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Mary Jane Carmichael

Hollins University, carmichaelmj@hollins.edu

Ashley M. Helton

University of Connecticut


Joseph C. White

Wake Forest University

William K. Smith

Wake Forest University

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1 **Standing dead trees are a conduit for the atmospheric flux of CH₄ and CO₂ from wetlands**

2

3 Mary Jane Carmichael^{1*}, Ashley M. Helton², Joseph C. White¹, and William K. Smith¹

4

5 1. Department of Biology, Wake Forest University, Winston-Salem, NC 27109

6 2. Department of Natural Resources & the Environment and the Center for Environmental

7 Sciences & Engineering, University of Connecticut, Storrs, CT, 06269

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***Corresponding author contact information:**

12

maryjcarmichael@gmail.com

Phone: (336) 830-4041

13

Fax: (336) 758-6008

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24 **Abstract**

25 In vegetated wetland ecosystems, plants can be a dominant pathway in the atmospheric
26 flux of methane, a potent greenhouse gas. Although the roles of herbaceous vegetation and live
27 woody vegetation in this flux have been established, the role of dead woody vegetation is not yet
28 known. In a restored wetland of North Carolina's coastal plain, static flux chambers were
29 deployed at two heights on standing dead trees to determine if these structures acted as a conduit
30 for methane emissions. Methane fluxes to the atmosphere were measured in five of the
31 chambers, with a mean flux of $0.4 \pm 0.1 \text{ mg m}^{-2} \text{ h}^{-1}$. Methane consumption was also measured in
32 three of the chambers, with a mean flux of $-0.6 \pm 0.3 \text{ mg m}^{-2} \text{ h}^{-1}$. Standing dead trees were also a
33 source of the flux of CO_2 ($114.6 \pm 23.8 \text{ mg m}^{-2} \text{ h}^{-1}$) to the atmosphere. Results confirm that
34 standing dead trees represent a conduit for the atmospheric flux of carbon gases from wetlands.
35 However, several questions remain regarding the ultimate source of these carbon gases, the
36 controls on the magnitude and direction of this flux, the mechanisms that induce this flux, and
37 the importance of this pathway relative to other sources at the landscape level.

38

39 **Keywords**

40 Carbon cycle, carbon dioxide, dead vegetation, decomposition, gas transport, methane, wetlands

41

42 **Data Availability**

43 The datasets analyzed during the current study are available from the corresponding author on
44 reasonable request.

45

46

47 **Introduction**

48 Carbon dioxide (CO₂) and methane (CH₄) are widely recognized as two of the most
49 important greenhouse gases due to their abundance in the atmosphere and strength as an agent of
50 global warming, respectively (Shindell et al. 2009; Hansen et al. 2013; Myhre et al. 2013).
51 Methane is recognized as a potent greenhouse gas, with a global warming potential ca. 28-34×
52 that of CO₂ over a 100 year period (Myhre et al. 2013). Atmospheric CH₄ concentrations are
53 once again on the rise (Saunois et al. 2016) after an almost two-decade period of oscillation
54 between stabilization and increase (Kirschke et al. 2013). The cause for this current increase is
55 currently unknown, but is likely attributed to increases in both anthropogenic (e.g. agriculture
56 and the fossil fuel industry) and natural (e.g. wetlands) sources (Saunois et al. 2016).

57 Quantitatively, wetlands represent the single largest source in the annual flux of CH₄ to
58 the atmosphere (Myhre et al. 2013; Schlesinger and Bernhardt 2013). In wetland ecosystems,
59 CH₄ is produced by methanogenesis, the terminal step in the anaerobic degradation of carbon,
60 which occurs in nutrient-depleted, anoxic microsites within sediments. Once CH₄ is produced, it
61 has a variety of fates in wetland systems, including escaping as a flux across the soil/sediment-
62 (Chanton et al. 1989; Morse et al. 2012), water- (Helton et al. 2014; Poindexter et al. 2016), or
63 plant-atmosphere (Schütz et al. 1991; Rusch and Rennenberg 1998) interface. Of these three
64 pathways, the plant-based pathway is arguably the least well understood, despite mounting
65 evidence that it may be a dominant pathway for CH₄ flux from vegetated wetland ecosystems
66 [see Carmichael et al. (2014) and references therein].

67 From a historical perspective, the role of both live and dead herbaceous vegetation as a
68 conduit for wetland CH₄ emissions has long been established (Dacey and Klug 1979; Sebacher et
69 al. 1985; Brix 1990; Smith and Lewis Jr. 1992). Schütz et al. (1991) first proposed that woody

70 vegetation (i.e. tree stems) might also be a source of CH₄ flux from wetlands, a pathway that was
71 confirmed in 1998 by Rusch and Rennenberg. A handful of studies have expanded on this initial
72 research, confirming live trees as a pathway for CH₄ emissions in both upland and wetland
73 systems [see review by Carmichael et al. (2014) and references therein, in addition to more
74 recent papers by Pangala et al. (2015), Terazawa et al. (2015), Machacova et al. (2016), Wang et
75 al. (2016), Wang et al. (2017), and Warner et al. (2017)]. In these studies, CH₄ flux occurred
76 across all possible exchanging surfaces at the plant-atmosphere interface, including the leaf,
77 stem, and trunk. In some cases, specialized wetland adaptations for tissue aeration (e.g.
78 aerenchyma, lenticels, and pneumatophores) have also been implicated as pathways for CH₄
79 flux; but, that is not universally the case, as stomata on leaf surfaces may also contribute to CH₄
80 flux (Garnet et al. 2005).

