et al., 2011). In contrast,  
202 relatively high rates of net CH<sub>4</sub> uptake have been observed previously within these soils, driven  
203 by methanotrophic bacteria (Heinemeyer et al., 2011).

### 204 **2.2.2 University of York managed grassland**

205 Investigations of managed grassland on the University of York campus (53° 56' 50" N, 1° 3' 26"  
206 W) occurred on April 21<sup>st</sup> and from 18<sup>th</sup>-19<sup>th</sup> August, 2011. The sample site was a tended lawn  
207 surface. As grasses are not particularly symbiotic with either arbuscular or ectomycorrhizal fungi  
208 we expected limited fungal influence, limiting CO<sub>2</sub> production within the soil to primarily roots  
209 or bacterial respiration. Rainfall during the August measurements significantly affected the soil  
210 pore water content, and localized pools of standing water were observed on both sampling days,  
211 likely limiting further the biogenic production and consumption of trace gases.

### 212 **2.2.3 Cors Fochno peat bog**

213 Cors Fochno is an estuarine raised bog in west-central Wales (centered on 52° 30'14" N, 4°  
214 00'47" W). Measurements at the site took place between 13<sup>th</sup> and 14<sup>th</sup> September, 2011 on a wet  
215 'lawn' (sensu Belyea and Clymo, 2001) dominated by the moss *Sphagnum pulchrum* (Lindb. ex  
216 Braithw.) Warnst. with a scattering of the sedge *Rhynchospora alba* (L.) Vahl. CH<sub>4</sub> is produced  
217 throughout the soil profile at Cors Fochno, including the upper layers (e.g., Green and Baird,  
218 2013; Comas et al., 2013). Respiration was expected to be primarily from surface peats and  
219 mosses, with some respiration from the sedge, *R. alba*. The water table across the lawn was at or  
220 close to the surface (within 2-3 cm of the top of the *Sphagnum* plants). Sections of wooden  
221 boardwalk were placed around the measurement area to minimize compression of the peat (soil)  
222 profile by observers.



223 The measurement period followed the landfall of a significant atmospheric depression. Wind  
224 gusts in excess of 50 mph were common on the 11<sup>th</sup> and 12<sup>th</sup>, and on the first day of sampling  
225 (the 13<sup>th</sup>) winds were often in excess of 20 mph. Winds had slowed considerably by the 14<sup>th</sup> to  
226 between 3.5 and 7 mph (1.5-3.0 m s<sup>-1</sup>).

#### 227 **2.2.4 Forsinard peat bog**

228 Measurements at Forsinard Flows Reserve (58° 21' 25" N, 3° 53' 48" W) took place from 13<sup>th</sup> -  
229 14<sup>th</sup> July, 2012. The reserve is a low altitude blanket bog in Caithness and Sutherland in northern  
230 Scotland. It is protected for its nature conservation interest by the Royal Society for the  
231 Protection of Birds (RSPB), and some areas are actively managed having previously been  
232 damaged by afforestation. Measurements took place in an unmanaged area of bog containing a  
233 mixed assemblage of vascular plants and bryophytes, including *Trichophorum cespitosum* (L.)  
234 Hartm., *Erica tetralix* L., *Eriophorum vaginatum* L. and *Sphagnum papillosum* Lindb. (Bellamy  
235 et al., 2012). The water table depths at our sampling locations in Forsinard were significantly  
236 lower than Cors Fochno (>10 cm).

#### 237 **2.3 Trace gas flux measurements**

238 Trace gas fluxes from the footprint of the toroid were estimated in the same way as for a  
239 conventional flux chamber; i.e. by measuring gas concentrations within the toroid over time and  
240 using the rate of change in concentration to calculate a flux (cf. Denmead, 2008). Fluxes were  
241 measured for a 3 × 3 matrix of local (≤1 m radius; isolated toroidal wind tunnel) and microscale  
242 (≥1 m radius; straight line wind tunnel) wind speeds, denoted 'zero', 'mid' and 'high' (Table 1).  
243 Replicate measurements were made for each wind state, and the order of tested sample  
244 conditions was randomized to avoid conflating temporal effects.

