1   **Title:** Deep rooting and global change facilitate spread of invasive grass

2   **Running head:** Deep rooting facilitates plant invasion

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19   **Type of paper:** Original research

20

21   **Abstract**

22   Abiotic global change factors such as rising atmospheric CO_2, and biotic factors such as exotic

23   plant invasion, interact to alter the function of terrestrial ecosystems. An invasive lineage of the

24   common reed, *Phragmites australis,* was introduced to the North America over a century ago,

25   but the belowground mechanisms underlying *Phragmites* invasion and persistence in natural

26   systems remain poorly studied. For instance, *Phragmites* has a nitrogen (N) demand higher than

27   native plant communities in many of the ecosystems it invades, but the source of the additional N

28   is not clear. We exposed introduced *Phragmites* and native plant assemblages, containing

29   *Spartina patens* and *Schoenoplectus americanus,* to factorial treatments of CO_2 (ambient or +300

30   ppm), N (0 or 25 g m^{-2} y^{-1}), and hydroperiod (4 levels), and focused our analysis on changes in

31   root productivity as a function of depth and evaluated the effects of introduced *Phragmites* on

32   soil organic matter mineralization We report that non-native invasive *Phragmites* exhibits a

33   deeper rooting profile than native marsh species under all experimental treatments, and also

34   enhanced soil organic matter decomposition. Moreover, exposure to elevated atmospheric CO_2

35   induces a sharp increase in deep root production in the invasive plant. We propose that niche

36   separation accomplished through deeper rooting profiles circumvents nutrient competition where

37   native species have relatively shallow root depth distributions; deep roots provide access to

38   nutrient-rich porewater; and deep roots further increase nutrient availability by enhancing soil

39   organic matter decomposition. We expect that rising CO_2 will magnify these effects in deep-

40   rooting invasive plants that compete using a tree-like strategy against native herbaceous plants,

41   promoting establishment and invasion through niche separation.

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Introduction

Human-induced global change is known to facilitate biological invasions while threatening ecosystem services (Vitousek et al. 1997, Dukes and Mooney 1999, Sorte et al. 2013). The economic impacts of invasive species and threats to biodiversity have resulted in losses exceeding $120 billion per year in the United States alone (Pimentel et al. 2005). Global change factors including rising atmospheric CO_2 concentrations, increased nitrogen (N) availability, and changes in precipitation have been demonstrated to favor introduced plant species (reviewed in Sorte et al. 2013). Invasion studies often provide insights into our understanding of landscape spread of the invader (Theoharides and Dukes 2007). In contrast, little is known about the effects of global change factors on the processes that lead to the establishment of self-sustaining plant populations and to expansion and invasion at the landscape level. Without such information, it is difficult to determine the extent to which global changes promote plant invasions in a rapidly changing world.

The ecosystem effects of changes in resource availability are more dramatic when expressed through changes in plant species composition than solely through physiological changes (Langley and Megonigal 2010, Hooper et al. 2012). Nowhere are biological-physical ecosystem feedbacks more important than in tidal wetlands, where plants produce organic matter and trap sediments that allow the soil surface to maintain a constant elevation relative to sea level (Kirwan & Megonigal 2013). Therefore, the introduction of new species or genetic lineages, such as introduced *Phragmites australis* in North America (Saltonstall 2002), *Spartina alterniflora* and *S. densiflora* on the Pacific Coast of North America (Daehler and Strong 1996), *S. anglica* in Europe (Nehring and Hesse 2008) and *S. alterniflora* in China (Qin and Zong 1992, Wang et al. 2006), that exhibit unique suites of physiological traits (Mozdzer and Zieman 2010,

67 Mozdzer and Megonigal 2012, Mozdzer et al. 2013, Caplan et al. 2014, Koop-Jakobsen and

68 Wenzhofer 2015), could have dramatic consequences for the geomorphology of coastal

69 wetlands. Successful invasion ultimately represents the ability of an invasive species to establish

70 among and outcompete native species. Two dominant factors that govern plant establishment and

71 competition in tidal wetlands are flooding tolerance and nutrient supply. Spatial variation in

72 nutrient availability and soil elevation (relative to flooding water) results in distinct plant

73 community zonation that reflects the combined effects of flood stress-tolerance and nutrient

74 competition in tidal marshes (Bertness and Ellison 1987, Ewanchuk and Bertness 2004). The

75 stress gradient hypothesis suggests that competition for nutrients is most intense in low flood-

76 stress areas of tidal marshes such as high elevation zones (Bertness and Callaway 1994).

77 Anthropogenic N pollution has been shown to favor invasive *Phragmites* by ameliorating

78 competitive effects (Bertness et al. 2002), but the success of this invasive species cannot solely

79 be attributed to N pollution because *Phragmites* also invades and dominates relatively pristine

80 tidal marsh habitats (McCormick et al. 2010) where *Phragmites* N demand exceeds the N supply

81 of the native ecosystem (Windham and Ehrenfeld 2003, Mozdzer and Zieman 2010). Moreover,

82 *Phragmites* expansion has accelerated in areas that have experienced decadal-scale declines in

83 nutrient loading (McCormick et al. 2010, Ruhl and Rybicki 2010). Thus, understanding the

84 mechanisms by which *Phragmites* acquires N to promote establishment and growth is a

85 significant challenge to advancing research on invasive species.

86   Important insights on how plants satisfy nutrient limitation have come from studies of

87 plant responses to elevated CO_2. Elevated CO_2 creates plant demand for soil nutrients – often N -

88 - that lead to progressive N limitation in the absence of either an external N source (van

89 Groenigen et al. 2011), or biogeochemical feedbacks that increase the N supply (Carney et al.

4

90   2007). Elevated CO_2 is known to stimulate deep root production in trees (Iversen 2010), where

91   promotion of root growth at depth is thought to serve as a nutrient foraging strategy to sustain

92   plant productivity in the face of enhanced nutrient demand (McKinley et al. 2009, Norby et al.

93   2010). However, an increase in deep root growth has not been observed in natural grasslands in

94   ecosystem-scale CO_2 experiments (Arnone et al. 2000, Iversen 2010). In contrast to CO_2 effects,

95   N typically reduces belowground biomass allocation and favors aboveground production

96   (Langley et al. 2009, Deegan et al. 2012). To understand the effects of several interacting global

97   change factors on plant invasion, we subjected two plant community types--native grass-sedge

98   and introduced *Phragmites*--to manipulations of atmospheric CO_2, soil N availability, and soil

99   surface elevation (a proxy for water table depth) in a factorial experiment. We focused on the

100   depth distribution of roots as a primary response for three reasons. First, a deeper rooting

101   distribution may reduce the importance of nutrient competition in the typical rooting zone.

