Title:

Impacts of moso bamboo (*Phyllostachys pubescens*) invasion on dry matter, and carbon and nitrogen stocks in a broad-leaved secondary forest located in Kyoto, western Japan

Authors:

Keitaro Fukushima 1, *, Nobuaki Usui 2, Ryo Ogawa 2, Naoko Tokuchi 1

Affiliation:

1: Field Science Education and Research Center, Kyoto University, Kyoto 606-8502, Japan

2: Graduate School of Agriculture, Kyoto University, Kyoto 606-8522, Japan

* Corresponding author; Keitaro Fukushima

(Present affiliation and address) Faculty of Urban Environmental Sciences, Tokyo Metropolitan University, 1-1 Minami-osawa, Hachioji city, Tokyo 192-0397, Japan

Tel; +81-42-677-1111

Email; ktaro.f@gmail.com

Abstract

In western and central Japan, the expansion of exotic moso bamboo (*Phyllostachys pubescens* Mazel ex J. Houz.) populations into neighboring vegetation has become a serious problem. Although the effects of bamboo invasion on biodiversity have been well studied, shifts in nutrient stocks and cycling, which are fundamental for ecosystem functioning, are not fully understood. To explore the effects of *P. pubescens* invasion on ecosystem functions, we examined above- and belowground dry matter, and carbon (C) and nitrogen (N) stocks, in a pure broad-leaved tree stand, a pure bamboo stand, and two tree–bamboo mixed stands with different vegetation mix ratios in the secondary forest of Kyoto, western Japan. In the process of invasion, bamboo shoots offset broad-leaved tree deaths; thus, no clear trend was apparent in total above- or belowground biomass or in plant C and N stocks during invasion. However, the ratio of aboveground to belowground biomass (T/R ratio at the stand level) decreased with increasing bamboo dominance, especially in the early stages of invasion. This shift indicates that rapid bamboo rhizomatous growth is a main driver of substantial changes in stand structure. We also detected rises in the C/N ratio of forest-floor organic matter during bamboo invasion. Thus major impacts of *P. pubescens* invasion into broad-leaved forests include not only early shifts in biomass allocation, but also changes in the distribution pattern of C and N stored in plants and soil.

Keywords: allocation pattern, bamboo invasion, carbon and nitrogen stocks, *Phyllostachys pubescens*, stand structure.

Introduction

Moso bamboo (*Phyllostachys pubescens* