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2   **Impacts of moso bamboo (*Phyllostachys pubescens*) invasion on dry matter, and carbon and**

3   **nitrogen stocks in a broad-leaved secondary forest located in Kyoto, western Japan**

4

5

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18

19 **Abstract**

20 In western and central Japan, the expansion of exotic moso bamboo (*Phyllostachys pubescens* Mazel

21 ex J. Houz.) populations into neighboring vegetation has become a serious problem. Although the

22 effects of bamboo invasion on biodiversity have been well studied, shifts in nutrient stocks and

23 cycling, which are fundamental for ecosystem functioning, are not fully understood. To explore the

24 effects of *P. pubescens* invasion on ecosystem functions, we examined above- and belowground dry

25 matter, and carbon (C) and nitrogen (N) stocks, in a pure broad-leaved tree stand, a pure bamboo

26 stand, and two tree–bamboo mixed stands with different vegetation mix ratios in the secondary

27 forest of Kyoto, western Japan. In the process of invasion, bamboo shoots offset broad-leaved tree

28 deaths; thus, no clear trend was apparent in total above- or belowground biomass or in plant C and N

29 stocks during invasion. However, the ratio of aboveground to belowground biomass (T/R ratio at the

30 stand level) decreased with increasing bamboo dominance, especially in the early stages of invasion.

31 This shift indicates that rapid bamboo rhizomatous growth is a main driver of substantial changes in

32 stand structure. We also detected rises in the C/N ratio of forest-floor organic matter during bamboo

33 invasion. Thus major impacts of *P. pubescens* invasion into broad-leaved forests include not only

34 early shifts in biomass allocation, but also changes in the distribution pattern of C and N stored in

35 plants and soil.

36

Introduction

39

40

41 Moso bamboo (*Phyllostachys pubescens* Mazel ex J. Houz.), one of the largest bamboo species in

42 the world, was introduced from China into western Japan about 300 years ago for use as human food

43 (young sprouts) and other products (adult culms) (Suzuki 1978; Shibata 2003). The species has been

44 transplanted across a wide range of areas in western and central Japan, where well-managed

45 plantation forests were established. Since the 1980s, most of these forests have been abandoned due

46 to rapid declines in domestic bamboo industries.

47 Like other bamboo species, *P. pubescens* has active rhizomatous clonal growth. The

48 belowground rhizome system is leptomorphic; it grows laterally, allowing rapid, widespread

49 expansion of ramets (Makita 1998). Furthermore, young shoots quickly reach full heights of 10–20

50 m matching those of well-developed canopy trees. These growth capabilities probably facilitate

51 invasions of neighboring secondary broad-leaved forests and/or coniferous plantations, whereby the

52 bamboos rapidly become dominant components of the vegetation and often form pure stands in

53 previously deciduous or coniferous vegetation (Isagi & Torii 1998; Suzuki & Nakagoshi 2011;

54 Suzuki 2014). A clear risk of losing biodiversity and ecosystem functioning exists when exotic giant

55 bamboos establish near-monospecific stands in previously diverse woodlands. Studies are urgently

56 required to identify the relationships between growth characteristics of *P. pubescens*, its

57 overwhelming invasion impacts, and ecosystem functioning.

58 Many studies have reported losses of plant diversity following *P. pubescens* invasion (Nakai &

59   Kisanuki 2006; Zhang *et al*. 2010; Akutsu *et al*. 2012; Bai *et al*. 2013). However, few studies have

60   reported on the effects of invasion on the sizes of carbon (C) and nitrogen (N) stocks or their cycling.

61   Information on these parameters is crucial for better understanding of ecosystem functioning before

62   and after invasion. However, data on the biogeochemical characteristics of pure bamboo forests are

63   available. For example, Isagi *et al*. (1997) showed that values of gross production and belowground

64   C allocation in *P. pubescens* stands are higher than those in temperate broad-leaved and/or

65   coniferous forest stands. The canopy of *P. pubescens* forest has higher N contents (Li *et al*. 1998)

66   and elevated transpiration rates (Komatsu *et al*. 2010) in comparison with broad-leaved and/or

67   coniferous forest, suggesting that the canopy photosynthetic rate may be higher in *P. pubescens*

68   stands than in native forest vegetation (Yen & Lee 2011). These characteristics are likely common to

69   other bamboo species under various climatic conditions (Isagi 1994; Tripathi & Singh 1996; Tu *et al*.

70   2013).

71   Previous research on the impacts of bamboo invasions and/or range expansions on C and N

72   biogeochemistry in Japan have focused on the understory dwarf species *Sasa kurilensis* (Rupr.)

73   Makino & Shibata, which has growth traits similar to those of *P. pubescens* with the exception of

74   culm height (Tripathi *et al*. 2005; Watanabe *et al*. 2013; Fukuzawa *et al*. 2014). These works have

75   shown that *S. kurilensis* contributes greatly to C and N retention and their cycling in broad-leaved

76   forest biomass and soils, but bamboo invasion and replacement of vegetation in native forests were

77   not included in the scope of these studies.

78   Thus, our objective in this study was to describe the effects of invasion of giant bamboo, *P*.

79   *pubescens*, into secondary broad-leaved forest on (i) dry matter mass, (ii) C stocks, and (iii) N stocks

80   in both plants and soils. We measured these parameters in above- and belowground plant parts, and

81   in soil horizons of a secondary forest, in a pure *P. pubescens* stand, and in two mixed forest stands

82   that differed in the degree of bamboo invasion.

83

84

85   **Materials and methods**

86

87   *Study site*

88

89   Fieldwork was conducted on Mt. Tennozan located on the boundary between Kyoto and Osaka

90   prefectures in western Japan (34°54′N, 135°46′E; Fig. 1). Mean annual temperature and precipitation

91   at the nearest weather station (AMeDAS) were 15.3°C (2001–2010, AMeDAS Kyotanabe, 34°50′N,

92   135°46′E) and 1459 mm (2001–2010, AMeDAS Nagaokakyo, 34°56′N, 135°41′E), respectively. The

93   bedrock geology of our study area comprised Mesozoic sedimentary sandstone, shale, and chert

94   belonging to Tamba terrane.

95   The native forest we studied was dominated by broad-leaved trees, including *Quercus serrata*

96   Thunb. and *Quercus variabilis* Blume, which are typical of Japanese temperate secondary

97   woodlands. *P. pubescens* was introduced a few hundred years ago in a patchy distribution pattern

98   through the region. The stands were well managed for the production of young bamboo sprouts as

99 human food. Broad-leaved secondary forests were established and cut for fuel. Broad-leaved trees

100 were harvested in our study area until the 1950s, but no anthropogenic disturbance has occurred for

101 at least 60 years (Tokuchi *et al*. 2010). *P. pubescens* plantations in this region have been abandoned

102 since the 1970s, and invading bamboo shoots were still expanding into neighboring broad-leaved

103 forests at the time of our study (Torii & Isagi 1997; Torii 1998). According to a vegetation census by

104 aerial photography in 2003, 46% of the areas around Mt. Tennozan (238.5 ha) are covered by

105 secondary broad-leaved forests, 41% by *P. pubescens* stands, and 7% by mixed

106 broad-leaved/bamboo stands (Tokuchi *et al*. 2010).

107   We selected vegetation stands dominated by (i) broad-leaved trees, (ii) *P. pubescens*, and (iii)

108 mixed stands of trees and bamboo along a ridge located on Mt. Tennozan. We established one square

109 plot (20 × 20 m) in broad-leaved tree forest stand (SF), one in a moso bamboo stand (BF), and two

110 plots containing mixed forest stands (MF1, MF2). According to the earlier aerial photographs (1961,

111 1974, and 2003), BF had been dominated by *P. pubescens* prior to 1974. The bamboo has been

112 invading MF1 since 1974 and MF2 since 1961. In plots MF1, MF2, and BF, expanding and

113 overcrowding bamboo shoots have not been cut or managed during recent decades. Thus, plots SF,

114 MF1, MF2, and BF represent a stage with no *P. pubescens* invasion, an early stage of invasion, a

115 mid-stage of invasion, and a last stage of invasion, respectively.

116

117 *Vegetation censuses and biomass estimation*

118

119   We measured diameters at breast height (DBHs; cm) and identified all trees and bamboo shoots

120   exceeding 1 cm in DBH.