102   Second, the introduction of oxygen or carbon-rich exudates in deep, largely root-free soil may

103   stimulate nutrient mineralization. Third, deeper rooting may influence the rate of soil organic

104   matter accumulation, which we propose initiates a positive feedback loop stimulating plant

105   invasion. We present a conceptual model of plant invasion that can be applied broadly to

106   wetland and grassland ecosystems, and couples biological invasions to changes in plant-mediated

107   biogeochemical cycles.

108   **Methods**

109   To evaluate how rooting depth varied between native and introduced plant communities,

110   a mesocosm experiment was performed in a brackish tidal creek within the Rhode River

111   (Kirkpatrick marsh: 38.8742°N, 76.5474°W), a sub-estuary of Chesapeake Bay. The facility is

112   part of the Smithsonian Global Change Research Wetland (GCREW) of the Smithsonian

113   Environmental Research Center in Edgewater Maryland. The site experiences a 44cm mean tidal

114   range, with a mean salinity of 10ppt (4-15 ppt range). The experimental design consisted of six

115   replicated "marsh organs", each enclosed by an open-top chamber, the design of which was

116   previously described in detail (Langley et al. 2013). Atmospheric CO_2 was maintained at either

117   ambient concentrations, or increased to ambient +300 ppm CO_2 (n=3) through the addition of

118   pure CO_2 into air blown into the floating chamber. Within each marsh organ, there were six

119   elevations or water table depths (+37 cm, +17cm, +2 cm, -8 cm, -18 cm, & -28 cm relative to

120   mean higher high water (MHHW) measured by a tidal gauge at our site. Elevations were chosen

121   to span the current range of marsh elevation (+37cm to +2cm) and simulating future sea levels (-

122   8 to -28). At each elevation, there were eight mesocosms, four containing *Phragmites* and four

123   containing the native mixed plant community of *Schoenoplectus americanus* and *Spartina patens*

124   (~1:1 at initial planting) (N=288). Half the mesocosms in each treatment received N addition

125   (NH_4Cl) equivalent to 25 g N m^{-2} y^{-1} (1.78 moles N m^{-2} $y^{-1)}$. Mesocosms were 72 cm tall, 10 cm

126   in diameter, and filled with reed-sedge peat (Baccto ® Peat, Michigan Peat Company, Houston,

127   TX) with free vertical drainage. Reed-sedge peat is a similar approximation to the organic soils

128   in our wetland that are > 80% organic. *Phragmites* plants were grown from seed to mimic the

129   process of establishment and invasion. Our goal in using seedlings was to assess how

130   *Phragmites* establishment can vary as a function of water level, CO_2, and nitrogen. Seeds were

131   germinated using standard techniques (Kettenring and Whigham 2009) in March, and transferred

132   to mesocosm pots in May with four seedlings per mesocosm and acclimated to 8 ppt salinity

133   water over the course of two weeks before deployment. Seeds were collected from four spatially

134   distinct populations at GRCEW, and one seedling from each population (n=4) was planted in

135   each mesocosm. The native plant community consisted of *Schoenoplectus americanus* and

136   *Spartina patens,* which were grown from rhizome fragments and plugs in the same year and

137   acclimated similarly (Langley et al. 2013). After one growing season in the *Phragmites*

138   experiment and two growing seasons in the native plant community experiment, total

139   belowground biomass was determined by destructively harvesting the belowground portion of

140   each *Phragmites* mesocosm (n=144) and in two of three replicates in the native- plant

141   assemblage mesocosms (N=98).   Plants did not survive in the lowest two elevations (-18 cm and

142   -28 cm) in any of the experimental plant communities, so these mesocosms were excluded from

143   the analysis. Additionally, two intact soil columns per treatment group were randomly selected

144   and were cut into 10-cm segments to evaluate the distribution of belowground biomass. The soils

145   were carefully washed away to recover roots and rhizomes, which were separated and oven-dried

146   to constant mass. Plant rooting depth distributions were fit to the β-distribution model of Gale

147   and Grigal (1987) in SAS (version 9.3) using proc NLIN. To evaluate the fixed effects of plant

148   community, CO_2, N, and water table depth on rooting depth distribution (the β parameter) we

149   first performed a 4 way ANOVA in SAS (proc GLM). Given the overwhelming effects of plant

150   community on rooting depth (Table 1), we performed subsequent three-way ANOVAs within

151   each plant community to better understand how each plant community and changes in resources

152   affect belowground biomass allocation (Table 2). To determine the effects of plant community,

153   CO_2, N, and water table depth on belowground biomass, data were analyzed using replicate

154   means within chamber using proc MIXED, with chamber as the random effect by plant

155   community.

156   We also examined how *Phragmites* affected decomposition of soil organic matter from

157   deep (below 50 cm) soil horizons that are relatively unexploited by shallow-rooting native plants.

158   To do so, a second mesocosm experiment was conducted in the same "marsh organ" facility in

159   2012. In this case, mesocosms were filled with homogenized soil collected from the study site at

160   a 50-100 cm depth with a $\delta^{13}C$ of -14.4‰, reflecting inputs from dominant C_4 grasses. As such,

161   it was possible to distinguish CO_2 generated by respiration of recent *Phragmites* photosynthate

162   (C_3-plant respiration and microbial respiration of recent C_3-plant litter and rhizodeposits) from

163   microbial respiration of C_4-derived soil organic matter using a stable carbon isotope partitioning

164   model (Wolf et al. 2007). In this experiment, mesocosms were placed at +17 cm, +2 cm and -18

165   cm relative to MHHW. At each elevation, 5 planted (treatment) and 5 unplanted (control)

166   mesocosms were deployed. There was poor survival at the -18 cm elevation, and these data were

167   excluded from analysis. Quantification of soil organic matter decomposition followed Mueller et

168   al (2015). Briefly, static opaque PVC chambers were placed on the mesocosms and sealed. The

169   headspace was flushed with CO_2-free air to remove atmospheric CO_2 and sampled through a

170   rubber septum after 4 h of incubation to reach $[CO_2] \geq 1000$ ppmv. Gas samples were transferred

171   into evacuated Labco exetainers (Labco Ltd, High Wycombe, UK) and analyzed for $\delta^{13}CO_2$ and

172   $[CO_2]$ at the UC Davis Stable Isotope Facility. The contributions of plant and soil organic matter

173   derived CO_2 to total CO_2 flux were calculated after equations in Fu and Cheng (2002) using the

174   $\delta^{13}C$ of the CO_2 emitted from control mesocosms as the soil end member (-16.8‰) and the $\delta^{13}C$

175   of dried plant tissue as the plant end member (-26.5‰), and data were analyzed by ANOVA in

176   STATISTICA 10 (StatSoft Inc).

177   We also assessed mineral N concentration throughout the depth profile to determine how

178   N availability varies with depth in the native marsh at the GCREW. These data were collected

179   from a native plant community exposed to a full cross of two manipulations, two levels of CO_2

180   (ambient and 700 ppm) and two levels of N (ambient and ambient+25 g m^{-2} yr^{-1}). Each of the

181   four treatments had five replicates for a total of 20 chambers as described in Langley et al.