81 Dead vegetation is an important component of forest carbon budgets (Litton et al. 2007)
82 that represents a substantial, dynamic carbon stock (Cornelissen et al. 2012). Deadwood and
83 litter represent a substantial aboveground C sink (Pacala et al. 2001), accounting for ca. 15% of
84 the global forest carbon storage (Pan et al. 2011). However, the role of standing dead trees in
85 wetland carbon dynamics has been largely ignored, despite the fact that ca. 15-30% of the
86 estimated total global wetland extent consists of forested ecosystems (Matthews and Fung 1987;
87 Lehner and Döll 2004). After tree death, water is evacuated from cavities and hydraulic elements
88 in the trunk, leaving an intricate network of open conduits within the plant tissue that provide a
89 continuum of connectivity, from soil/sediment to the atmosphere. In wetland systems, dead trees
90 likely possess a suite of structural adaptations already honed for gas transport from the
91 atmosphere to above- and belowground tissues (Hook 1984a). Barriers to diffusion in the inner
92 bark and xylem are generally viewed as resistors to gas exchange in woody tissue; however, as

93 the decay process begins, microbial and insect activity could lead to increased wood porosity via
94 the formation of additional channels within plant tissue that may facilitate gas exchange with the
95 atmosphere (Teskey et al. 2008). Interestingly, Hook and Brown (1972) observed that
96 microscopic pores as small as 2-5 μm in diameter were large enough to permit gas exchange
97 across the cambium in *Nyssa aquatica* L. (water tupelo) and *Fraxinus pennsylvanica* Marshall
98 (green ash), two common wetland species. Thus, it is possible that the open conduit systems in
99 dead trees may provide a pathway for the atmospheric flux of sediment-borne greenhouse gases
100 from wetland systems [as suggested previously by Carmichael et al. (2014) and Oberle et al.
101 (2017)].

102 In order for standing dead trees (hereafter snags) to act as a source of the atmospheric
103 flux of greenhouse gases, two conditions must occur: (1) gas evolution and/or accumulation
104 within the trunk airspace of a dead tree and (2) flux of this gas across the plant atmosphere
105 interface (Carmichael and Smith 2016b). A recent study described the potential for snags to act
106 as conduits for CH_4 and CO_2 emissions from wetland ecosystems (Carmichael and Smith 2016b),
107 providing evidence that snags accumulate carbon-based greenhouse gases within trunk airspace
108 at significantly higher concentrations than the atmospheric samples taken immediately outside of
109 the trunk, thus establishing a concentration gradient that would be expected for a plant-
110 atmosphere flux to occur. But, several questions remained, namely the ultimate source of these
111 carbon gases (i.e. sediment- or plant-based decomposition pathways) and whether the gases
112 actually escape from snags as a flux to the atmosphere. Therefore, we conducted a study in the
113 summer of 2016 to determine if snags represent a conduit for the flux of CH_4 and CO_2 to the
114 atmosphere from wetland ecosystems.

115 **Materials and Methods**

116 *Site Description*

117 Due to the potential for highly productive croplands, much of North Carolina's
118 Albemarle-Pamlico peninsula was converted from wetland habitat to farmland in the 1970's
119 (Carter 1975). However, land in the region drains poorly (Titus and Richman 2001; Sallenger Jr.
120 et al. 2012; Hauer et al. 2016) and farmlands must be intensively managed, often through the
121 installation of drainage canals and pump stations, to prevent soil waterlogging and declines in
122 crop productivity. In the late 1990's, the Great Dismal Swamp Mitigation Bank, LLC purchased
123 the former Timberlake Farms to restore the site as a compensatory mitigation bank. The
124 Timberlake Observatory for Wetland Restoration (hereafter TOWeR) is a 1,700 ha site located
125 on the Albemarle-Pamlico peninsula (35°54'22"N, 76°09'25"W, Fig. 1). Detailed descriptions of
126 the region, site, and restoration practices and management can be found in Needham (2006),
127 Ardón et al. (2010a), and Ardón et al. (2010b).