121   Above- and belowground biomasses of broad-leaved trees in all plots were estimated using

122   allometric equations relating DBH and height developed by different author earlier (Nishioka *et al*.

123   1982; Goto *et al.* 2006; Ogawa & Kira 1977; Nagano & Kira 1978; Ogino 1977). Broad-leaved tree

124   biomasses allocated to stems (main trunks, W_s; kg), branches (W_b; kg), and leaves (W_l; kg) were

125   calculated thus:

126            $W_s = 0.02644 \times (DBH_{0.1}{}^2 \times H)^{0.9688}$ (1)

127            $W_b = 0.01262 \times DBH_{0.1}{}^{2.364}$ (2)

128            $W_l = 0.005921 \times DBH_{0.1}{}^{2.288}$,   (3)

129   where H is tree height (m), which we estimated using the following relationship:

130            $1/H = 1/(a \times DBH^b) + 1/H_{max}$,   (4)

131   where *a* and *b* are constants, and H_{max} is the asymptotic maximum height (m; Ogawa & Kira 1977).

132    $DBH_{0.1}$ is stem diameter (cm) for a position located one-tenth of the way along the maximum trunk

133   length; $DBH_{0.1}$ was estimated from the measured DBH using the following empirical equation,

134   which was developed for a warm–temperate secondary oak forest by Nagano and Kira (1978):

135            $DBH_{0.1} = 0.941 \times DBH + 0.734$.   (5)

136   We calculated the biomass of broad-leaved tree coarse roots ($\geqq 2$ mm in diameter) (W_{below}; kg)

137   using the following extended allometric equation:

138            $W_{below} = 0.082 \times DBH^2$.   (6)

139   Eq. 6 was developed for a cool–temperate beech forest by Ogino (1977). We estimated the biomass

140   of broad-leaved tree fine roots (<2 mm in diameter) by soil block sampling (see below).

141   To estimate the aboveground biomass of *P. pubescens* shoots, we applied the allometric equation

142   developed for a site close to one of our study plots (BF) by Abe and Shibata (2009) in June 2006:

143        $W = a \times DBH^{b}$,   (7)

144   where parameters *a* and *b* were estimated individually for culms, branches, and leaves. The

145   allometric relationship between the dry weight of each component and culm DBH was calculated

146   separately for current-year shoots and shoots older than 1 year (Abe & Shibata 2009). The

147   parameters are summarized in Table 1.

148   We used two methods of soil-block sampling to estimate the belowground biomass of *P.*

149   *pubescens* shoots. One method estimated the "stump," which we define here as the culm between the

150   soil surface and rhizome (stump-block); the second method was used for root estimation (root-block).

151   In the first procedure, we carefully excavated three soil blocks (each 50 × 50 cm to 50 cm depth)

152   centered around bamboo shoots by using a shovel and saw within the pure *P. pubescens* stand

153   located outside plot BF in August 2006. We cut free the aboveground part, dug into the soil, and

154   carefully excavated the subterranean parts of the shoot. The stump-blocks were washed with tap

155   water to remove mineral soils. The remaining root systems were separated into the stump and other

156   components. The stumps were dried at 40°C for 1 week and then weighed. We constructed an

157   allometric equation from the relationship between the dry weight of stump per shoot and culm DBH

158   (see Eq. 7), and subsequently estimated the total bamboo stump biomass within our plots as a portion

159 of the belowground biomass components.

160   In the second procedure, we collected two soil blocks (50 × 50 cm to 30 cm depth) inside each

161 plot in the period from February to April 2006 for our calculations of root biomass per unit area and

162 the extent of bamboo rhizome lateral extension. These root-block samples were divided into vertical

163 portions 0–5, 5–10, 10–20, and 20–30 cm downward from the soil surface.

164   Within plots MF1, MF2, and BF, we found several centimeter-thick layers of live fine- and

165 coarse-roots between the mineral and organic layers (see below). We termed this layer the "root mat"

166 (RM) and separated it out from the other layers in the root-blocks. The living roots in the RM and

167 mineral soil layers were divided into those from broad-leaved trees and those from *P. pubescens*, and

168 sorted by hand into categories of fine roots, coarse roots, and bamboo rhizomes in the laboratory.

169 Each component was carefully separated according to illustrations in Suzuki (1978) and Makita

170 (1998). We distinguished rhizomes from roots by the presence of nodes in the former. The various

171 components were dried at 40°C for 72 h and weighed. The area-based biomasses of these

172 components were determined by calculation for these soil blocks.

173   Finally, we used the predictions of our allometric regressions for stand-level integration of the

174 biomasses of stems, branches, leaves, and coarse roots of broad-leaved trees, and the biomasses of

175 culms, branches, leaves, and stumps of *P. pubescens*. We used the root-block predictions to integrate

176 area-based biomasses of tree fine roots, and bamboo coarse roots, fine roots, and rhizomes in the RM

177 and mineral soil layers.

178

179   *Soil sampling*

180

181   We estimated the dry masses of organic matter in the organic soil layers of the four plots. Four

182   frames (20 × 20 cm) were deployed haphazardly on the surface soils in the period February–April

183   2006, and from these, we collected all forest-floor organic matter in the litter (Oi) and humus layers

184   (Oe+Oa). Samples of this organic matter were dried at 40°C for 1 week and weighed.

185   We used soils collected in the root-blocks to determine soil bulk density. After removing roots

186   and rhizomes, we divided the dry weight of fine mineral soil that passed through a 2-mm sieve by

187   the total dry weight of bulk soil for each soil layer. Organic matter and mineral soils were also

188   present in the RM layer. Consequently, we used a 4-mm mesh to sieve the RM samples collected

189   from the root-blocks in preparation for soil analysis.

190

191   *Chemical analysis*

192

193   Bamboo organs (leaves, branches, culms, fine and coarse roots, and rhizomes), forest-floor organic

194   matter, and mineral soils were ground in a mill prior to measurements of C and N contents with a

195   NC analyzer (NC-22A; Sumigraph, Osaka, Japan). We assumed that the C and N contents of

196   bamboo stumps were the same as those in bamboo rhizomes. Reports have indicated that the C and

197   N contents of *P. pubescens* leaves vary significantly by culm age (Li *et al*. 1998). Thus, we made

198   separate measurements of aboveground compartments of *P. pubescens* on current-year shoots and

199 those older than 1 year. We obtained C and N contents of most broad-leaved tree organs from

200 previous reports (Tsutsumi *et al*. 1968; Katagiri & Tsutsumi 1975), but our data on fine and coarse

201 roots were obtained by the analyses described above. By multiplying the dry weights of plant organs

202 or soil organic matter in the soil layers by the respective C and N contents and summing, we were

203 able to estimate the total area-based C and N stocks in each plot.

204

205 *Data analysis*

206

207 We used paired *t*-tests to detect significant differences in the C and N contents of *P. pubescens* leaves,

208 branches, and culms between current-year shoots and those older than 1 year. The Kruskal-Wallis

209 test was used to test the effect of stand characteristics on the mean C and N contents in coarse and

210 fine roots of bamboo and broad-leaved trees, and in bamboo rhizomes and stumps. We also used the

211 Stell-Dwass post hoc test for multiple comparisons to detect differences in the mean C and N

212 contents in these components between pairs of stand types. Significant differences in the mean C and

213 N contents in the soil organic matter within each layer (forest floor, RM, and 0–10-cm and 10–30-cm

214 layers) among stand types were also analyzed by the Kruskal-Wallis test followed by the

215 Steel-Dwass post hoc test. Statistical analyses were performed using R software (R Development

216 Core Team 2010).

217

218

219   **Results**

220

221   *Stand structure*

222

223   Stem and culm densities, mean DBH, total basal area (BA), proportion of *P. pubescens* in BA,

224   numbers of species, and dominant broad-leaved tree species in SF, MF1, MF2, and BF are

225   summarized in Table 2. As the proportions of *P. pubescens* in BA increased, the numbers of plant

226   species in the plots decreased (Table 2). Patterns of DBH frequency distribution differed

227   dramatically among plots (Fig. 2). Thus, DBH distributions of broad-leaved trees were positively

228   skewed in plots SF, MF1, and MF2, while DBH distributions of bamboo shoots showed a normal

229   curve in plots MF1, MF2, and BF. In mixed stands (plots MF1 and MF2), distributions showed a

230   bimodal curve with one smaller mode comprising the DBH distribution of broad-leaved trees and the

231   larger mode comprising that of bamboo shoots. Mean DBH values of bamboo culms were similar

232   among the plots regardless of differences in culm density (Table 2). As bamboo culm densities

233   increased, the frequencies of broad-leaved trees with DBH values <12 cm decreased dramatically

234   (e.g., in plot MF2); we found no trees with DBH values >12 cm in plot BF (Fig. 2).