182 (2009). Porewater was sampled from triplicate sampling wells at each of three depths: 15, 30 and

183 75 cm, Porewater was sampled every 1 to 3 months throughout the growing season and analyzed

184 for ammonium concentration (Keller et al. 2009). In these anaerobic soils, porewater nitrate is

185 typically below detection limits and does not contribute substantially to total mineral N

186 availability. We analyzed porewater NH_4^+ availability averaged over three growing seasons

187 (2006-2008) using a three-way ANOVA (CO_2 x N x depth, n=5) in JMP (Version 11.0, SAS

188 Institute).

189 **Results**

190 *Belowground productivity*

191   Both water table depth and plant community significantly affected root depth distribution

192 (β distribution *sensu* Gale & Grigal 1987) (four-way ANOVA, elevation & type effects; Table

193 1), with elevated CO_2 causing root distribution to shift deeper in the invasive plant community at

194 high elevations (plant assemblage $\times$ CO_2 $\times$ elevation effect; P=0.040) (Figure 1 & Table 1). At

195 all elevations, *Phragmites* had deeper root depth distributions than the native plant community

196 (Figure 1 & Table 1), and N had no effect on root depth distribution (Table 1), but there was a

197 non-significant trend toward a shallower rooting profile (Figure 2a). In the native plant

198 community, more than 90% of the biomass was found in the top 30 cm, regardless of elevation;

199 whereas this was only the case for the lowest elevation in *Phragmites* (Figure 1).

200   Elevated CO_2 affected root depth distribution only in *Phragmites* (CO_2 effect, p= 0.0127,

201 Table 2), but had no effect in the native plant community (CO_2 effect, p= 0.2325, Table 2). In the

202 *Phragmites* community, elevated CO_2 had the greatest effects at the highest and lowest

203 elevations in (CO_2 $\times$ elevation effect, p=0.046, Figure 1, Table 2). *Phragmites* had the deepest

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204 root depth distribution at the highest elevation (+37cm), distribution with more than 50% of its

205 biomass below 20 cm in depth, in contrast to the native plant community that had < 30% of its

206 biomass below 20 cm in depth. These CO_2-induced effects on rooting distribution persisted in

207 elevations two (+17 cm) and three (+2 cm), with the invasive plant rooting significantly deeper

208 in all but the lowest elevation (i.e. wettest) treatments (Figure 1, Table 1).

209   Carbon dioxide increased belowground biomass in the invasive *Phragmites* community

210 (CO_2 effect, p=0.030 Tables 4 & 5), with no effect of CO_2 in the native plant community (CO_2,

211 p=0.83), (Fig 2a, Table 4 & 5). Nitrogen increased total belowground biomass in both the native

212 and *Phragmites* plant communities (N effect, p=0.006 & p<0.001, respectively, Table 4), but

213 increased flooding experienced as lower relative elevation significantly decreased belowground

214 biomass in both plant communities (elevation effect, p<0.001,Table 4), with the native plant

215 community exhibiting greater belowground biomass given the extra year of growth than

216 *Phragmites* (Table 3).

217 *Soil organic matter decomposition*

218       $\delta^{13}C$ of emitted CO_2 differed significantly between planted (high elevation: mean $\pm$ SD =

219 -18.4 $\pm$ 1.0‰; mid elevation: -20.08 $\pm$ 1.4‰) and unplanted mesocosms (high elevation: mean $\pm$

220 SD = -16.8 $\pm$ 0.4‰; mid elevation: -16.8 $\pm$ 0.17‰; p<0.001), reflecting the fact that CO_2 from

221 respiration of recent photosynthate (plant respiration or microbial respiration of recent plant litter

222 or rhizodeposits) was ^{13}C-depleted compared to CO_2 from microbial respiration of soil organic

223 matter. Soil organic matter decomposition rate was significantly enhanced in the presence of

224 *Phragmites* (p<0.0001), but decomposition rates did not vary by elevation (p=0.58). At the

225 highest elevation in the second experiment (+17 cm), the decomposition rate was far more rapid

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226   in the presence of *Phragmites* (mean ± SD = 2.84 ± 0.59 g C m^{-2} d^{-1}) than in plant-free

227   mesocosms (1.03 ± 0.19 g C m^{-2} d^{-1}) (*post hoc* Tukey HSD, p<0.001), and the same pattern

228   occurred at the mid (+2 cm) elevation (2.70 ± 0.57 g C m^{-2} d^{-1} vs 0.93 ± 0.05 g C m^{-2} d^{-1}) (*post*

229   *hoc* Tukey HSD, p<0.001) (Figure 3). Due to post-photosynthetic fractionation processes, the

230    $\delta^{13}C$ of plant tissue can diverge from the $\delta^{13}C$ of the respired CO_2 (Bowling et al. 2008, Zhu and

231   Cheng 2011). However, the magnitude of this effect in *Phragmites* is <1‰ as determined in

232   plants from the adjacent marsh platform (compare Mueller et al. 2016 for methodological detail),

233   and therefore   too small to change the conclusion that plants greatly enhanced soil organic

234   matter decomposition rate.

235   *Porewater nutrient analysis*

236   Porewater ammonium availability in plots dominated by native plants at the Smithsonian

237   GCREW increased sharply with depth (three-way ANOVA, depth, p<0.0001), with

238   concentrations over ten times greater at 80 cm in depth than at 20 cm depth. Nitrogen

239   fertilization increased porewater [NH_4^+] by 9-72% at 40 and 80 cm (three-way ANOVA, depth x

240   N, p=0.0257) (Figure 2B). Porewater ammonium availability decreased with elevated CO_2

241   (three-way ANOVA, CO_2, p = 0.0220) and increased with N treatment at the 20 cm depth (*post*

242   *hoc* Student's t, p<0.005).

Discussion

244   Previous studies have noted that the high N demand of invasive *Phragmites* exceeds N

245   supply based on nutrient budgets (Meyerson et al. 2000, Windham and Meyerson 2003).