128 Restoration was completed at TOWeR in 2007 when the pump station at the northern end
129 of the site was disabled, hydrologically reconnecting the site to surrounding waters. With the
130 restoration of historical hydrology, several areas within the site that were not previously farmed
131 converted into ghost forest landscapes (Fig. 2a and b), as flood-intolerant species (e.g. *Acer*
132 *rubrum* L.) succumbed most likely to the stress associated with living in a permanently
133 inundated environment (Hook 1984b; Kozłowski 1997). To date, living trees persist, but are
134 restricted to either flood-tolerant species such as *Taxodium distichum* (L.) Rich., *Nyssa aquatica*
135 L., *Nyssa sylvatica* Marshall var. *biflora* (Walter) Sarg. or raised hummock microsites. The
136 selected research sites for the present study consisted of two ghost forest landscapes (Fig. 1a),
137 one located in the northwestern quadrant of the TOWeR property, and the second within a
138 permanently inundated section of the restored wetland.

139 *Site mesoclimate and additional environmental measurements*

140 Environmental variables were continuously measured at each sampling location (Fig. 1a)
141 in July 2016 and compared to historical data from the State Climate Office of North Carolina's
142 Climate Retrieval and Observations Network of the Southeast (CRONOS) Database monitoring
143 station #311949 located within 2 km of TOWeR in the Gum Neck Community of Tyrrell
144 County, North Carolina. Air temperature and relative humidity were measured continuously at 2
145 m above ground using a HOBO Pro V2 sensor and data logger (Model U23-001, Onset, Bourne,
146 MA) shielded from direct sunlight and the nighttime sky.

147 Daily water quality measurements were taken in each ghost forest landscape at three
148 representative locations as described in Carmichael and Smith (2016a). Salinity was monitored
149 using a YSI EcoSense EC300A portable conductivity, salinity, and temperature meter (YSI,
150 Yellow Springs, OH). Surface water pH was monitored using a YSI EcoSense pH100A portable
151 pH, mV, and temperature meter. All instruments were calibrated in the field prior to
152 measurements. In addition to mesoclimate and water quality measurements, tree diameter at
153 breast height (DBH, 1.37 m) and the water depth next to each tree and each floating static flux
154 chamber (see below) were measured.

155 *Plant-Atmosphere greenhouse gas fluxes*

156 We used a static chamber approach (Livingston and Hutchinson 2009) to measure plant-
157 atmosphere greenhouse gas fluxes on ten trees in the northwest quadrant of the TOWeR property
158 (Fig. 1a). Snags were systematically selected to ensure that each tree was located in standing
159 water (mean water depth 0.23 ± 0.03 m, range 0.10–0.38 m) and was structurally sound enough to
160 support static flux chambers and withstand drilling. An effort was made to repeat measurements
161 on as many trees as possible from a 2014 study (Carmichael and Smith 2016b).

162 Chambers (Fig. 2c) were constructed based on a modified version of the chamber design
163 described in Pangala et al. (2012). The description and dimensions of the chambers matched
164 those described in Pangala et al. (2012) with the following exceptions: chambers were
165 constructed of 3 mm clear Lexan and gas-impermeable closed cell foam (MD Building Products,
166 Oklahoma City, OK) was used to provide a seal between the two halves of the chambers. Each
167 chamber contained two gas sampling ports [8 mm Suba Seal stoppers (Sigma-Aldrich, St. Louis,
168 MO) sealed in place with 100% Silicone caulk (General Electric, Fairfield, CT)] and an internal
169 fan (Jameco Electronics, Belmont, CA), which was used to ensure that the air in each chamber
170 was well-mixed during incubations and sampling. Central chamber openings were custom fit to
171 the diameter of each tree using 5 mm closed cell resilient sealing tape (Advanced Acoustics,
172 Mansfield, UK). After each chamber was mounted and secured in place, gas-impermeable PTFE
173 tape (3M, St. Paul, MN) was used as a secondary sealant over each joint. Two chambers were
174 deployed on each tree, one chamber located at 10-50 cm above water level and a second at 60-
175 100 cm, as studies from living trees indicate an inverse relationship between CH₄ flux and
176 distance above the soil surface (Pangala et al. 2012).

177 At the beginning of each sampling interval, air temperature, barometric pressure, and
178 wind speed were recorded using a Kestrel 4000 weather and environmental meter (Kestrel
179 Instruments, Boothwyn, PA). Ten mL gas samples were collected from each chamber in
180 triplicate at seven time points over an 80 minute incubation: 0, 5, 10, 20, 50, 60, and 80 minutes.
181 Gas samples were injected into pre-evacuated 9 mL glass vials (Teledyne Tekmar, Mason, OH),
182 providing an overpressure to prevent atmospheric gas from leaking into the sample vial.

183 *Greenhouse gas sampling from trunk airspace*

184 To confirm the presence of greenhouse gases in trunk airspace, a protocol inspired by
185 Covey et al. (2012) and described in detail in Carmichael and Smith (2016b) was utilized on the
186 ten trees selected for greenhouse gas flux measurements. Sampling occurred immediately after
187 the static flux chambers were removed from the trees. Three holes were drilled to center of each
188 tree using a 5/16 in drill bit: one at 30 cm and a second at 80 cm above water level (the mid-point
189 height of each static flux chamber), with a third hole at breast height (1.37 m) to have a
190 standardized height on each tree. Immediately after drilling, each hole was plugged with an 8
191 mm SubaSeal stopper (Sigma-Aldrich, St. Louis, MO) and a gas-tight syringe was used to
192 extract a single 10 mL sample of gas from the trunk airspace at 30 cm above water level. The
193 sample was injected into a pre-evacuated 9 mL glass vial (Teledyne Tekmar, Mason, OH),
194 providing an overpressure to prevent atmospheric gas from leaking into the sample vial.
195 Immediately after sampling the trunk airspace, a second sample was taken as described above
196 from the atmosphere directly next to the trunk at 30 cm above water level. This procedure was
197 then repeated at 80 cm above water level and at breast height. After trunk greenhouse gas
198 sampling was completed, samples of ambient air (n= 3 daily) were taken at a TOWeR location
199 away from any obvious CH₄ sources to obtain background concentrations for atmospheric
200 greenhouse gases for the site.

201 *Water-Atmosphere greenhouse gas fluxes*

202 To compare the relative importance of greenhouse gas flux pathways, water-atmosphere
203 greenhouse gas fluxes were also measured using a static chamber approach following a protocol
204 that had been used successfully at TOWeR (Helton et al. 2014). Floating static flux chambers
205 (Fig. 2d) were constructed from 10 L gas sampling bags as described in detail in Helton et al.
206 (2014). Static flux chambers (n=8) were deployed at three locations within a ghost forest

207 landscape in the restored wetland (Fig. 1a). At the beginning of each sampling interval, air
208 temperature, barometric pressure, and wind speed were recorded using a Kestrel 4000 weather
209 and environmental meter (Kestrel Instruments, Boothwyn, PA). Triplicate 10 mL gas samples
210 were collected from each chamber as described in Helton et al. (2014) at three time points over
211 24 hour incubation: 0, 8, and 24 hours.

212 *Gas analyses*

213 All gas samples were stored at room temperature for less than one week before analysis
214 via gas chromatography at the Duke River Center. Gas samples were analyzed for CH₄ and CO₂
215 concentrations at the Duke River Center following protocol outlined in Morse et al. (2012),
216 Helton et al. (2014), and Carmichael and Smith (2016b). Samples were injected by a Tekmar
217 7050 Headspace Autosampler into a Shimadzu 17A gas chromatograph with electron capture
218 detector and flame ionization detector (Shimadzu Scientific Instruments, Columbia, MD)
219 retrofitted with sixport valves and a methanizer to allow the determination of the three gases
220 from the same sample. Ultra-high purity N₂ was used as the carrier gas, and a P5 mixture served
221 as the make-up gas for the electron capture detector. A Nafion tube (Perma Pure, Toms River,
222 NJ) and counter-current medical breathing air were used to remove water vapor from the sample
223 stream. Gas concentrations were determined by comparing the peak areas of samples and
224 certified primary standards (range of standards 0.3–5,000 μL L⁻¹ for CH₄ and 100–10,000 μL L⁻¹
225 for CO₂; Airgas, Morrisville, NC) using GCsolution software (Shimadzu Scientific Instruments).

226 *Plant-Atmosphere and Water-Atmosphere greenhouse gas flux calculations*

227 Under ideal conditions in static chamber incubations, gases either accumulate or are
228 consumed linearly over time (Livingston and Hutchinson, 2009); gas fluxes are determined by
229 regression analysis of the change in gas concentration over time in the chamber. Static flux

230 chambers are sensitive to disturbance, so rigorous quality control measures (see description
231 below) must be applied. Measured gas concentrations were initially converted using the ideal gas
232 law and field measurements of air temperature and barometric pressure from ppmv to $\mu\text{g m}^{-3}$.
233 Quality control measures, as described in detail in Helton et al. (2014) and McInerney and
234 Helton (2016), were then applied to the data set.

235 For gas flux calculations, we began by calculating the average of all sample replicates
236 that were within 10% of one another (McInerney and Helton 2016). Next, we used these values
237 to calculate the minimum detectable concentration difference (MDCD) for each sampling date
238 (Yates et al. 2006): incubations that did not exceed the MDCD were excluded from the analysis.
239 Gas fluxes are reported as a flux per unit exchanging surface area. Therefore, some additional
240 transformations were required before regression analyses could be completed. For plant-
241 atmosphere gas fluxes, the volume of each static flux chamber was obtained by subtracting the
242 volume of each stem in a chamber (approximated as a truncated cone) from the total chamber
243 volume. The exchanging surface area of the trunk was approximated as a truncated cone. These
244 two numbers were used to calculate the volume to surface area ratio, which was then used to
245 report flux rates by surface area. For water-atmosphere fluxes, the volume to surface area ratio
246 for the static flux chambers obtained by Helton et al. (2014) was used for conversions. Once
247 these conversions were completed, linear regression was used to calculate gas fluxes. An
248 incubation met the assumption of linearity when $r^2 > 0.85$; all incubations below this value were
249 discarded from analysis.