235

236   *Above- and belowground biomasses*

237

238   We used an allometric equation (Eq. 7) describing the relationship between culm DBH and stump

239 dry weight to predict biomasses of belowground stumps of *P. pubescens* shoots; the calculated

240 values of parameters *a* and *b* were 7.71×10^{-2} and 1.434 ($r^2 = 0.954$), respectively.

241   Figure 3 depicts the vertical distribution of belowground biomasses of coarse and fine roots, and

242 rhizomes of *P. pubescens* shoots per unit area in plots MF1, MF2, and BF. Fine roots of *P. pubescens*

243 occurred most densely in the 0–5-cm mineral soil layer; coarse roots and rhizomes occurred most

244 densely below 5 cm soil depth (Fig. 3).

245   Details of aboveground and belowground biomasses of each compartment, and total biomasses

246 are presented in Fig. 4 and Appendix A. No increasing or decreasing trends were observed in

247 aboveground and total biomasses. However, belowground biomass increases were associated with *P.*

248 *pubescens* invasions (Fig. 4). At the stand level, the dry mass ratio of non-photosynthetic organs to

249 photosynthetic organs (culm/foliage ratio, C/F; Iwaki 1958) increased from 22.7 to 35.8 (Fig. 5a),

250 while the dry mass ratio of aboveground organs to belowground organs (top/root ratio, T/R)

251 decreased from 3.41 to 1.39 as the proportion of bamboo increased in BA (Fig. 5b). The C/F ratio of

252 broad-leaved trees remained constant among plots other than BF (Fig. 5a), in which all large canopy

253 trees had disappeared as a result of the bamboo invasion (Fig. 2). No differences were detected in the

254 C/F ratio of *P. pubescens* shoots across our plots (Fig. 5a). Among plots, the T/R ratio of

255 broad-leaved trees was lowest in BF; the T/R ratio of *P. pubescens* tended to increase with increasing

256 proportions of bamboo in BA (Fig. 5b).

257

258 *Organic matter mass at the forest floor level and the bulk density of mineral soil*

259

260 Values of forest-floor organic matter mass in the Oi layer were not significantly different among

261 plots (Kruskal-Wallis test, $P > 0.05$), but those in the Oe+Oa layer were significantly larger in plot

262 SF than in the other plots (Kruskal-Wallis and Steel-Dwass tests, $P < 0.05$; Table 3).

263 The bulk density of mineral soil that passed through a 2-mm sieve tended to increase with depth

264 and decrease with the proportion of bamboo in BA (Table 4). The RM layer, which appeared to have

265 developed between the organic and the mineral soil layers in the presence of *P. pubescens*, included

266 a small amount of mineral soil (Table 4).

267

268 *C and N contents and stocks in plants and soils*

269

270 Details of the mean C and N contents in each compartment of *P. pubescens* and broad-leaved trees

271 are listed in Table 5. In *P. pubescens*, the C contents in leaves, branches, and culms were not

272 significantly different between current shoots and shoots older than 1 year (paired *t*-test, $P > 0.05$;

273 Table 5), and the N contents in leaves, branches, and culms did not vary between the two age classes

274 of shoots (paired *t*-test, $P > 0.05$; Table 5). The leaves and the branches of *P. pubescens* contained

275 less C and more N than equivalent organs of broad-leaved trees. The culms of *P. pubescens*

276 contained less C than the stems of broad-leaved trees; the N contents in bamboo culms and tree

277 stems were closely similar (Table 5). The coarse and fine roots of *P. pubescens* contained less C and

278 N than those of the broad-leaved trees (Table 5). C and N contents in the rhizomes, stumps, and

279   coarse roots of *P. pubescens* were closely similar.

280   C and N contents of each soil layer in the four plots are detailed in Table 6. C and N contents in

281   the Oi layer differed significantly among plots (Kruskal-Wallis and Steel-Dwass tests, $P < 0.05$). As

282   the proportion of bamboo BA increased in the stands, the C and N contents in this layer decreased

283   (Table 6).

284   Values of C stocks in plants and soils in the stands ranged from 83.4 to 108.2 MgC ha^{-1} in

285   aboveground parts, from 28.7 to 64.6 MgC ha^{-1} in belowground parts, and from 45.0 to 54.0 MgC

286   ha^{-1} in soils (Fig. 6a, Appendix B). The values of N stocks ranged from 0.44 to 0.57 MgN ha^{-1} in

287   aboveground parts, from 0.38 to 0.60 MgN ha^{-1} in belowground parts, and from 2.13 to 2.98 MgN

288   ha^{-1} in soils (Fig. 6b). Forty to sixty percent of C was stored in aboveground parts, but >70% of the

289   stand N stock was stored in the soils (Fig. 7). The proportion of total stand C stored in belowground

290   parts increased with increasing proportions of bamboo BA, but the proportions of N shifted little in

291   response to increasing bamboo BA (Fig. 7).

292

293

294   **Discussion**

295

296   *Stand structure and biomass in vegetation dominated by broad-leaved trees and bamboo*

297

298   The dominant tree species in our stands were *Q. serrata* and/or *Q. variabilis*, which are typical of the

299 secondary forest around Mt. Tennozan (Table 2). The above- and belowground biomasses in a pure

300 stand of broad-leaved trees (SF) were 211.8 and 62.1 Mg ha^{-1}, respectively (Fig. 4, Appendix A);

301 these values exceed those previously reported for forests with similar tree species composition in the

302 other areas (Table 7). The differences between studies is likely attributable the greater stand age (~60

303 years) and a higher density of trees with DBH >5 cm in our data set. Surviving large trees with DBH

304 values exceeding 30 cm on Mt. Tennozan also contributed significantly to the large biomass values

305 we calculated.

306   Culm density (9675 ha^{-1}; Table 2) and aboveground biomass (182.1 Mg ha^{-1}; Fig. 4, Appendix

307 A) in the abandoned pure *P. pubescens* stand (BF) were within the range of previously reported

308 values for equivalent vegetation, but belowground biomass we measured (127.1 Mg ha^{-1}; Fig. 4,

309 Appendix A) exceeded previously reported values (Table 8). *P. pubescens* biomass surveys in

310 various regions of Japan have detected an exponential relationship between BA and above- or

311 belowground biomasses (FFPRI 2009). Using this regression relationship, we calculated biomasses

312 in our *P. pubescens* stand (BA = 88.3 m^2 ha^{-1}; Table 2) of 181.2 Mg ha^{-1} above ground and 91.4 Mg

313 ha^{-1} below ground, which fit our empirical estimates for aboveground biomass but not those for

314 belowground biomass. The discrepancy between estimates is likely due to the difficulty in accurately

315 defining the belowground compartment of bamboo species, especially for the leptomorph types like

316 *P. pubescens*. Comprehensive inclusion of all belowground compartments requires estimation of the

317 spatial extent of rhizome and root system biomasses in addition to stump estimates derived from the

318 allometric relationship with DBH. Previous studies may not have implemented this inclusive

319   procedure and therefore underestimated belowground biomass. We believe that our comprehensive

320   approach provides reliable values.

321   We calculated T/R values of 3.41 and 1.39 in the secondary broad-leaved (SF) and *P. pubescens*

322   stands (BF; Fig. 5b), respectively. According to Saito (1989), T/R falls within the range of 3–7 and is

323   close to unity in broad-leaved/coniferous forest stands and grasslands. Thus, our measure of stand

324   structure in *P. pubescens* vegetation was close to that of grassland meadows, but bamboo biomass

325   was comparable to that of a well-developed secondary forest.

326

327   *Changes in stand structure and biomass as bamboo invasion proceeds*

328

329   In our study sites, bamboo density and percentage of bamboo in total BA was higher in the plot

330   where the number of years passed after *P. pubescens* invasion was longer (Table 2), indicating that

331   the dominance of *P. pubescens* in the plot represents a stage of invasion.