245 During the experiments, trace gas concentrations in the toroidal wind tunnel were continuously  
246 measured using a Los Gatos Research Fast Greenhouse Gas Analyzer (FGGA; Los Gatos  
247 Research, Mountain View, CA, USA). The instrument is capable of measuring both CH<sub>4</sub> and  
248 CO<sub>2</sub> simultaneously. The measurement interval at the forest, the managed grassland, and the  
249 Forsinard peat bog sites was every second (1 Hz) while at Cors Fochno peat bog it was every 5

250 seconds (0.2 Hz). At this sampling interval instrumental precision is better than  $\pm 1\%$  for both  
251 gases. Air from within the toroid was drawn from the East vent lid, 16 cm above the  
252 anemometers and 38 cm above the soil surface, into the FGGA, where it was analyzed, via off-  
253 axis Integrated Cavity Output Spectroscopy, in a non-destructive manner (Baer et al., 2002), and  
254 returned to the toroid at the West vent lid. The FGGA has a flow rate of  $0.45 \text{ L min}^{-1}$ .

255 For all but the first set of measurements on a given day (the first sampled combination of wind  
256 speeds and pressure), the measurements were only initiated after the straight line wind tunnel and  
257 toroid gas concentrations returned to approximately ambient concentrations (1.8-2.0 ppmv for  
258  $\text{CH}_4$ ; 385-400 ppmv for  $\text{CO}_2$ ). These starting conditions were confirmed through continuous  
259 FGGA sampling and analysis of the toroidal and straight line wind tunnel concentrations  
260 between sampling measurements and usually (see below) normalized rapidly, within 2-3  
261 minutes. Once the next sampling period was ready to begin, the fans in the toroid and straight-  
262 line tunnel were engaged at the appropriate settings; zero, mid or high. The toroid was then  
263 isolated from external air masses by placing the vent lids on silicone gaskets and weighing them  
264 down with lead-shot-filled tubing. The toroid remained isolated from exterior air masses, for ~6  
265 minutes during sampling, after which the fans in the toroid and wind tunnel were powered down,  
266 the vent lids removed and the system left to re-equilibrate to ambient conditions. At Forsinard,  
267 and only Forsinard, 90 minute gaps were allowed between each faster wind sampling state, and  
268 in these conditions flux measurements at zero-wind speed (both within and without the toroidal  
269 wind tunnel) were taken prior to further testing to ensure that fluxes had returned to their original  
270 zero-wind range (as described in the Results section). Care was taken at all sites to minimize the  
271 amount of pressure placed upon nearby soils prior to and during sampling.

272 Pressure differential, soil temperature, ambient air temperature and internal wind speeds were  
273 measured within the isolated toroid and straight line wind tunnels during each measurement  
274 period. Wind speeds remained steady during each placement (Table 1) but differed significantly  
275 between sites. In situ wind speeds were significantly reduced, due to friction from the ground  
276 surface and, in the case of the straight line wind tunnel, alternative wind paths along the tunnel  
277 wall.

## 278 **2.4 Flux estimates**

279 Trace gas fluxes were estimated using the HMR method (Pedersen et al., 2010). This method  
280 fits, where appropriate, a non-linear (exponential) equation to the gas concentration vs time data.  
281 The method is also able to distinguish when gas concentrations vs time are linear or when they  
282 are essentially flat so that the flux is zero. Data retrieved from the FGGA from each 6-minute  
283 sampling period were manually analyzed. Up to the first 2 minutes of data were discarded due to  
284 pressure-based fluctuations associated with setting up the equipment and starting the test. The  
285 amplitude and duration of these initial fluctuations were compared to set wind speeds and no  
286 correlation was observed. After the initial disturbance both CO<sub>2</sub> and CH<sub>4</sub> proceeded to increase  
287 or decrease in a monotonic fashion for the duration of the remainder of the experiment (< 6 min).  
288 We utilized the earliest 120 – 180 second period during which both CO<sub>2</sub> and CH<sub>4</sub> gas  
289 concentrations either rose or fell monotonically.

290 Trace gas fluxes are likely to be significantly different for different trace gas species, both  
291 temporally and spatially. To compare trace gas fluxes across different dates and locations, the  
292 average of measured fluxes from the zero-wind treatments, where wind speeds in both the toroid  
293 and straight-line outer wind tunnels were zero, was taken as a baseline condition, and set to  
294 represent a value of 1.0. All other treatments were then compared relative to this value so that the  
295 relative flux for each trace gas was equal to:

$$296 \quad F_R = F_T / F_0 \quad (1)$$

297 where  $F_R$  is the relative flux for each gas under each set of conditions,  $F_T$  is the treatment flux  
298 and  $F_0$  is the appropriate average baseline flux. Using these relative measures, trace gas fluxes  
299 can be compared across space (between and within ecosystems) and time.