250 *Statistical analyses*

251 For gas samples obtained from trunk airspace, paired t-tests were used to evaluate
252 measured differences in greenhouse gas concentrations between trunk airspace and the air next to

253 the trunk at a given height. A one-way analysis of variance was used to evaluate both the
254 comparison between trunk airspace greenhouse gas concentrations at all heights above water
255 level and the comparison between greenhouse gas concentrations in the air next to the trunk at all
256 heights above water level.

257 To test for the effect of height above water level on plant-atmosphere greenhouse gas
258 fluxes, t-tests were used to compare plant-atmosphere flux measurements from the two static flux
259 chambers on each tree. T-tests were also used to compare the magnitude of plant-atmosphere
260 fluxes to the flux associated with the water-atmosphere interface and to compare the magnitude
261 of carbon (CO₂ and CH₄) fluxes across the water-atmosphere interface.

262 In all cases described above, a Shapiro-Wilk test was used to test for normality. If
263 normality assumptions were violated, a non-parametric equivalent (i.e. Wilcoxon Signed Rank
264 Test, Kruskal-Wallis one-way ANOVA on ranks with a Tukey test for multiple comparisons,
265 or Mann-Whitney Rank Sum Test) was utilized. Statistical analyses were conducted using Sigma
266 Plot v.12 (Systat Software, San Jose, CA) and R 3.0.1 (R Core Team).

267 **Results**

268 *Site mesoclimate and additional environmental measurements*

269 Mesoclimate data indicate that the daily temperature profile in July 2016 was similar to
270 both the 10 year weather averages and the 30 year climate normal for Tyrrell County, North
271 Carolina. Fresh surface water conditions (salinity = 0.1±0.0 ppt) and relatively constant surface
272 water pH (pH = 4.69±0.07) were maintained throughout the study period: these observations are
273 consistent with long-term observations (unpublished site monitoring data). The mean water depth
274 at standing dead tree locations was 0.23±0.03 m (range, 0.0–0.5 m). DBH ranged from 2.0–16.0

275 cm, with an average value of 7.9 ± 0.6 cm. The mean water depth at water-atmosphere static flux
276 chamber locations was 0.31 ± 0.03 m (range, 0.19–0.45 m).

277 *Greenhouse gas sampling from trunk airspace*

278 The trunk airspace CH_4 and CO_2 concentrations were significantly elevated ($P<0.01$) at
279 30 and 80 cm compared to the air immediately outside of the trunk (Fig. 3). Trunk airspace CH_4
280 and CO_2 concentrations were also significantly elevated ($P<0.05$) at 30 cm compared to breast
281 height. There were no significant differences in trunk airspace greenhouse gas concentrations
282 between either 30 cm and 80 cm or 80 cm and breast height, possibly due to high variability in
283 the dataset.

284 Mean concentrations of CH_4 and CO_2 in the air immediately outside of the trunk (Fig. 3)
285 fell within the 95% confidence intervals for CH_4 and CO_2 measured in the ambient air at the site,
286 indicating that atmospheric greenhouse gas concentrations near the trunk were not significantly
287 elevated as compared to background concentrations reported on the sample date. The single
288 exception was the concentration of CH_4 in the air outside of the trunk at 30 cm (5.1 ± 1.1 $\mu\text{L L}^{-1}$),
289 which was slightly elevated compared to the background concentration in ambient air on sample
290 days (2.7 ± 0.1 $\mu\text{L L}^{-1}$). There were no significant differences in the concentrations of either CH_4
291 or CO_2 in the air immediately outside of the trunk at the base of the trunk (30 cm) compared to
292 80 cm and 1.37 m, which is indicative of atmospheric mixing.

293 *Plant-Atmosphere greenhouse gas fluxes*

294 Of the twenty static flux chambers that were used to measure greenhouse gas fluxes
295 across the plant-atmosphere interface, eight (40%) passed quality control standards (Table 1).
296 Methane production was measured in five (62%) of the chambers, with an average flux of
297 0.4 ± 0.1 $\text{mg m}^{-2} \text{h}^{-1}$ (range, 0.1–0.7 $\text{mg m}^{-2} \text{h}^{-1}$). Methane consumption was measured in three

298 (38%) of the chambers, with an average flux of $-0.6 \pm 0.3 \text{ mg m}^{-2} \text{ h}^{-1}$ (range, -0.3 – $-1.2 \text{ mg m}^{-2} \text{ h}^{-1}$)
299 ¹). For CO₂, seven (88%) of the chambers were a source of carbon flux to the atmosphere (mean
300 $114.6 \pm 23.8 \text{ mg m}^{-2} \text{ h}^{-1}$, range 42.1 – $224.9 \text{ mg m}^{-2} \text{ h}^{-1}$). A single chamber provided evidence of
301 CO₂ consumption at a rate of $-29.6 \text{ mg m}^{-2} \text{ h}^{-1}$. For both CH₄ and CO₂, there were no significant
302 differences in fluxes based on location of chamber placement (i.e. bottom vs. top) ($P > 0.05$).