332   As *P. pubescens* invaded our secondary forest sites, numbers of plant species decreased and total

333   basal area increased. Okutomi *et al*. (1996) observed similar shifts in the vegetation during a study

334   of plant spatial distributions and canopy structures in a mixed broad-leaved tree/bamboo forest,

335   although they did not determine biomasses. At our study site, the above- and belowground

336   biomasses of broad-leaved trees decreased as those of *P. pubescens* increased, but no monotonous

337   trends were apparent in the summed biomass data (Table 5c). These relationships might be

338   explainable as follows. In the early stages of invasion, smaller trees are replaced by small numbers

339   of bamboo culms, with consequent decreases in whole stand biomass (plot MF1). Only large trees

340   survive as the invasion proceeds. During the mid-stages of the invasion process, bamboo density

341   increases and stand biomass reaches a maximum (as in plot MF2). Finally, whole stand biomass

342   decreases when high densities of bamboo cause the deaths of large broad-leaved trees (perhaps due

343   to competition for light, water, and/or mineral nutrients), as in plot BF.

344   An increase in the C/F ratio as bamboo dominance increased indicates that the proportion of

345   photosynthetic organs in the aboveground biomass increased at the stand level (Fig. 5a). *P.*

346   *pubescens* is a highly productive plant that produces more leaves on fewer culms (stems) than

347   woody species (Isagi *et al.* 1997; Yen & Lee 2011). In addition, the leaf N contents of *P. pubescens*

348   exceeded those of woody plants (Table 5, Li *et al.* 1998), suggesting that *P. pubescens* has a higher

349   photosynthetic capacity (Reich *et al.* 1997). Isagi *et al.* (1997) measured high gross production rates

350   in a *P. pubescens* stand. They also pointed out that a large proportion of the photosynthetic products

351   was allocated to belowground systems and then transported to newly developing bamboo shoots

352   (Isagi *et al.* 1997).

353   In stands where bamboo had invaded secondary forest (plots MF1 and MF2), the belowground

354   biomass of *P. pubescens* exceeded aboveground biomass (Fig. 4c, Appendix A), and the stand T/R

355   ratio declined dramatically (Fig. 5b). These trends indicate that the ramet population of *P. pubescens*

356   initially expands its root system into adjacent forest stands, a process that results in rapid changes in

357   stand biomass distribution.

358

359   *Changes in C and N stocks in forest stands following bamboo invasion*

360

361   Although aboveground compartments of *P. pubescens* had lower C and higher N contents than those

362   of broad-leaved trees (Table 5), total aboveground C and N stocks did not change monotonically

363   following *P. pubescens* invasion of secondary forest stands (Fig. 6) due to an aboveground biomass

364   buildup during invasion. The C and N contents in the belowground compartments of broad-leaved

365   trees exceeded those of bamboo (Table 5). C stocks per unit area in belowground compartments and

366   total belowground biomass approximately doubled during *P. pubescens* invasions (Fig. 6a, Appendix

367   B), but N stocks did not change (Fig. 6b, Appendix B). This indicates that the difference of not only

368   the dry matter mass but also the chemical content of each plant compartment between broad-leaved

369   tree and *P. pubescens* can largely affect the element stock and distribution in the forest stand. These

370   physiological characteristics of *P. pubescens* including higher productivity, greater belowground

371   allocation, and lower C and/or higher N contents in leaves rather than those of trees are partly

372   reported in cases of some other bamboo species, such as *P. bambusoides* Sieb. et Zucc. in western

373   Japan (Isagi *et al.* 1993), *Bambusa* spp. in Puerto Lico (O'Connor et al. 2000), and *Dendrocalamus*

374   *strictus* (Roxb.) Nees in India (Tripathi & Singh 1996). Because these studies only described the

375   stand structure and/or nutrient dynamics in bamboo forest, further researches are necessary to

376   elucidate their changes by bamboo invasion into the native forest in each area.

377   When total values were calculated by summing the stocks for plants and soil organic matter in

378   each plot, the ratio of belowground C in total C stocks increased during bamboo invasion of

379   secondary forest (Fig. 7a). Thus, the development of *P. pubescens* root systems may greatly change

380   the C distribution in forest stands.

381   More than 70% of N was stored in the soils (Fig. 7b). In general, microbial decomposition of

382   organic matter in forest soils releases C as gaseous CO_2 into the atmosphere, but N is largely

383   immobilized and retained underground (e.g., Vitousek et al. 1979; Johnson *et al.* 2000; Berg &

384   McClaugherty 2014). This results in little effect of invasions by *P. pubescens* on N stock size or its

385   distribution.

386   The C/N ratio of organic matter in the surface soil layer (on a weight basis) is a useful indicator

387   of the degree of decomposition (Berg & McClaugherty 2014), net nitrification rate (Goodale & Aber

388   2001; Fukushima *et al.* 2011) and leaching of mineralized N from forest soils (Lovett *et al*. 2004).

389   When forest-floor organic matter with a relatively high C/N ratio decomposes, organic N is generally

390   mineralized but then rapidly immobilized by heterotrophic soil microbes. When the C/N ratio of soil

391   organic matters decreases as decomposition progresses, microbe demand for mineral N becomes

392   satiated; inorganic N is then nitrified by autotrophic nitrifiers and subsequently leached from the soil.

393   The C/N ratio of the forest-floor organic matter at our study site increased monotonically with

394   bamboo shoot density (Table 9). Previous studies revealed that understorey dwarf bamboo like *S.*

395   *kurilensis* in a broad-leaved secondary forest in northern Japan (Tripathi *et al.* 2005; Watanabe *et al.*

396   2013) and *Chusquea culeou* E. Desv. in an old-growth broad-leaved forest in Patagonia (Austin &

397   Marchesini 2012) plays a key role in retaining mineral N in soil through N uptake by bamboo and N

398   immobilization during bamboo litter decomposition. The giant bamboo has greater biomass, litter

399   fall, and productivity than dwarf bamboo. Hence, the process of *P. pubescens* invasion into

400   secondary forest may depress the rate of N cycling and prevent the loss of inorganic N from soils.

401   Moreover, Umemura & Takenaka (2014a) demonstrated that soil pH increases as *P. pubescens*

402   invades surrounding evergreen coniferous forests, which may greatly affect the net nitrification rates

403   in soil because some groups of ammonia-oxidizing bacteria can deactivate and some groups of

404   ammonia-oxidizing archaea can activate under low pH (Nicol *et al.* 2008). Overall, *P. pubescens*

405   invasion into forest stands clearly alters N cycling between plants and soil due to changes in soil

406   organic matter quality (e.g., the C/N ratio) and physicochemical parameters (e.g., pH). The details of

407   these processes should be studied by examining changes in soil N dynamics during invasion.

408

409

410   **Conclusion**

411

412   In our secondary forest located in western Japan, stand structure and the distribution of plant

413   biomass were affected by *P. pubescens* dominance, which is almost equal to the degree of *P.*

414   *pubescens* invasion. The changes in (i) standing biomass, (ii) C and N stocks in plants and soil, and

415   (iii) their distributions during bamboo invasion were likely triggered by the rapid bamboo

416   rhizomatous clonal growth and the deaths of large(L412-414) broad-leaved trees. Nevertheless, few

417   differences in biomass or C and N stock sizes were observed between a broad-leaved forest stand

418   and a pure *P. pubescens* stand, suggesting that the capabilities for storing C and N in plants and soil

419 are comparable in broad-leaved and bamboo forests. In contrast, the allocation of C into

420 belowground biomass (T/R ratio), the N content of leaves, the C/F ratio in aboveground vegetation,

421 and the C/N ratio in forest-floor organic matter shifted markedly in response to invasion. These

422 shifts are likely driven by the physiological attributes of invading *P. pubescens*, and may have large

423 effects on the rates of C and N cycling and loss in forest ecosystems during early invasion. To better

424 understand the effects of *P. pubescens* invasion on ecosystem functions, future studies on soil N

425 dynamics and N retention will be required.

426

427 **Acknowledgments**

428

437

438 **References**

439

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599

600

601   **Table 1**. The parameters of regression equations predicting biomasses of each *P. pubescens* organ

602   from diameters at breast height (DBH). Data are from Abe and Shibata (2009).