246   However, these studies have not considered the possibility that *Phragmites* can access N in pools

247   below the rooting depth of native plants. In this system, native plants have a relatively shallow

248 rooting depth distribution regardless of their zonation, with > 90% of the mass in the top 20 cm

249 (Saunders et al 2006, Figure 1), while porewater N concentrations increase dramatically with

250 depth below the rooting zone of the native plant community (Figure 2). This pattern suggests that

251 deep-rooting plants, such as *Phragmites,* have access to a large N pool, free of competition with

252 native plants. Indeed, data from our research group has demonstrated that *Phragmites* exceeds

253 our reported rooting depths (>3 meters) and actively takes up N at depths exceeding 70 cm,

254 whereas active N uptake by the native plant community occurs within the top 20 cm of the soil

255 profile (Meschter 2015). Invasive *Phragmites* also exceeds the rooting depth of many native salt

256 marsh plants in New England (Moore et al. 2012), suggesting that our observations can be

257 generalized to other tidal marshes invaded by *Phragmites*.

258   In addition to accessing unexploited plant-available soil nutrients, deep rooting may also

259 increase the soil N supply by enhancing N mineralization from soil organic matter. We found

260 that the decomposition of relatively old soils recovered from below the native community

261 rooting zone (50-100 cm) increased by approximately three-fold in the presence of *Phragmites*

262 roots as compared to plant-free soils. Recent work of our lab group demonstrated that priming

263 effects in tidal wetland systems are largely driven by aboveground biomass (Mueller et al. 2016).

264 We acknowledge, that mesocosms may have affected biomass production and thus indirectly

265 also affected the magnitude of observed priming effects. However, *Phragmites* biomass in this

266 experiment was relatively poorly developed with total belowground biomass <6 g DW

267 mesocosm^{-1} and aboveground biomass <5 g DW mesocosm^{-1} at both elevations. Therefore, we

268 expect priming effects to be even larger under mature clones in a field setting. The presence of

269 roots can greatly accelerate decomposition of recalcitrant soil organic (Fig 3) matter by

270 "priming" the microbial community with energy-rich carbon sources (Cheng 2009) or by

271   introducing oxygen into anoxic soil layers (Wolf et al. 2007). Because N, P and other nutrients

272   are also released in the mineralization process, we propose that deep roots increase the nutrient

273   supply through enhanced mineralization of soil organic matter, which would otherwise remain

274   highly inert. Thus, enhanced rates of microbial activity may mineralize buried nutrients, making

275   them available for plant uptake and transport to the soil surface, where they recycle internally to

276   further increase productivity. The net effect of these changes may be a positive feedback to

277   future *Phragmites* growth and invasion. Although we demonstrated that *Phragmites* has the

278   potential to strongly accelerate the decomposition of old, recalcitrant organic matter in the

279   present study, future research will have to investigate the magnitude of priming effects at

280   different soil depths in order to demonstrate deep-root priming.

281   Our results suggest differences in rooting depth are likely ontogenic, and will likely be

282   magnified in a field setting. In our experiment, we used *Phragmites* seedlings, and found that

283   from the onset, *Phragmites* rooted deeper than the native plant community under nearly every

284   treatment combination. Although the native plant community had greater absolute belowground

285   biomass than the *Phragmites* community, this was likely due to the additional season of growth

286   (1 year – *Phragmites* vs. 2 years – native), and this additional biomass in the native community

287   was always in the top 20 cm of the soil profile. It is likely that the rooting patterns observed in

288   *Phragmites* would strengthen when left to mature in the field and increase its stature several-fold

289   in both height and mass (Windham and Lathrop 1999, Mozdzer et al. 2013, Caplan et al. 2015).

290   In contrast, the native mesocosms already reflected plant densities and biomass dimensions that

291   are similar to those found in the field (Langley et al. 2013). As such, our data suggest inherent

292   developmental differences in rooting depth that promote early establishment of *Phragmites*.

13

293   Deep rooting may have other important consequences for invasion biology. Deep rooting

294   may allow invasive plants with unusually high N demand, such as *Phragmites* (Windham and

295   Meyerson 2003), to become established in undisturbed natural ecosystems. In the present study,

296   *Phragmites* seedlings grown in the absence of interspecific competition developed root systems

297   that were deeper than native species in one growing season. Because *Phragmites* often

298   establishes by seed (McCormick et al. 2010), we suggest that new *Phragmites* seedlings may be

299   able to escape intense nutrient competition through niche separation in a relatively short period

300   of time following establishment. Once the plant becomes established, clonal integration may

301   facilitate expansion (Amsberry et al. 2000) into lower elevation areas by subsidizing clones with

302   soil nutrients derived from deep sources. Indeed, *Phragmites* populations at the Smithsonian

303   GCREW (our study site) established at relatively high elevation creek banks, and are presently

304   invading marshes of lower elevation (Mozdzer *personal observation*). This hypothesis is also

305   supported by literature from other sites that describe *Phragmites* establishing at higher

306   elevations, and then spread vegetatively into lower elevations of the marsh (Windham and

307   Lathrop 1999, Bertness et al. 2002). Once *Phragmites* becomes established at higher elevations

308   through niche separation, invasion may progress through competitive exclusion because of

309   *Phragmites'* tall stature (>3 m in height), which effectively excludes native competitors by

310   intercepting light both in the growing plant canopy and the thick understory litter layer

311   (Holdredge and Bertness 2011). We acknowledge that N fixation by invaders can also influence

312   invasion (Ehrenfeld 2003), however, there is limited evidence of N fixation by *Phragmites* and in

313   this instance, N-fixation activity is lower than native competitors (Burke et al. 2002)

314   We propose that establishment and subsequent invasion of *Phragmites* is aided by

315   inherent species-level differences in access to deep soil nutrients and escape from nutrient

316 competition, which can occur at the seedling stage. Our data further suggest that these

317 differences in rooting depth will be enhanced by elevated CO_2, which significantly deepened the

318 root depth distribution in invasive *Phragmites,* but not the native plant community. Although a

319 deepening of the root zone under elevated CO_2 has been well-documented for woody plants

320 (Arnone et al. 2000, Iversen 2010) given higher water and/or nutrient demands in forested

321 ecosystems, our findings are novel for non-woody plants. Our data also suggest that rising CO_2

322 concentrations possibly have played a role in the spread of *Phragmites* in the past few decades,

323 and that rising CO_2 concentrations will also enhance future invasions. Indeed NPP is 2-3 times

324 greater in *Phragmites* dominated ecosystems at GCREW when exposed to near future

325 concentrations of CO_2 (700 ppmv) or N pollution, in contrast to the native mixed plant

326 community (C3-C4) where the effects of global change on NPP are minimal (Caplan et al 2015).