303 *Water-Atmosphere greenhouse gas fluxes*

304 All eight floating static flux chambers passed quality control standards for water-
305 atmosphere fluxes of CH₄ and CO₂. The mean water-atmosphere flux of CO₂ ($343.9 \pm 16.1 \text{ mg m}^{-2} \text{ h}^{-1}$)
306 was an order of magnitude greater than the mean water-atmosphere flux of CH₄ (30.9 ± 6.1
307 $\text{mg m}^{-2} \text{ h}^{-1}$, Table 1). For CH₄, water-atmosphere fluxes demonstrated some spatial
308 heterogeneity, ranging from 10.2 – $63.3 \text{ mg m}^{-2} \text{ h}^{-1}$. This was also the case for CO₂, but fluxes
309 were much less variable (range, 274.2 – $417.9 \text{ mg m}^{-2} \text{ h}^{-1}$). Water-atmosphere CO₂ fluxes were
310 significantly higher ($P < 0.001$) than those associated with CH₄. In addition, water-atmosphere
311 CH₄ and CO₂ fluxes were significantly higher than those across the plant-atmosphere interface
312 ($P < 0.001$). The water-atmosphere flux of CH₄ was roughly two orders of magnitude greater than
313 that of the plant-atmosphere flux, whereas the water-atmosphere flux of CO₂ was ca. $4 \times$ greater
314 than the flux associated with snags.

315 **Discussion**

316 Our results identify standing dead trees as a pathway for the flux of CH₄ and CO₂ from
317 wetland ecosystems providing an increased resolution to the pathways responsible for the
318 atmospheric flux of greenhouse gases from wetlands. Snags were sources of the atmospheric
319 flux of CO₂, but were both sources and sinks of the more potent greenhouse gas, CH₄, with
320 measured CH₄ fluxes quantitatively offsetting one another in the present study.

321 *Greenhouse gas sampling from trunk airspace*

322 Results from trunk airspace greenhouse gas sampling confirmed the development of a
323 concentration gradient across the snag-atmosphere interface, a necessary first step for snags to
324 act as a source of carbon flux to the atmosphere. These data are consistent with results from a
325 2014 pilot project at TOWeR (Carmichael and Smith 2016b) that demonstrated both the
326 accumulation of carbon-based greenhouse gases within the trunk airspace of snags and the
327 establishment of a concentration gradient within trunk airspace. However, as in Pitz and
328 Megonigal (2017), methodological limitations in our study did not allow for the determination of
329 the source of the accumulated gases. Potential sources of gas production include chemically-
330 driven degradation of methoxyl groups in plant tissue (Keppler et al. 2006; McLeod et al. 2008;
331 Vigano et al. 2008), microbial decomposition of woody tissue in the snag (Zeikus and Ward
332 1974; Covey et al. 2012; Lenhart et al. 2012; Hietala et al. 2015; Wang et al. 2017), and/or plant-
333 mediated transport from the sediment (Gauci et al. 2010; Pangala et al. 2012; Terazawa et al.
334 2015).

335 As a result of internal barriers to diffusion in the inner bark and xylem, it is not unusual
336 to observe high gas concentrations in trunks and stems relative to atmospheric air (Teskey et al.
337 2008), a pattern that has been observed in both living trees (Teskey et al. 2008; Covey et al.
338 2012; Wang et al. 2017) and deadwood stocks (Covey et al. 2016; Warner et al. 2017). Several
339 studies, as reviewed in Teskey et al. (2008) and as observed in Wang et al. 2017, have noted a
340 positive correlation between internal concentrations of stem gases and measured efflux across the
341 plant-atmosphere interface. Therefore, chamber-based work was necessary to 1) confirm if the
342 high internal gas concentrations observed in this study escaped the plant-atmosphere interface as

343 a flux and 2) more finely resolve if deadwood stocks, such as snags, represent a source or a sink
344 of carbon flux to the atmosphere.

345 *Plant-Atmosphere greenhouse gas fluxes*

346 Snags were confirmed here as a conduit for the flux of carbon gases from wetlands. In the
347 present study, there were no clear spatial patterns in the data that were collected and many of the
348 chambers did not meet quality control standards, indicating either the absence of fluxes from an
349 individual snag or that some fluxes may be too small to be detected due to instrumentation limits.
350 However, among detectable fluxes, there was evidence of both CH₄ and CO₂ production and
351 consumption across the plant-atmosphere interface. For both CH₄ and CO₂, plant-atmosphere
352 fluxes were lower in magnitude than those measured across both the water- (this study) and soil-
353 atmosphere interfaces (Morse et al. 2012) at TOWeR. Plant-atmosphere fluxes of CH₄ in this
354 study were similar in magnitude to those measured from both live trees and coarse woody debris
355 in other studies of both wetland (Pangala et al. 2012) and upland (Wang et al. 2016; Wang et al.
356 2017; Warner et al. 2017) systems. However, fluxes of CH₄ in this study exceeded those
357 measured in other studies from live trees in both wetland (Gauci et al. 2010; Machacova et al.
358 2013) and upland (Machacova et al. 2016; Pitz and Megonigal 2017) systems by up to 3 orders
359 of magnitude. It is not uncommon to observe high spatial and temporal variation in studies that
360 measure plant-atmosphere greenhouse gas fluxes. Although CO₂ fluxes from woody vegetation
361 are rarely reported in the literature related to the role of vegetation in the flux of greenhouse
362 gases from wetland systems, the values in our study largely agree with those measured in live
363 trees and coarse woody debris in upland systems by Warner et al. (2017).