603

		a	*b*	*n*	r^2
Leaf	Current year	1.149×10^{-2}	1.515	7	0.853
	$\geqq 1$ year	4.774×10^{-3}	1.976	8	0.851
Branch	Current year	1.045×10^{-1}	1.185	7	0.722
	$\geqq 1$ year	4.647×10^{-2}	1.483	8	0.74
Culm	Current year	6.210×10^{-2}	2.261	7	0.951
	$\geqq 1$ year	1.305×10^{-1}	2.052	8	0.915

604

605

606 **Table 2** Densities of broad-leaved tree stems and bamboo shoots, mean diameter at breast height (DBH) of broad-leaved trees and bamboo shoots, total basal

607 area (BA), proportion of bamboo in BA, number of plant species, and dominant tree species in our study plots.

Plot	Stem density	Culm density	Mean DBH of woody trees	Mean DBH of bamboos	Total BA	Percentage of bamboo in BA	Number of Species	Dominant tree species[b]
	(No. ha^{-1})	(No. ha^{-1})	(cm)	(cm)	(m^2 ha^{-1})[a]	(%)	(No. plot^{-1})	
SF	6600	0	7.29	n.a.	52.9	0	19	*Quercus serrata* (19.3), *Myrica rubra* (19.0), *Q. variabilis* (15.1), *Ilex pedunculosa* (12.3)
MF1	6225	1275	5.88	10.03	46.1	20.0	17	*Q. serrata* (27.2), *I. pedunculosa* (22.9), *Chamaecyparis obtusa* (16.8)
MF2	2375	5575	7.28	10.51	76.1	69.1	14	*Q. variabilis* (18.3), *Q. serrata* (5.4), *Q. glauca* (4.0)
BF	150	9675	1.97	10.52	88.3	99.9	4	

a Total basal area (BA) at the breast height
b Order of relative dominant woody tree species was based on BA. Percent of total BA in parentheses.
DBH; diamter at the breast height
n.a.; not available

608

609   **Table 3** Mean dry weights of organic matter in the Oi and Oe+Oa soil layers ($n = 4$). SD in

610   parentheses.

611

Layer	SF		MF1		MF2		BF	
Oi (Mg ha^{-1})	4.05	(0.767)	4.08	(0.874)	5.25	(2.32)	3.47	(1.69)
Oe+Oa (Mg ha^{-1})	20.6	(6.05)*a*	1.89	(0.598)*b*	1.4	(0.984)*b*	1.53	(0.291)*b*

612   Different letters (*a*, *b*) indicate significant differences among plots ($P < 0.05$, Kruskal-Wallis test

613   followed by Steel-Dwass post hoc test).

614

615 **Table 4** Mean soil bulk density in the root mat and mineral soil layers (*n* = 2).

Layer	SF	MF1	MF2	BF
RM (Mg ha^{-1})	n.a.	19.3	14.8	19.2
0-5cm (Mg ha^{-1})	462.6	360	314.5	241.8
5-10cm (Mg ha^{-1})	534.8	373.6	403.2	263.6
10-20cm (Mg ha^{-1})	937.3	901.2	798	640.9
20-30cm (Mg ha^{-1})	919.3	760.5	658.8	821.5

616 n.a.; not available

617

618

619

620 **Table 5** Mean C and N contents in each organ of *P. pubescens* and broad-leaved trees. SD in

621 parentheses. Both C and N contents in leaves, branches, and culms of bamboo shoots were not

622 significantly different between current shoots and shoots older than 1 year (paired *t*-test, $P > 0.05$).

		Total C (%)		Total N (%)		*n*
Phyllostachys pubescens						
Leaf	Current	41.9	(1.72)	2.43	(0.30)	3
	≧1 year	43.2	(0.46)	2.03	(0.19)	3
Branch	Current	46.4	(0.23)	0.55	(0.17)	3
	≧1 year	45.8	(1.11)	0.51	(0.25)	3
Culm	Current	46.3	(0.69)	0.18	(0.043)	3
	≧1 year	46.8	(1.22)	0.19	(0.050)	3
Coarse root		44.2	(0.32)	0.23	(0.015)	9
Fine root		43.2	(0.50)	0.51	(0.044)	9
Rhizome and stump		44.3	(0.15)	0.26	(0.029)	9
Broad-leaved tree						
Leaf		52.6 †		1.57 ‡		
Branch		51.8 †		0.38 ‡		
Stem		50.9 †		0.19 ‡		
Coarse root		46.1	(0.48)	0.59	(0.049)	9
Fine root		46.7	(0.54)	0.77	(0.040)	8

623 †; Data are from Katagiri and Tsutsumi (1975). ‡; Data are from Tsutsumi *et al*. (1968).

624 **Table 6** Mean C and N contents in soil organic matter in each soil layer. SD in parentheses ($n = 5$).

	Soil layer	SF			MF1			MF2			BF		
C(%)	Oi	46.2	(0.36)	a	45.6	(0.68)	ab	43.5	(0.95)	b	39.8	(0.59)	c
	Oe+Oa	28.7	(7.91)		27.7	(10.1)		39.3	(2.86)		31.5	(4.29)	
	RM	n.a.			28.7	(10.1)		26.6	(8.99)		22.9	(7.64)	
	0-10 cm	2.92	(0.99)		3.44	(0.946)		3.25	(1.68)		3.34	(0.86)	
	10-30 cm	0.69	(0.13)		0.71	(0.13)		1.57	(0.87)		2.11	(0.46)	
N(%)	Oi	1.02	(0.17)	a	0.99	(0.073)	a	0.85	(0.17)	ab	0.64	(0.11)	b
	Oe+Oa	1.59	(0.21)		1.22	(0.41)		1.61	(0.14)		1.35	(0.13)	
	RM	n.a.			1.22	(0.33)		1.36	(0.50)		1.21	(0.38)	
	0-10 cm	0.16	(0.058)		0.16	(0.045)		0.18	(0.088)		0.22	(0.039)	
	10-30 cm	0.042	(0.001)		0.041	(0.006)		0.099	(0.041)		0.11	(0.014)	

625 Different letters (*a*, *b, c*) indicate significant differences among plots ($P < 0.05$, Kruskal-Wallis test followed by Steel-Dwass post hoc test).

626 RM; root mat layer. n.a.; not available.

627

628   **Table 7.** Above- and belowground biomass in *Quercus serrata* secondary forest from previous studies and this study.

Site	Age (year)	Aboveground biomass (Mg ha^{-1})	Belowground biomass (Mg ha^{-1})	Reference
Shimane Prefecture	40	96.3 - 218.0	n.a.	Katagiri (1988)
Kyoto Prefecture	n.a.	102	23.4	Goto *et al.* (2003); Dannoura *et al.* (2006)
Okayama Prefecture	58 - 61	79.2 - 161.3	n.a.	Goto *et al.* (2006)
Miyazaki Prefecture	60 - 62	118.5 - 127.4	n.a.	Kai (1984)
Iwate Prefecture	36	131.1	n.a.	Segawa and Kato (1970)
Nagano Prefecture	16	132.2	24.1	Katakura *et al.* (2007)
Toyama Prefecture	33 - 35	114.8 - 206.8	n.a.	Hasegawa (1989)
Kyoto Prefecture	60 ~	211.8	62.1	This study (plot SF)

629   n.a.; not available.

630

631   **Table 8**. Aboveg- and belowground biomass in un-managed *Phyllostachys pubescens* forest from previous studies and this study.

632

Site	Culm density (shoots ha^{-1})	Aboveground biomass (Mg ha$^{-1)}$)	Belowground biomass (Mg ha^{-1})	Reference
Kagoshima Prefecture	5000 - 6130	82.8 - 146.6	n.a.	Kumemura *et al.* (2009)
Kyoto Prefecture	7700	137.9	44.6	Isagi *et al.* (1997)
Central Taiwan	6996 - 7188	81.6 - 96.8	n.a.	Yen and Lee (2011)
Kyoto Prefecture	7967 - 8300	217 - 224	n.a.	Abe and Shibata (2009)
Aichi Prefecture	2400 - 4790	31.4 - 107	36 - 67.5	Umemura and Takenaka (2014b)
Gifu Prefecture	8125 - 16300	42.1 - 83.5	89.1 - 98.5	Goto *et al.* (2008)
Kyoto Prefecture	9675	182.1	127.1	This study (plot BF)

633   n.a.; not available

634 **Table 9** C/N ratios of aboveground and belowground compartments and soil layers, their respective

635 subtotals, and total values.