300

## 301 **3 Results**

### 302 **3.1 Wind speed differences versus pressure differentials**

303 Our data show that wind speed was better at predicting trace gas fluxes than pressure  
304 differentials (Figs. 2, 3, and 4). While the physical relationship between pressure and wind is

305 well established, wind speed is not strongly correlated with pressure differences measured  
306 between the toroidal and straight line wind tunnels (Fig. 2;  $r^2 = 0.63$ ). Of particular interest to the  
307 comparison of wind speed and pressure differential as explanatory variables are measurements  
308 taken during the managed grassland measurement campaign where warming within the toroid  
309 (from residual thermal energy from the soil surface) led to an increase in pressure within the  
310 instrument. The observed differences in pressure (+) were opposite to those expected due to  
311 ongoing higher wind speeds within the toroid (-). When pressure is higher within the toroid one  
312 might expect air within it to be driven into the soil, reducing gas fluxes from the soil to the  
313 atmosphere. However, CH<sub>4</sub> and CO<sub>2</sub> fluxes between soil and atmosphere were substantially  
314 higher within these treatments, suggesting that fluxes were more strongly influenced by  
315 measurable wind speed than by measured pressure changes (Tables 1-3).

### 316 **3.2 Wind speed effects on trace gas fluxes**

317 Wind speeds internal and external to the toroidal wind tunnel affected CH<sub>4</sub> and CO<sub>2</sub> fluxes in a  
318 planar fashion ( $r^2 = 0.67$ ; Figs 3a-c). CH<sub>4</sub> and CO<sub>2</sub> fluxes are enhanced as wind speeds directly  
319 above the soil surface increase (i.e., within the toroid) (+55% flux relative to zero-wind  
320 conditions per m s<sup>-1</sup>) but are reduced as wind speeds external to the toroid increase (i.e., within  
321 the straight line wind tunnel but outside the toroid) (-13% flux relative to zero-wind conditions  
322 per m s<sup>-1</sup>). Under open field wind conditions, where internal and external wind speeds are  
323 similar, trace gas fluxes increase by 42% per m s<sup>-1</sup> wind speed relative to zero-wind conditions  
324 (Fig. 3a). Although fluxes increased linearly across the range of wind speeds (and wind speed  
325 differentials) considered here (Fig. 3a), it is important to note that they could exhibit a different  
326 functional form over a wider range of speeds. For example, trace gas fluxes may approach an  
327 asymptote at very high wind speeds.

328 The relationships identified above are irrespective of the initial flux direction (efflux or influx).  
329 When CH<sub>4</sub> is taken up by soils, increased wind speeds in the isolated toroid led to greater CH<sub>4</sub>  
330 uptake while higher wind speeds within the straight line wind tunnel reduced CH<sub>4</sub> uptake (Fig.  
331 3c; Table 3). The observed wind speed-trace gas flux correlation was consistent for both gases  
332 measured over all ecosystems, and was reproducible both within and between sampling  
333 campaigns (Tables 2, 3; Figs 3a-c).

### 334 **3.3 Abrupt flux transitions driven by high wind speeds**

335 Data collected from the Forsinard peat bog site provides compelling evidence of abrupt flux  
336 transitions. During this campaign it became clear that, unlike other study sites, it was impossible  
337 to obtain reproducible results while randomly selecting toroid and wind tunnel wind speed  
338 conditions. At this location surface soil pore spaces were purged under short exposure (< 10 min)  
339 to ‘high’ wind speed conditions ( $\sim 2.0 \text{ m s}^{-1}$  within the toroid) and required up to an hour to re-  
340 equilibrate to their original zero-wind fluxes (Fig. 5). The evergreen forest experiment showed a  
341 similarly abrupt transition in flux (a 30% reduction in zero-wind fluxes after a single long term  
342 exposure to high winds within both the isolated toroid and the linear wind tunnel).

343 Increases in fluxes at higher wind speeds, followed by periods of lower fluxes have previously  
344 been reported for eddy correlation measurements (Sachs et al., 2008; Wille et al., 2008; Schrier-  
345 Uijl et al., 2012). Likewise, internal wind-speed effects on instantaneous chamber fluxes have  
346 been documented (e.g. Denmead, 2008; Xu et al., 2006). These previous studies have allowed  
347 these effects to be measured, but mostly as a by-product of trying to reduce or evaluate poorly-  
348 constrained errors in measurement methods. Our study is the first to consider both wind and  
349 pressure effects simultaneously in a replicated study for realistic ranges of wind speeds and  
350 pressure differentials and is the first to quantify the duration of the wind-driven evacuation effect  
351 on fluxes.