327 To the extent that deep rooting response enhances nutrient supply, deep rooting may also help to

328 maintain the growth response of *Phragmites* to elevated CO_2 over long periods of time, avoiding

329 the tendency of CO_2-driven growth responses to diminish over time because of progressive N

330 limitation (Luo et al. 2004).   We acknowledge that N competition was not directly assessed in

331 this study, but differences in rooting depth may alleviate nutrient competition in the shallow

332 rhizosphere. We also have no evidence of root zone deepening in the native C_3-C_4 plant

333 community in our mesocosms (Fig 2), suggesting that these mechanisms exhibited are plausible.

334   Enhanced root productivity at lower elevations with elevated CO_2 may also enhance the

335 ecological range where *Phragmites* establishes in the near future. Currently, *Phragmites*

336 establishes in the high elevations of a tidal marsh (Bertness et al. 2002), which we hypothesize is

337 facilitated by deep rooting and access to untapped nutrients, in a zone typified by intense nutrient

338 competition (Bertness et al. 2002). Our data also suggest that elevated CO_2 can alleviate abiotic

339   flooding stress, potentially changing plant community zonation as predicted by the stress

340   gradient hypothesis (Bertness and Ellison 1987, Ewanchuk and Bertness 2004). Specifically,

341   elevated CO_2 enhanced root productivity in *Phragmites* at our lowest elevation, presumably

342   increasing its competitive ability (Fig 1c-d). Therefore, changes in CO_2 may increase the

343   frequency and location of *Phragmites* invasion as it become more competitive at lower

344   elevations*,* where it is currently excluded due to abiotic flooding stresses including salinity and

345   sulfide (Chambers et al. 1998, Chambers et al. 2003).

346   Changes to root depth distributions may also influence patterns of vertical elevation gain.

347   Elevation gain in tidal wetlands is highly dependent on root growth (Kirwan and Megonigal

348   2013), particularly in sediment-poor environments (Langley et al. 2009). The combination of

349   high rates of root production and deep, anoxic soils where decomposition is slow may help

350   explain limited evidence that *Phragmites*–dominated ecosystems exhibit greater surface

351   elevation gain than those dominated by native species (Rooth et al. 2003). As an ecosystem

352   engineer, the ability to build soils vertically at greater rates than native plants provides a

353   mechanism for the invasive plant to keep pace with rising seas.   Elevated CO_2 significantly

354   increased belowground growth in *Phragmites* (Fig 2), most likely in response to a large increase

355   in photosynthesis (Caplan et al 2015). Previous studies have demonstrated a correlation between

356   increases in root growth and elevation gain (Langley et al. 2009), suggesting that *Phragmites*-

357   dominated marshes may also be better adapted to rising sea levels than native plant-dominated

358   marshes given the potential for greater belowground growth. However, this must be interpreted

359   cautiously without data on accretion rates, subsidence, and mineral inputs into the ecosystem.

360   Finally, it is possible that root zone deepening may also be a mechanism by which *Phragmites*

361   may access less saline ground waters, thereby also allowing Phragmites to invade more saline

362   habitats, that are typically resistant to invasion (Chambers et al. 1998, Chambers et al. 2003).

363   **A conceptual model of plant invasion**

364   We propose that invasion by species with deep root-depth distributions fundamentally

365   alters biogeochemical processes, creating a positive feedback that intensifies plant invasion, and

366   that these feedbacks are enhanced by elevated CO_2. We put forward a conceptual model that

367   illustrates how deep rooting causes a positive feedback that further promotes invasion, and

368   accounts for how these feedbacks are intensified by rising CO_2 (Figure 4). Initially, niche

369   separation via deep rooting during establishment provides *Phragmites* access to an untapped pool

370   of nutrients, thereby promoting establishment. Next, priming microbial decomposition processes

371   in the rhizosphere further enhances nutrient availability, alleviating nutrient limitation of plant

372   growth and facilitating invasion into less hospitable, low-elevation areas by clonal expansion.

373   The success of the invading plant is furthered by competitive exclusion via competition for light.

374   As *Phragmites* invades the ecosystem, we propose that the combination of greater root

375   productivity and deep root production promotes soil elevation gain by adding soil volume, which

376   further improves the growth of *Phragmites* (Figures 1, 2). In addition, by bringing formerly

377   buried and inaccessible N to the soil surface where it can be recycled through uptake, senescence

378   and decomposition (Megonigal and Neubauer 2009), *Phragmites* is self-fertilizing the ecosystem

379   and amplifying its own growth.

380   We suggest that rooting depth is a key factor that drives plant invasion but has eluded

381   scientists due to the difficulty in accurately assessing belowground growth, particularly in

382   sensitive, experimental research plots. Most studies rely solely on aboveground responses;

17

383 however perennial invasive grasses such as *Phragmites* have below- to aboveground biomass

384 ratios that exceed 3:1. It is not known how common deeper rooting profiles are among other

385 invasive grasses, but invasive *Phragmites* rooting profiles are more similar to woody functional

386 types such as shrubs and trees (Jackson et al. 1996), which commonly out-compete grasses as

387 they invade into grasslands (Rundel et al. 2014). Root zone deepening by shrubs similarly fills an

388 open niche or provides access to water. In contrast to grasslands, deep rooting in wetlands

389 requires specialized architecture to deal with anoxic soils. *Phragmites* is one of the few wetland

390 plants that employs pressurized gas flow to enhance oxygen transport to the rhizosphere and

391 simultaneously remove rhizospheric CO_2, methane, and toxic sulfides. Thus deep rooting may

392 prove to be a diagnostic trait of invasive wetland plant species, and may be associated with other

393 prominent invasive plants including *Agrypyron cristatum, Arundo donax, Phalaris arundinacea,*

394 and *Typha spp.* We put forward our conceptual model to be tested broadly in genetically diverse

395 ecosystems in wetland ecosystems and in grasslands where both deep-rooting grasses and shrubs

396 can alter biogeochemical pathways to promote species shifts.

397

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549

550

551   Table 1. Results of 4-way ANOVA to evaluate the effects of plant assemblage, nitrogen

552   pollution (N), elevated CO_2 (CO_2), and elevation (elevation) on the rooting depth distribution (β)

553   (*sensu* Gale & Grigal 1987). Significant effects on of type, elevation, and CO_2 on β distribution

554   are in bold font.