364 Despite the growing body of literature on the role of plants in the flux of carbon gases
365 from wetland systems, much is yet to be learned about this pathway, a statement that is

366 especially relevant for the newly recognized pathway of snags. First, it is still unclear whether
367 the ultimate source of the carbon gases in this study was decomposition of woody tissue, plant-
368 mediated transport of sediment-borne gases, or a combination of both. Future experiments
369 focused on measuring the potential for CH₄ production and oxidation in tissue harvested from
370 snags could help to clarify this unknown. In addition, stable isotopic studies of gases trapped in a
371 flux chamber might also be a useful approach [similar to Schwietzke et al. (2016)], though
372 identifying sources of CH₄ using this technique can be somewhat complicated (Newton 2016).

373 Second, the abiotic and biotic controls on the magnitude and direction of carbon fluxes
374 from snags are currently unknown. A variety of abiotic factors have been shown to impact decay
375 rates in deadwood: surface area exposed to ground contact and/or physical position (Harmon
376 1982; Oberle et al. 2017), exposure to radiation and wind (Harmon 1982), the chemical
377 composition of wood (Zanne et al. 2015), the water content of wood (Wang et al. 2017), and the
378 availability of carbon substrates (Covey et al. 2016). In addition, any factor that impacts
379 properties associated with diffusion in deadwood would likely also affect gas fluxes across the
380 plant-atmosphere interface (Covey et al. 2016). For example, the state of decay (Warner et al.
381 2017), wood density (Pangala et al. 2012), woody porosity (Visser and Bögemann 2003), and the
382 diameter of stems or trunks (Covey et al. 2016) are all factors that likely influence fluxes from
383 snags. Plant-microbe interactions may also act as a control on the strength and direction of
384 fluxes. Negative CH₄ fluxes were measured in this study, and a comparison of gas concentration
385 values in dead trunk airspace to those in experimental models of biologically inert trunks (2"
386 PVC columns, unpublished data) provides evidence that dead trunks, as biologically active
387 structures, may actually play a role in mediating CH₄ flux. Methanotrophic symbionts are known
388 to colonize wetland plant tissue (Raghoebarsing et al. 2005), and it is possible this relationship

389 could turn an individual plant from a source of CH₄ to a sink if rates of CH₄ consumption were
390 high enough.

391 Third, the mechanisms that induce the flux of carbon gases across the plant-atmosphere
392 interface are yet to be elucidated. A flux could purely be diffusive, but it is also likely that
393 environmental conditions such as wind exposure may drive and/or enhance fluxes across the
394 plant-atmosphere interface. During one sampling event, a storm system was moving through the
395 area. When having difficulty extracting a gas sample from a packed column at water level, a gust
396 of wind pulsed through the site and the sample was easily extracted. According to Bernoulli's
397 principle, as fluid speed increases, fluid pressure drops. Therefore, fast moving air generates a
398 lower pressure than still air. It is possible that this burst of wind could create a vacuum,
399 suctioning accumulated gases out of the column airspace, and pointing towards a potential
400 mechanism for the induction of fluxes across the plant-atmosphere interface in snags. In fact,
401 Bernoulli's principle has been demonstrated to induce gas flows in other non-living structures
402 built from biological activity (Vogel et al. 1973), and low-air-pressure events, such as those
403 associated with storm systems, can induce CH₄ fluxes across both the soil- (Clements and
404 Wilkening 1974) and water-atmosphere (Mattson and Likens 1990) interface.

405 Finally, from a source-strength perspective, little is known about 1) diurnal and/or
406 seasonal fluctuations in the magnitude of CH₄ and CO₂ fluxes across the plant-atmosphere
407 interface in snags and 2) the current spatial extent of ghost forests within coastal landscapes.
408 However, it is clear that ghost forest landscapes will become increasingly common in the future,
409 as stressors associated with global climate change represent a present and imminent threat to
410 coastal wetlands. This is particularly true for wetlands of the United States' Atlantic and Gulf

411 coasts, where an estimated 58,000 km² of land lies less than 1.5 m above sea level (Titus and
412 Richman 2001).