352

## 353 **4 Discussion**

### 354 **4.1 Which is the more effective predictor of trace gas fluxes: wind speed or** 355 **pressure differential?**

356 Our results demonstrate that both wind speed and pressure differential are correlated to surface  
357 fluxes of trace gases (Figs. 3a-c, 4). Wind speed, however, is consistently a better predictor than  
358 pressure differential. Furthermore, soil pore spaces buffer, through expansion and contraction of  
359 soil pore air, local boundary layer air pressures (Xu et al., 2006). Our observations support the  
360 concept of pressure buffering. One of the aspects of the system that is not described explicitly by  
361 Xu et al. (2006) is the effect of temperature on the chamber pressure. In our experiments the

362 internal temperature of the isolated toroid was, at times, 10° C warmer than the air within the  
363 linear wind tunnel, due to transfer of residual heat from the soil surface to the enclosed air within  
364 the toroid. Using the Ideal Gas Law we would expect the pressure differential (straight line wind  
365 tunnel minus isolated toroid) under these conditions to be -34 hPa but the observed pressure  
366 differential was much less, -0.18 hPa. To place this in context, it would require 80 m s<sup>-1</sup> wind  
367 speeds to generate the same pressure differential generated by a 10°C temperature difference.

368 A further complication to common use of pressure differential measurements is the placement of  
369 the pressure gauge. We suggest that an aboveground placement is not particularly helpful, since  
370 it does not address the soil-boundary layer buffering previously described. However, sub-surface  
371 placements become problematic due to problems associated with standardization of depth and of  
372 disturbance. More broadly, the criteria for pressure differential gauge placement have not been  
373 standardized, which has significant implications for comparing published results from different  
374 studies. Therefore, it may be argued that obtaining data on pressure differentials for the purposes  
375 of trace gas flux measurements is not practical. A more tractable, plausible, measureable quantity  
376 is local wind speed, although some standardization of measurement heights and locations will be  
377 necessary; most published data to date have utilized measurement heights from 0.2 to 5.0 meters  
378 from the soil surface.

## 379 **4.2 Wind speed effects on soil-atmosphere exchange of trace gases: A revised** 380 **conceptualization**

381 Measurements taken under realistic surface wind speeds indicate that gas exchange rates are  
382 considerably influenced by both wind speed and the spatial distribution of local winds. This  
383 implies that the commonly used conceptual model based on simple 1-dimensional diffusion is  
384 insufficient, and that a revised model of soil-atmosphere exchange is required. In particular we  
385 propose to build upon the Massman model (Massman, 2006), developed for soil and snow  
386 surfaces, by the inclusion of a near-surface mixed layer.

387 We propose that boundary layers develop at the near surface within soils, similar to that of plant  
388 canopies or the near-surface ocean. The oceanic mixed layer develops according to local solar  
389 radiation, wind speeds, and wind duration. In the case of soils, the mixed layer develops due to

390 the interplay between abiotic factors and biological processes. The latter are production and  
391 consumption, while the former include:

392 (i) Wind speed. We have demonstrated that there exist positive correlations between local wind  
393 speed and trace gas fluxes (Fig. 3a).

394 (ii) Wind duration. We tested this hypothesis briefly in Wheldrake Forest where we subjected the  
395 soil surface to bursts of high winds (bursts in this case equates to gusts of alternating zero/high  
396 winds for 1 minute intervals over a 6 minute period). These bursts caused a ~+40% increase in  
397 CO<sub>2</sub> flux relative to zero-wind conditions ( $1.7 \pm 0.3$  versus  $1.2 \pm 0.7$   $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , Table  
398 2) but was less than that of consistent high wind exposure (Table 2;  $2.4 \pm 0.7$   $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ).  
399

400 (iii) Water table depth. Our data suggest that, under conditions when the water table is near the  
401 surface, the proposed mixed layer does not develop (Tables 2, 3).

402 (iv) Soil porosity.

403 This new model would explain the observed results through enhanced mixing of soil pore space  
404 air with overlying air and the development of horizontal concentration gradients within the soil  
405 profile.