555

Source	DF	F Value	Pr > F
Plant assemblage	1	30.30	**<0.0001**
Elevation	3	16.30	**<0.0001**
CO_2	1	6.50	**0.014**
N	1	0.01	0.915
Elevation × CO_2	3	0.54	0.658
Elevation × N	3	0.80	0.503
CO_2 × N	1	0.20	0.654
Elevation × CO_2 × N	3	1.20	0.324
Plant assemblage × CO_2	1	0.39	0.534
Plant assemblage × N	1	1.06	0.310
Plant assemblage × Elevation	3	0.45	0.712
Plant assemblage × Elevation × CO_2	3	3.05	**0.040**

556

557

558   Table 2. Results of two-way ANOVA to evaluate the effects of elevated CO_2, and elevation

559   (water table depth) within each plant assemblage on the rooting depth distribution (β) (*sensu*

560   Gale & Grigal 1987). Significant effects on of elevation and CO_2 on β distribution are in bold

561   font.

562

Source	DF	F Value	Pr > F
Native assemblage			
Elevation	3	7.37	0.0011
CO_2	1	1.5	0.2325
Elevation X CO_2	1	1.16	0.346
Phragmites			
Elevation	3	11.03	<.0001
CO_2	1	7.26	0.0127
Elevation X CO_2	1	3.11	0.0454

563

564

565

566

567 Table 3. Effects of Elevated CO_2 and elevation (water table depth) relative to MHHW on mean
568 belowground biomass (g) ± (SE) in the native plant *and Phragmites* assemblages.
569

	Native assemblage				*Phragmites*			
Elevation	Ambient CO_2		Elevated CO_2		Ambient CO_2		Elevated CO_2	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
+37	47.5	2.2	33.9	7.4	26.0	2.1	32.5	3.1
+17	32.6	2.2	32.4	5.4	20.1	1.8	23.9	1.8
+2	13.7	7.9	25.0	6.1	11.1	1.4	15.4	2.4
-8	5.9	3.0	14.8	5.0	6.8	1.8	7.5	2.0

570
571

572   Table 4. Results of 3-way ANOVA to evaluate the effects of elevated CO_2, N, and elevation

573   (water table depth) on belowground biomass in the native and *Phragmites* plant assemblage

574   mesocosms. Significant effects are highlighted in bold font.

575
576

Source	DF	F Value	Pr > F
Native Community			
elevation	3	18.28	**<0.0001**
CO_2	1	0.04	0.838
N	1	10.64	**0.006**
Phragmites			
elevation	3	148.1	**<0.0001**
CO_2	1	5.22	**0.0304**
N	1	83.69	**<.0001**

577

578   **Figure Legends:**

579   Figure 1. Effects of elevated CO_2 on the mean proportion of belowground biomass of invasive

580   introduced *Phragmites australis* and the native plant assemblage (*Schoenoplectus americanus* &

581   *Spartina patens*) at elevations (A) +37 cm, (B) +17 cm, (C) +2 cm, and (D) -8 cm relative to

582   mean higher high water (MHHW) exposed to ambient or elevated CO_2. Seasonal mean water

583   table depth is indicated by the dashed line. β distribution values (*sensu* Gale & Grigal 1987) are

584   presented in each panel for each species and treatment. Significant effects of vegetation type

585   (Type) or elevated CO_2 on β are indicated in each panel.

586

587   Figure 2. (A) Effects of elevated CO_2 and nitrogen addition on belowground biomass

588   distribution of invasive *Phragmites australis* at an above MHHW where invasive *Phragmites*

589   *australis* typically establishes at the Smithsonian Global Change Research Wetland (our high

590   elevation scenario). Elevated CO_2 and CO_2+N cause root distribution to shift deeper in the soil

591   profile. (B) Mean porewater NH_4^+ (μM) availability at the Smithsonian Global Change Research

592   Wetland, demonstrating decreased porewater $[NH_4^+]$ with elevated CO_2, but increasing $[NH_4^+]$

593   with depth.

594

595   Figure 3. The influence of *Phragmites* plants on soil organic matter decomposition at high (+17

596   cm to relative to MHHW) and mid (+2 cm to relative to MHHW) water table depths. Presence

597   of *Phragmites* significantly increased decomposition rate ($p<0.0001$), and elevation had no effect

598   on decomposition rate ($p>0.05$). Post-hoc tests indicated *Phragmites* plants significantly

599   increased soil organic matter decomposition at both the high- (p=0.0003) and mid-water table

600   (p=0.0003) depths relative to unplanted controls.

601   Figure 4. Conceptual diagram illustrating our interpretation on how deep-rooting invasive plants

602   gain access to nutrients below the rooting depth of native plants. Priming of the microbial

603   community deep within the soil profile further increases nutrient availability, thereby increasing

604   plant growth and facilitating invasion into the ecosystem via competitive exclusion.

605   Belowground growth builds soils, engineering the ecosystem to be drier and more suitable for

606   *Phragmites* than the native plant community as *Phragmites* invades into lower elevations. Once

607   deep nutrients are brought to the surface, *Phragmites* self-fertilizes the ecosystem resulting in a