		SF	MF1	MF2	BF
Aboveground	Leaf	33.5	32.3	27.6	21.2
	Branch	136.3	130.7	111.8	89.4
	Stem and Culm	268.6	265.8	256.9	246.8
	Subtotal	189.7	187.3	182.3	174.9
Belowground	Coarse root	78.4	93.7	121.9	192.7
	Fine root	60.9	81.2	84.8	85.4
	Rhizome	n.a.	169.2	169.2	169.2
	Stump	n.a.	169.2	169.2	169.2
	Subtotal	75.9	97.2	107.0	132.9
Soil	Oi layer	45.4	45.9	51.3	62.1
	Oe+Oa layer	18.1	22.8	24.4	23.4
	Root mat layer	n.a.	23.6	19.5	19.0
	0-10 cm	17.8	21.9	18.3	15.3
	10-30 cm	16.7	17.5	15.9	19.6
	Subtotal	17.9	21.2	17.7	18.3
Total		50.2	56.2	53.0	50.4

636 n.a.; not available.

637   Figure legends

638

639   **Fig. 1** Location of the study site.

640

641   **Fig. 2** Diameter at breast height (DBH) frequency distributions of *P. pubescens* (■) and other plants

642   (□) in the study plots: (a) plot dominated by secondary broad-leaved forest (SF), (b) mixed

643   bamboo/broad-leaved forest plot subjected to bamboo invasion since 1974 (MF1), (c) mixed

644   bamboo/broad-leaved forest plot subjected to bamboo invasion since 1961 (MF2), (d) plot

645   dominated by bamboo (BF).

646

647   **Fig. 3** Vertical distributions of biomass in *P. pubescens* roots ($n = 2$ for the root mat layer, $n = 4$ for

648   each mineral soil layer in the 0–30 cm depth range, and $n = 2$ for rhizomes). Error bars are standard

649   deviation (SDs).

650   * RM; root mat

651

652   **Fig. 4** (a) Aboveground and (b) belowground biomasses of broad-leaved trees and *P. pubescens*

653   organs; (c) total biomass.

654

655   **Fig. 5** (a) Ratios of non-photosynthetic organ to photosynthetic organ dry weights (C/F); (b) ratios of

656   aerial organ to root dry weights (T/R) for whole plants, broad-leaved trees, and *P. pubescens*.
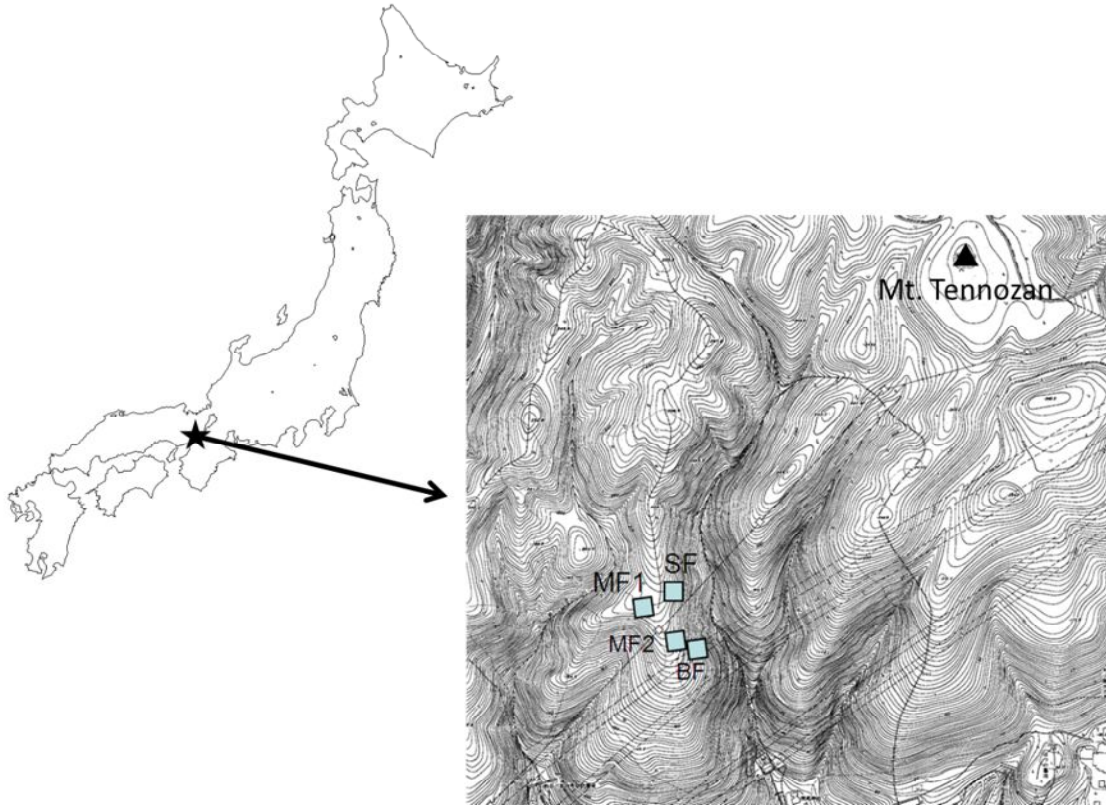
657

658   **Fig. 6** (a) Carbon and (b) nitrogen stocks in all aboveground and belowground compartments and in

659   each soil layer.

660

661   **Fig. 7** The proportion of above- and belowground compartments and soils to total (a) carbon and (b)