406 Previous soil-atmosphere models cannot explain the full range of soil-atmosphere fluxes that we  
407 observed. In the simple diffusive model, CH<sub>4</sub> travels 70% faster than CO<sub>2</sub>, (Sahoo and Mayaa,  
408 2010) which contrasts with our observed, similar response of CH<sub>4</sub> and CO<sub>2</sub> to increased winds  
409 over multiple soil types. External wind speed effects are particularly difficult to reconcile with  
410 this simple model since diffusion is a relatively slow process while the patterns we observed  
411 occurred rapidly (< 2 min).

412 Pressure differentials, leading to expansion or contraction of air within soil pores, leading to  
413 greater and more rapid mixing within pores, have been proposed as a mechanism by which air  
414 may be mixed between soil pore spaces and the overlying atmosphere (i.e., ‘pressure-pumping’)  
415 (Denmead, 1979; Yonemura et al., 2000; Takle et al., 2004; Xu et al., 2006; Flechard et al.,  
416 2007; Reicosky et al., 2008; Rey et al., 2012). However, the effects of high external winds within  
417 the linear wind tunnel on trace gas fluxes from low or moderate wind environments within the

418 isolated toroid (the isolated toroid in this scenario is similar to the real world scenarios of (i) a  
419 forest verge, nearby an open field, (ii) an open field surrounding a slight depression with deeper  
420 grass depth providing a protected canopy, or (iii) a hedgerow) cannot be explained through this  
421 pressure-pumping model. While pressure waves have been demonstrated to travel up to 50 cm  
422 within soils (Takle et al., 2004; Flechard et al., 2007; Reicosky et al., 2008) such waves, under  
423 high external wind conditions, would lead to lower relative pressure in the soil below the toroid.  
424 A lower pressure below the toroid would lead to a reduction in, or neutral impact, on fluxes of  
425 CO<sub>2</sub> (similar concentrations, but lower pressure, in soil pores would mean similar diffusive  
426 fluxes, but potential for atmosphere-to-soil transfer to maintain pressure equilibrium). Similarly,  
427 lower pressures in the soil would likely lead to greater uptake of CH<sub>4</sub>. Our observed results show  
428 neither an increase in CH<sub>4</sub> uptake concurrent with decreases in CO<sub>2</sub> fluxes, nor do they  
429 demonstrate an overall neutral impact.

430 Furthermore, the correlation between pressure differential and flux is significantly weaker than  
431 the correlation observed for wind speeds (Fig. 4;  $r^2 = 0.37$  for pressure differential vs. Fig. 3a;  $r^2$   
432 = 0.67 for wind speed). If neither the diffusion gradient model nor the pressure-pumping model  
433 is capable of explaining the available data then a revised model is needed.

434 Our proposed 'mixed layer' conceptualization of the soil-atmosphere interface is described  
435 below. In the zero-wind condition (where there is no wind inside either the linear external wind  
436 tunnel or the isolated toroidal wind tunnel, and representative of long term, no wind conditions  
437 on either side of a natural boundary), soil concentration gradients are identical on either side of  
438 the boundary and fulfill the smooth gradient expectations of the current 1-dimensional gradient  
439 diffusive soil model.

440 Alternatively, when the nested wind tunnel is set so that faster winds are experienced within the  
441 toroid than in the linear wind tunnel (similar to an open soil surface nearby a rock-covered  
442 surface, or an open field near a forest verge), we hypothesize that a mixed layer develops in local  
443 soils under high surface winds (directly under the toroidal wind tunnel) while soils, external to  
444 the isolated toroid and under zero surface winds, retain their diffusion-controlled soil gradient. In  
445 this scenario the developing mixed layer either 'mines' the soil of high concentration gases or



446 delivers higher concentration, atmospheric gases to consumption zones, leading to enhanced soil-  
447 atmosphere fluxes regardless of whether consumption or production processes dominate.

448 Under the opposite condition, where local surface winds are negligible and microscale surface  
449 winds are high (so that there are zero-, or low winds within the toroid and faster winds within the  
450 straight line wind tunnel) the mixed layer develops away from the site of interest (in this case,  
451 below the toroid) creating a horizontal concentration gradient within surface soils which  
452 competes with the vertical concentration gradient at the soil surface, lowering observed fluxes  
453 relative to zero-wind conditions.