413 *Water-Atmosphere greenhouse gas fluxes*

414 These data also provided supporting evidence for the quantitative importance of water-
415 atmosphere carbon fluxes from wetland ecosystems, an often overlooked component of gas
416 transport processes in lentic and lotic freshwater systems (Bastviken et al. 2011; Poindexter et al.
417 2016; Stanley et al. 2016). Recent experimental evidence indicates that carbon fluxes across the
418 water-atmosphere interface are likely a dominant transport pathway in wetland systems,
419 especially during ebullition events (Walter et al. 2006; DelSontro et al. 2014) and over nighttime
420 hours (Poindexter et al. 2016), a window in which greenhouse gas flux measurements are rarely
421 completed. In the present study, water-atmosphere fluxes of CH₄ and CO₂ were significantly
422 higher (ca. two orders of magnitude and 4× respectively) than fluxes across the plant-atmosphere
423 interface. For CH₄, water-atmosphere fluxes were consistently higher than those measured at
424 similar sites in TOWeR in July 2012 [Helton et al. (2014), CO₂ fluxes were not reported in this
425 study]. In addition, water-atmosphere fluxes of CH₄ were an order of magnitude higher than
426 mean soil-atmosphere fluxes measured in a multi-year study at TOWeR; for CO₂, the ranges of
427 water- and soil- atmosphere fluxes were within the same order of magnitude and overlapped
428 Morse et al. (2012). Though the focus of the present study was not necessarily hydrodynamic
429 transport processes, our data indicate that water-atmosphere flux of CH₄ and CO₂ may be a
430 quantitatively important pathway in the atmospheric flux of greenhouse gases from wetland
431 ecosystems.

432 *Conclusions*

433 Results from this study have identified standing dead trees as a previously unrecognized
434 pathway in the flux of CH₄ and CO₂ from wetland ecosystems. However, several key questions
435 remain regarding 1) the ultimate source of these carbon gases, 2) the abiotic and biotic controls
436 on the magnitude and direction of this flux, 3) the mechanisms that induce this flux, and 4) the
437 importance of this pathway relative to other sources at the landscape level. Over time, knowledge
438 regarding the mechanisms that induce and control carbon fluxes from snags could lead to the
439 development of management strategies for decreasing greenhouse gas emissions from wetlands,
440 as suggested in McNerney and Helton (2016). Though stocks of deadwood in forests are
441 notoriously difficult to estimate (Woodall et al. 2012), globally stressors associated with global
442 climate change (i.e. sea level rise, saltwater incursion, and extreme episodic events such as
443 intense drought or hurricanes) are already leading to the conversion of large swaths of coastal
444 forested wetlands to ghost forest landscapes, increasing the spatial footprint of snags in coastal
445 landscapes (Gilbert et al. 2012; Melillo et al. 2014) and the quantitative importance of standing
446 dead trees in wetland carbon dynamics.

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659 **Table 1** Plant-atmosphere and water-atmosphere carbon fluxes at TOWeR in July 2016. Values are reported as mean±standard error
 660 and only represent chambers that met quality control criteria as outlined in the methods. Sample sizes are given in parentheses
 661

	CH₄ (mg m⁻² h⁻¹)		CO₂ (mg m⁻² h⁻¹)	
	Plant-Atmosphere	Water-Atmosphere	Plant-Atmosphere	Water-Atmosphere
Production	0.4±0.1 (<i>n</i> =5)	30.9±6.1 (<i>n</i> =8)	114.6±23.8 (<i>n</i> =7)	343.9±16.1 (<i>n</i> =8)
Consumption	-0.6±0.3 (<i>n</i> =3)	–	-29.6 (<i>n</i> =1)	–

662

663 **Figure Captions**

664 **Fig. 1** Site map of the Timberlake Observatory for Wetland Restoration (a) in relation to the state
665 of North Carolina and the Albemarle-Pamlico Peninsula (b). The circle in panel 1a marks the
666 location of the ghost forest stand where plant-atmosphere greenhouse gas fluxes were measured.
667 The white square denotes the location of the chambers used to measure water-atmosphere
668 greenhouse gas fluxes. Both panels were created using Google Earth; image is copyrighted by
669 DigitalGlobe (2016)

670 **Fig. 2** Representative ghost forest landscapes at the Timberlake Observatory for Wetland
671 Restoration in Tyrrell County, North Carolina and field equipment used to measure trace
672 greenhouse gases: a) deepwater site for the measurement of plant-atmosphere fluxes, b) ghost
673 forest where water-atmosphere flux chambers were deployed, c) static flux chambers for plant-
674 atmosphere gas fluxes, and d) static flux chambers for water-atmosphere gas fluxes

675 **Fig. 3** CH₄ (a) and CO₂ (b) concentrations in trunk airspace compared to the ambient air
676 immediately outside of the trunk at 30 cm, 80 cm, and breast height (1.37 m). Values given as
677 mean±standard error. Asterisks indicate significantly elevated greenhouse gas concentrations
678 within the trunk airspace compared to the ambient air immediately outside of the trunk at a given
679 height. The solid line represents the mean greenhouse gas concentration in ambient air at the site,
680 whereas the dotted lines indicate the 95% confidence interval of the mean