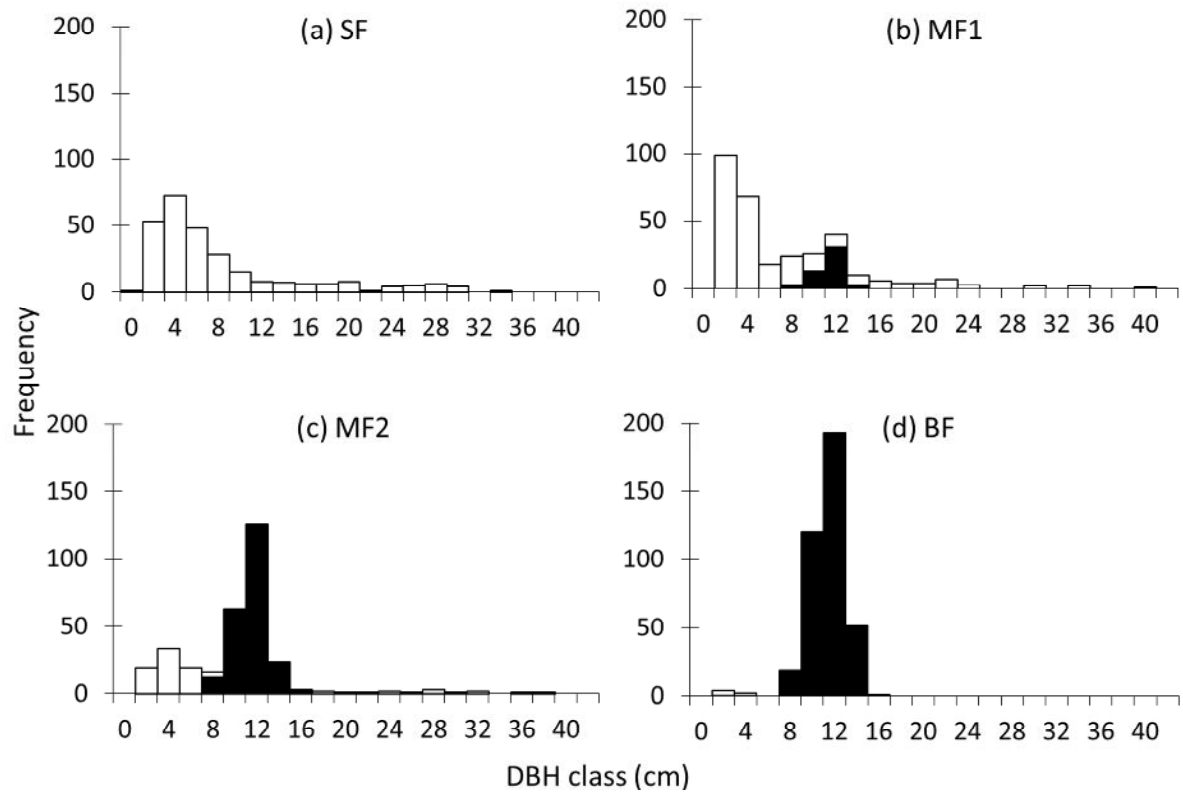662   nitrogen stocks for four plots.
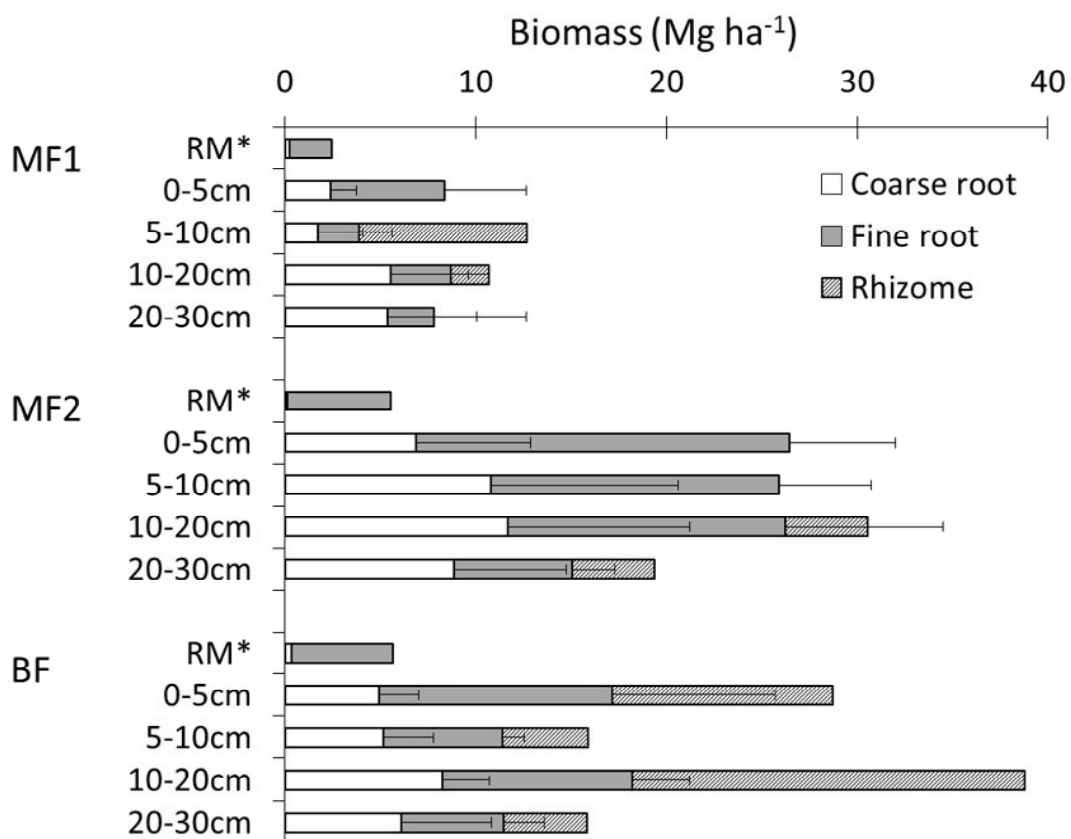
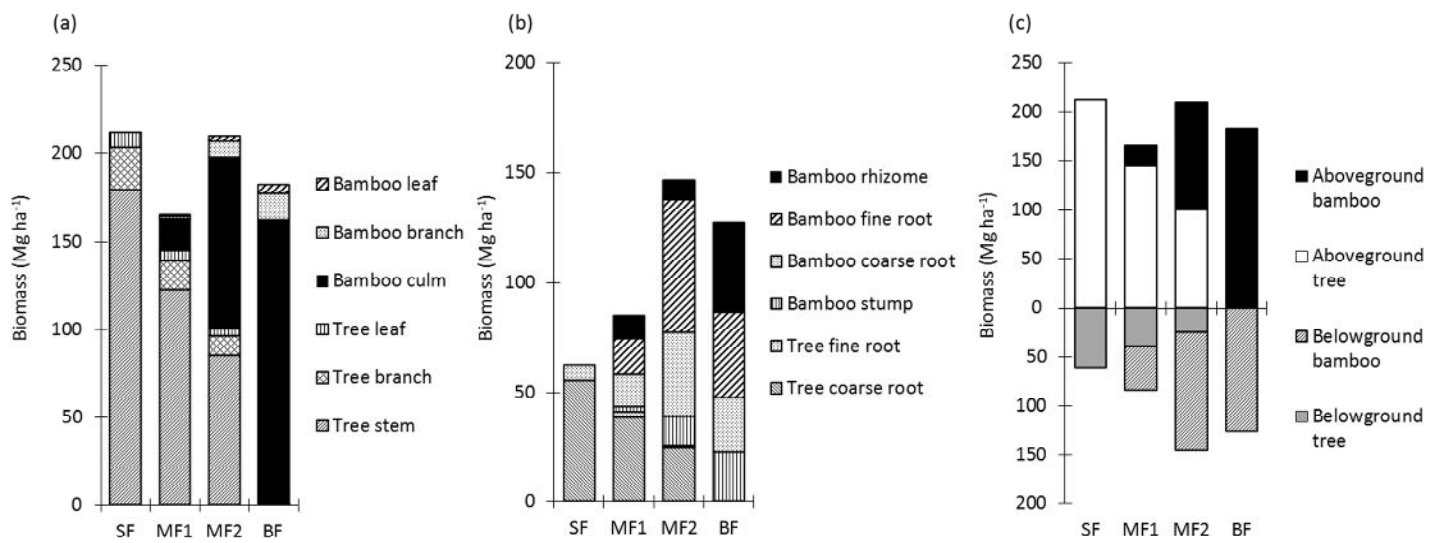663