454 When fast winds are experienced across an ecosystem equally (as in the case where both linear  
455 and toroidal wind tunnels are exposed to fast winds) fluxes are enhanced over zero-wind  
456 conditions despite the development of competitive horizontal gradients.

457 We found two conditions under which the observed relationship between wind speeds and trace  
458 gas fluxes break down, neither of which conflict with our proposed hypothesis that surface wind  
459 speeds affect the rate of greenhouse gas exchange between soils and the atmosphere through the  
460 development of a mixed layer. The first occurs when there is little or no concentration gradient  
461 between the atmosphere and the soil profile, leading to zero-wind fluxes that are essentially zero.  
462 In this situation the development of a mixed layer under elevated wind speeds merely mixes  
463 equivalent concentration gases between soil and atmosphere, leading to zero net transfer. This  
464 condition was observed for CH<sub>4</sub> fluxes at the managed grassland and Forsinard peat bog sites.  
465 The second condition occurs when the water table is very close to the soil surface (< 4 cm), as  
466 occurred at Cors Fochno peat bog, where both CO<sub>2</sub> and CH<sub>4</sub> fluxes were affected (Tables 2, 3).  
467 In this situation, it is likely that a mixed layer is unable to develop rapidly due to a combination  
468 of water acting as a diffusive/advective barrier within near-surface soils as well as increased  
469 hydrostatic pressure from the overlying water column.

470 The mixed layer model explicitly allows the disruption of smooth concentration gradients under  
471 moderate surface wind conditions and is better able to describe abrupt flux transitions over short  
472 timescales (Fig. 5).

473 **The model has implications for all current measurement techniques, above and beyond**  
474 **theoretical considerations of wind speed impacts on boundary interactions. In flux chamber**

475 research the effects of concurrent, external winds on trace gas fluxes have not been well  
476 quantified or incorporated into flux estimates (Xu et al., 2006). We suggest that these wind  
477 effects may reduce observed within-chamber fluxes in several ways, including the development  
478 of competitive horizontal gradients within surface soils (Fig. 3) and after-effects in chambers  
479 placed during or directly after strong local winds (Fig. 5). Eddy covariance measurements are  
480 also likely to perform poorly under high wind states. The effects of terrain obstacles on ambient  
481 flow and non-uniformity in source surface strengths continue to be challenges for accurate flux  
482 estimates (Massman and Lee, 2002) and this model suggests that they may be more significant  
483 than currently appreciated. Furthermore, high wind effects may be underestimated in eddy  
484 covariance analyses because they often do not incorporate pressure flux or quasi-advective terms  
485 (Massman and Lee, 2002).

486 The implications from the new mixed-layer model suggest that estimates of soil-atmosphere  
487 fluxes should be revisited, given that regional fluxes represent the net balance of multiple small,  
488 local fluxes. Indeed, spatial variation in near-surface wind speeds exists in all ecosystems and  
489 will affect overall ecosystem flux. The concept of flux measurements using traditional  
490 techniques as accurate portrayals of soil-atmosphere exchange becomes, in this model, more  
491 relativistic.

492 A mixed layer in surface soils changes our understanding of gross budgets for many trace gases.  
493 For instance, up to 90% of CH<sub>4</sub> generated within soils may be consumed in situ (Segers, 1998).  
494 The mixed layer model implies that a significantly greater fraction of microbially-produced CH<sub>4</sub>  
495 will avoid in situ consumption through rapid mixing with overlying air under windy conditions.  
496 This effectively increases soil-atmosphere flux of CH<sub>4</sub> relative to no wind conditions, even if  
497 production rates are equal within the soil column.

498

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616 Environment Research Council (NE/H01182X/1).

617 Figure 1. The nested wind tunnel system. Note high speed fans within the toroid at East and  
618 West compass points, with anemometers measuring wind speeds at points North and South.  
619 Toroid vents are open at this point and all internal fans are off. Wind tunnel sides are PAR  
620 transparent in this picture and drum fans at the end of the agricultural tunnel are off. Pressure  
621 differential gauges can be seen above fan banks and the PAR sensor is front and center on the top  
622 of the flux chamber.

623

624 Figure 2. The relationship between wind speed and measured pressure differential (outer wind  
625 tunnel minus inner toroid). The planar surface indicates best fit to data ( $r^2 = 0.63$ ,  $z$  (hPa) =  $-0.03$   
626  $+ 0.07 \times \text{IT WS (m s}^{-1}) + 0.01 \times \text{OWT WS (m s}^{-1})$ ). Note insensitivity of pressure to external wind  
627 speeds.