608   positive feedback loop of high productivity stimulating further invasion.
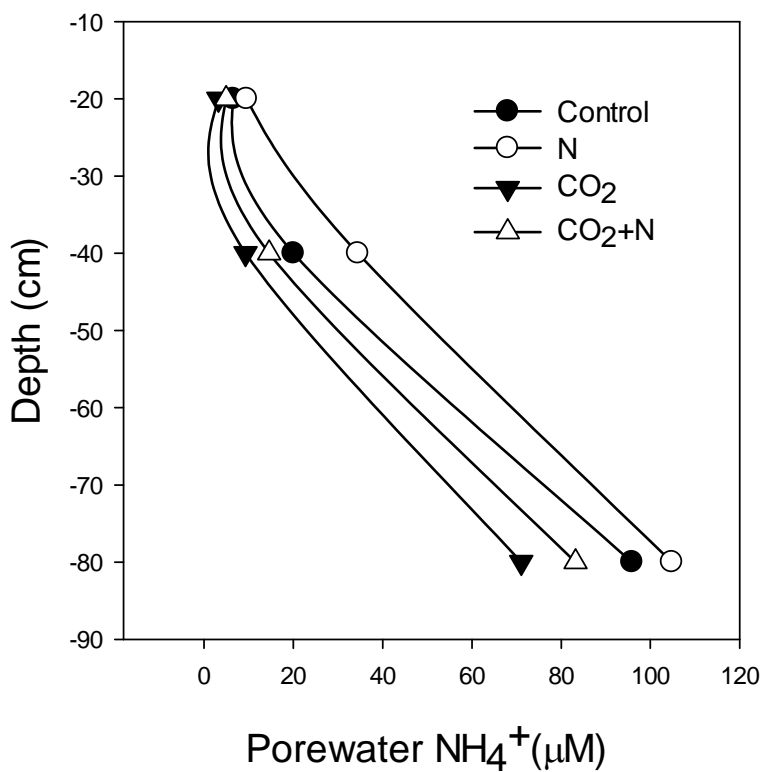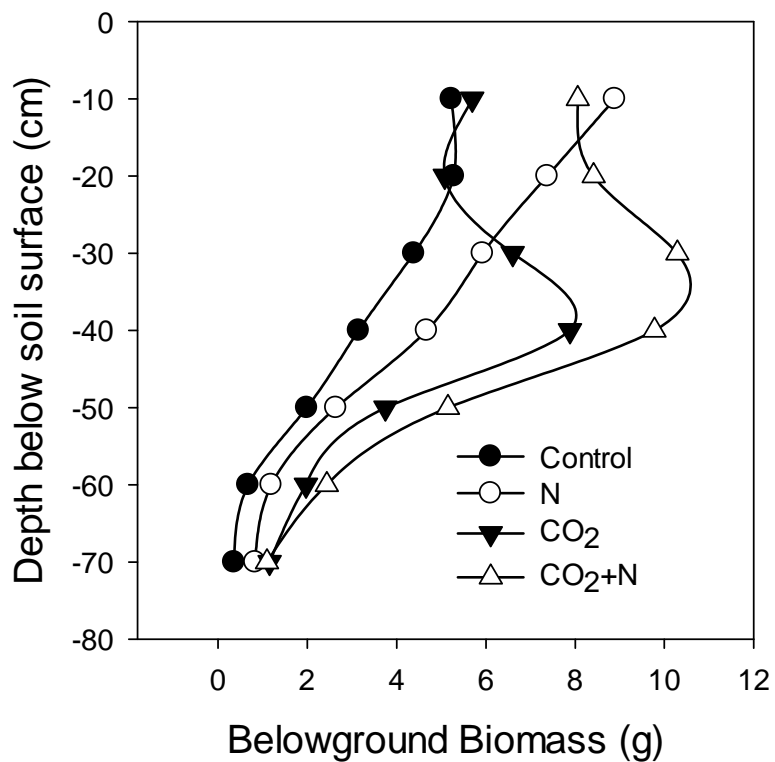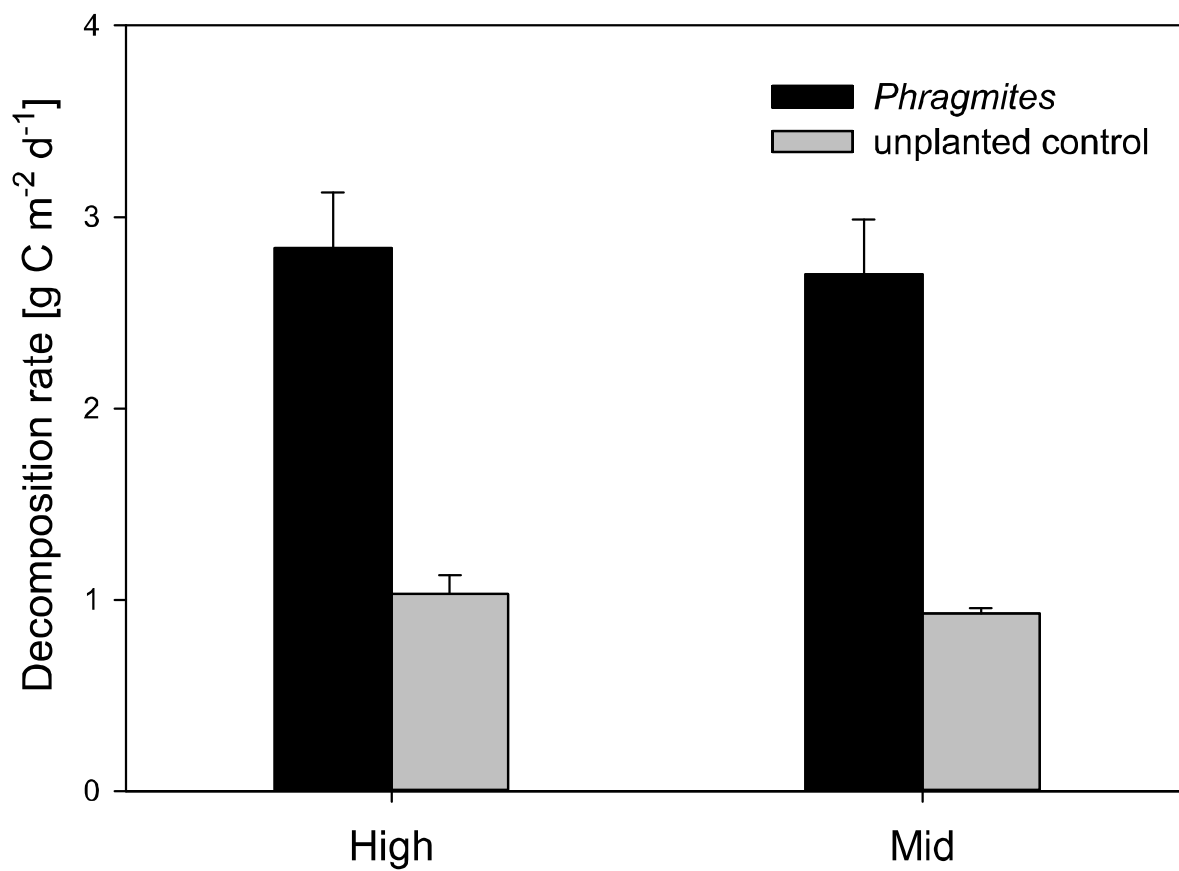
609