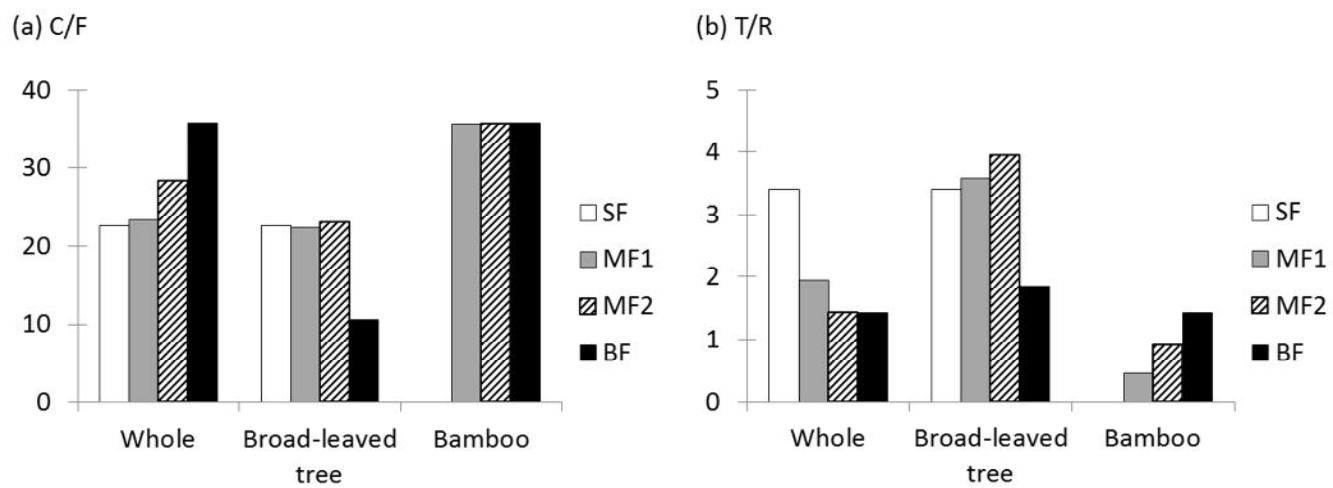664   Fig. 1

665

666

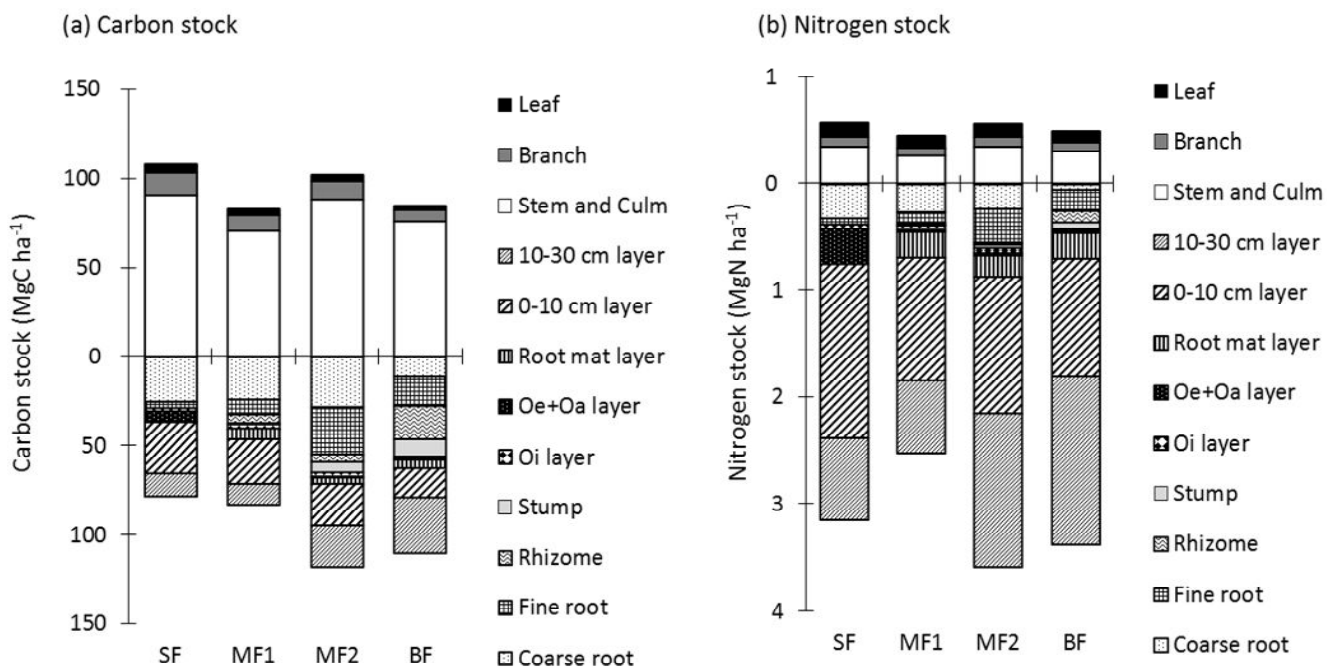667   Fig. 2

668

669

670   Fig. 3

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672

673   Fig. 4

674

675

676   Fig. 5

(a) C/F

(b) T/R

677

678

679   Fig. 6
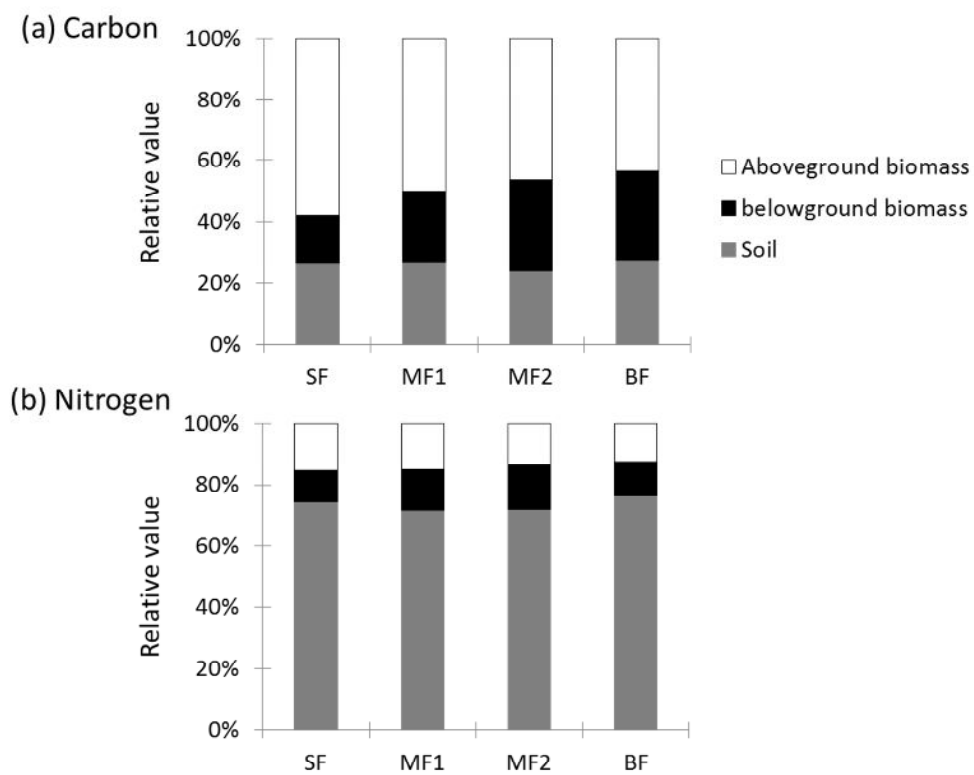

(a) Carbon stock

(b) Nitrogen stock

680

681

682

683   Fig. 7

684

685

686   Appendix A. Biomass of above- and belowground compartments, their respective totals, and total values.

687

| Mg ha-1 | Broad-leaved tree | | | | | | | Bamboo | | | | | | | | | Total biomass |
| | Aboveground | | | | Belowground | | | Avobeground | | | | Belowground | | | | | |
Plot	Leaf	Branch	Stem	Total	Coarse root	Fine root	Total	Leaf	Branch	Culm	Total	Stump	Coarse root	Fine root	Rhizome	Total	
SF	8.95	23.8	179.1	211.8	55.2	6.93	62.1	0	0	0	0	0	0	0	0	0	273.9
MF1	6.21	16.4	122.4	145.1	38.3	2.14	40.5	0.54	1.66	17.7	19.9	2.5	15.1	16.0	10.8	44.4	249.8
MF2	4.16	11.2	84.6	100.1	24.3	0.99	25.3	2.98	9.08	97.5	109.6	13.4	38.2	60.8	8.6	121.1	356.1
BF	0.01	0.02	0.07	0.10	0.05	0.00	0.05	4.94	15.1	162.0	182.1	22.3	24.7	39.1	41.0	127.1	309.4

688

689

690 Appendix B. Carbon and nitrogen stocks in aboveground and belowground compartments and in

691 each soil layer, their respective subtotals, and total values.

		SF	MF1	MF2	BF
C (MgC ha-1)					
Aboveground biomass	Leaf	4.7	3.5	3.5	2.1
	Branch	12.3	9.3	10.0	6.9
	Stem and Culm	91.2	70.6	88.7	75.9
	Subtotal	108.2	83.4	102.2	85.0
Belowground biomass	Coarse root	25.5	24.4	28.1	10.9
	Fine root	3.2	7.9	26.7	16.9
	Rhizome	n.a.	4.8	3.8	18.2
	Stump	n.a.	1.1	5.9	9.9
	Subtotal	28.7	38.1	64.6	55.9
Soil	Oi	1.9	1.9	2.3	1.4
	Oe+Oa	5.9	0.5	0.6	0.5
	RM	n.a.	5.5	3.9	4.4
	0-10	29.1	25.3	23.3	16.9
	10-30	12.8	11.8	22.8	30.9
	Subtotal	49.7	45.0	53.0	54.0
Total		186.6	166.5	219.8	194.9
N (MgN ha-1)					
Aboveground biomass	Leaf	0.14	0.11	0.13	0.10
	Branch	0.090	0.071	0.089	0.078
	Stem and Culm	0.34	0.27	0.35	0.31
	Subtotal	0.57	0.44	0.56	0.49
Belowground biomass	Coarse root	0.32	0.26	0.23	0.057
	Fine root	0.053	0.098	0.32	0.20
	Rhizome	n.a.	0.028	0.023	0.11
	Stump	n.a.	0.006	0.035	0.058
	Subtotal	0.38	0.39	0.60	0.42
Soil	Oi	0.041	0.040	0.045	0.022
	Oe+Oa	0.33	0.023	0.023	0.021
	RM	n.a.	0.24	0.20	0.23
	0-10	1.63	1.15	1.28	1.10
	10-30	0.77	0.67	1.44	1.58
	Subtotal	2.77	2.13	2.98	2.96
Total		3.72	2.96	4.15	3.86

692 n.a.: not available.