628

629 Figure 3a. Relationship between wind speeds internal and external to the toroid and relative flux  
630 rates for both  $\text{CO}_2$  ( $n = 27$ ) and  $\text{CH}_4$  ( $n = 12$ ). Planar surface indicates best fit to data ( $z = 0.99 +$   
631  $0.55 \times \text{IT WS} - 0.13 \times \text{OWT WS}$ ;  $r^2 = 0.67$ ). The shaded red line represents equal wind speeds  
632 inside and outside the flux chamber, where  $z = 0.99 + 0.42 \times \text{IT/OWT WS (m s}^{-1})$ . Separate  $\text{CO}_2$   
633 and  $\text{CH}_4$  flux relationships are shown in Figs. 3b, 3c.

634 Figure 3b. The relationship between wind speeds internal and external to the toroid and relative  
635 CO<sub>2</sub> fluxes ( $n = 27$ ). All details as shown in Fig. 3a. Planar surface indicates best fit to data ( $z =$   
636  $1.01 + 0.52 \times \text{IT WS} - 0.12 \times \text{OWT WS}$ ;  $r^2 = 0.66$ ).

637 Figure. 3c. The relationship between wind speeds internal and external to the toroid and relative  
638 CH<sub>4</sub> fluxes ( $n = 12$ ). All details as shown in Fig. 3a. Planar surface indicates best fit to data ( $z =$   
639  $0.94 + 0.61 \times \text{Internal WS} - 0.14 \times \text{External WS}$ ;  $r^2 = 0.69$ ).

640  
641 Figure 4. The relationship between measured pressure differential (outer wind tunnel minus inner  
642 toroid, in hPa) and flux relative to zero wind conditions ( $F_R$ ). For direct comparison, only data  
643 included in Fig. 3 have been included in this figure. Solid fill symbols indicate CO<sub>2</sub> flux ratios  
644 while open symbols show CH<sub>4</sub> flux ratios (Tables 2, 3). Trend line indicates best fit for data ( $r^2 =$   
645  $0.37$ ,  $y = 4.85 \times \text{Pressure differential (hPa)} + 1.13$ ).

646  
647 Figure 5. Flux recovery from peat soils after high wind events. Open circle (o) represents fluxes  
648 taken under zero wind conditions prior to wind events. Gray squares (■) represent fluxes  
649 measured under zero wind conditions after wind events. The logarithmic trend line indicates best  
650 fit to data ( $y = 1.01 \times \ln(t(\text{min})) - 1.46$ ;  $r^2 = 0.77$ ). Error bars indicate standard deviation;  $n \geq 3$ .

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653

654 Table 1. Average chamber wind speed and pressure differential for various inner toroid - outer  
 655 wind tunnel treatments. *Italicized, top values are for data collected in April 2011(Grassland and*  
 656 *Forest) and September 2011 (Peat Bog) while non-italicized bottom values indicate data*  
 657 *collected in December and August 2011 and September 2012 for Forest, Grassland and Peat*  
 658 *Bog, respectively. Upper values are wind speeds (inner toroid; outer wind tunnel) and are listed*  
 659 *in m s<sup>-1</sup>. No standard deviations are listed since wind speeds were consistent to ±0.1 m s<sup>-1</sup> at each*  
 660 *emplacement. Pressure differential (defined as outer wind tunnel pressure minus inner toroid*  
 661 *pressure) is listed below wind speeds, and is shown in hPa.*

Isolated Toroid Wind Speed ↓	Linear Wind Tunnel Wind Speed →								
	Forest Soils			Managed Grassland Soils			Peat Bog		
	Zero	Mid	High	Zero	Mid	High	Zero	Mid	High
Zero	<i>0; 0</i> -0.074  0; 0.2 0.025	   0; 2.4 -0.010	   0; 3.2 0.001	<i>0; 0</i> -0.183  0; 0 0.072	   0; 2.0 0.038	   0; 3.2 0.012	<i>0; 0</i> 0.009  0; 0 0.003	     	<i>0; 2.0</i> 0.003    
Mid	   0.9; 0.2 0.070	   0.9; 2.4 0.047	   0.9; 3.2 0.042	   2.0; 0 0.005	   2.0; 1.9 0.095	   2.0; 3.2 0.064	<i>1.1; 0</i> 0.054  0.8; 0 0.016	     	     
High	<i>0; 2.5</i> 0.160  1.7; 0.2 0.187	   1.7; 2.4 0.179	   1.7; 3.2 0.171	<i>0; 2.6</i> 0.169  3.2; 0 0.151	   3.2; 1.9 0.150	   3.2; 3.6 0.215	<i>2.0; 0</i> 0.132  1.4; 0 0.049	     	<i>2.0; 1.4</i> 0.090  1.4; 2.5 0.056