610   Figure 1.

Culmulative proportion of belowground biomass   Culmulative proportion of belowground biomass
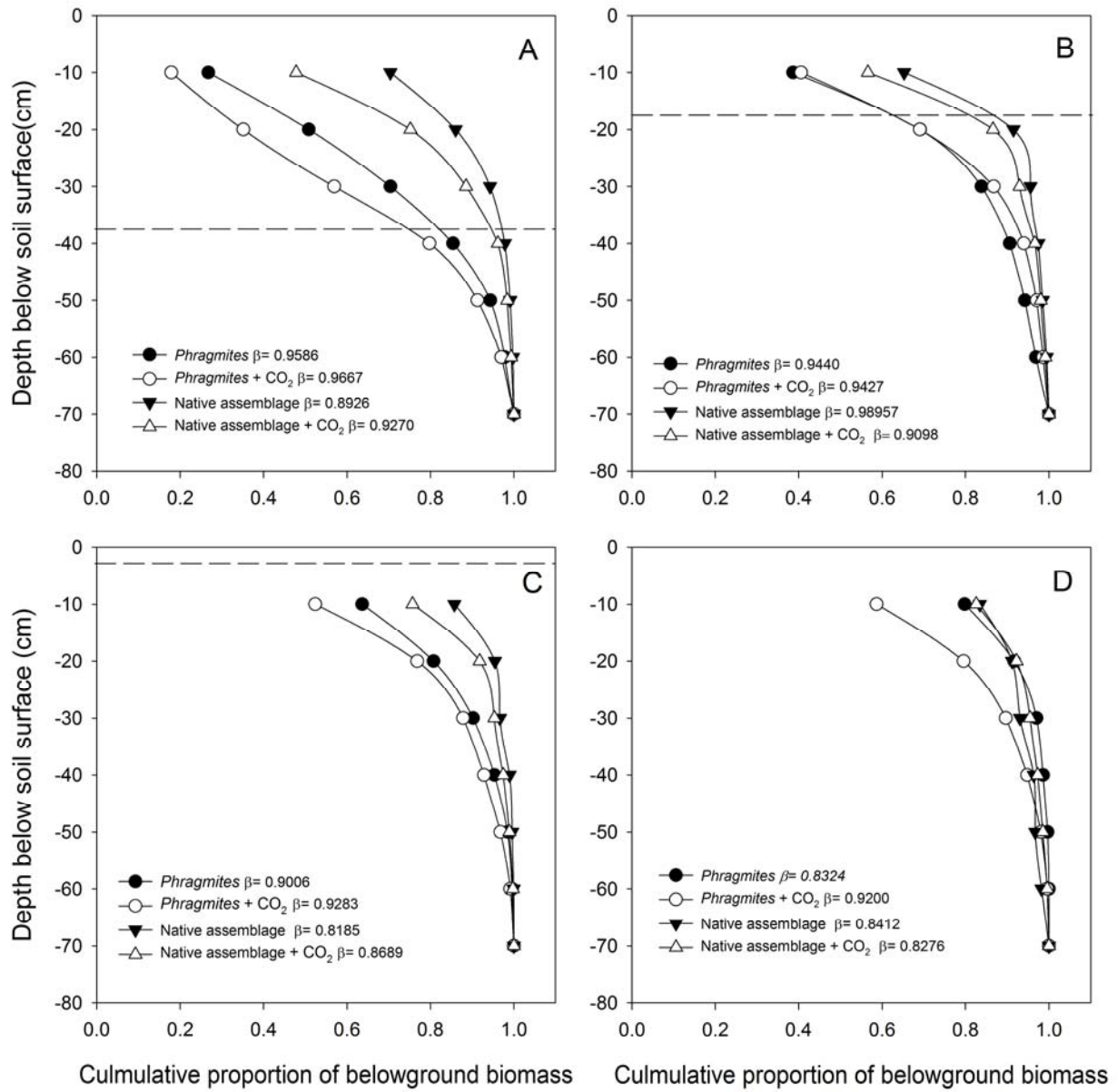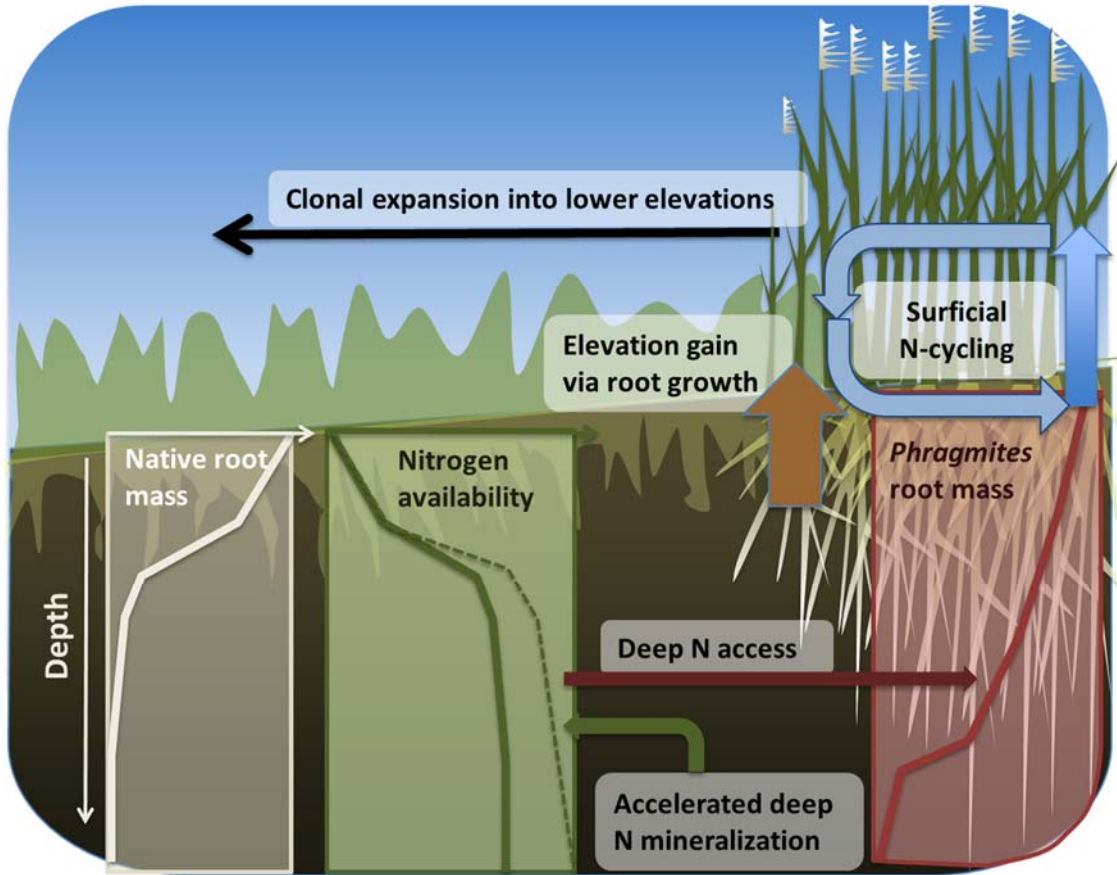
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614   Figure 2.

616   Figure 3.

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619   Figure 4.

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