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668 Table 2. Average CO<sub>2</sub> fluxes (in  $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )  $\pm$  standard deviation for each component of  
 669 the inner toroid-outer wind tunnel matrix. *Italicized, top values are for data collected in April*  
 670 *2011(Grassland and Forest) and September 2011 (Peat Bog) while non-italicized bottom values*  
 671 *indicate data collected in December and August 2011 and September 2012 for Forest, Grassland*  
 672 *and Peat Bog, respectively. By convention positive values indicate efflux of CO<sub>2</sub> from the soil*  
 673 *surface into the atmosphere.*

Isolated Toroid Wind Speed ↓	Linear Wind Tunnel Wind Speed →								
	Forest Soils			Managed Grassland Soils			Peat Bog		
	Zero	Mid	High	Zero	Mid	High	Zero	Mid	High
Zero	<i>1.1±0.4</i> (n=4)			<i>6.3±0.5</i> (n=3)			<i>3.4±1.1</i> (n=8)		<i>3.8</i> (n=1)
	1.2±0.7 (n=7)	1.1±0.5 (n=6)	1.0±0.1 (n=6)	6.4±5.8 (n=3)	3.1±2.5 (n=3)	4.8±4.2 (n=3)	1.2±0.5 (n=3)		
Mid							<i>3.4±1.3</i> (n=2)		
	2.0±0.4 (n=6)	1.3±0.2 (n=6)	1.4±0.3 (n=6)	10.9±3.3 (n=3)	10.1±0.8 (n=3)	11.6±3.8 (n=3)	1.1±0.2 (n=5)		
High	<i>2.9±0.4</i> (n=2)			<i>26.1±2.6</i> (n=3)			<i>6.3±2.2</i> (n=4)		<i>3.5</i> (n=1)
	2.4±0.7 (n=6)	1.9±1.2 (n=6)	1.5±0.7 (n=6)	13.9±2.1 (n=4)	14.5±1.6 (n=3)	15.7±2.3 (n=3)	1.1±0.2 (n=4)		1.1±0.5 (n=3)

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681 Table 3. Average CH<sub>4</sub> fluxes (in  $\mu\text{g CH}_4 \text{ m}^{-2} \text{ hr}^{-1}$ )  $\pm$  standard deviation for each component of  
 682 the inner toroid -outer wind tunnel matrix. *Italicized*, top values are for data collected in April  
 683 2011(Grassland and Forest) and September 2011 (Peat Bog) while non-*italicized* bottom values  
 684 indicate data collected in December and August 2011 and September 2012 for Forest, Grassland  
 685 and Peat Bog, respectively. By convention positive values indicate efflux of CH<sub>4</sub> from the soil  
 686 surface into the atmosphere.

Isolated Toroid Wind Speed ↓	Linear Wind Tunnel Wind Speed →								
	Forest Soils			Managed Grassland Soils			Peat Bog		
	Zero	Mid	High	Zero	Mid	High	Low	Mid	High
Zero	<i>-70±40</i> (n=4)			<i>-36±8</i> (n=3)			<i>-5±41</i> (n=7)		<i>-22</i> (n=1)
	-150±80 (n=7)	-110±30 (n=6)	-120±50 (n=6)	-10±2 (n=3)	-10±12 (n=3)	-16±14 (n=3)	2600±1000 (n=3)		
Mid							<i>69±52</i> (n=2)		
	-150±30 (n=6)	-150±60 (n=6)	-110±40 (n=6)	-13±4 (n=3)	-23±4 (n=3)	3±8 (n=3)	2800±200 (n=5)		
High	<i>-250±20</i> (n=2)			<i>-68±3</i> (n=3)			<i>41±40</i> (n=4)		<i>6</i> (n=1)
	-250±110 (n=6)	-280±200 (n=6)	-220±100 (n=6)	-13±9 (n=4)	-25±10 (n=3)	-3±19 (n=3)	2200±100 (n=4)		2600±100 (n=3)

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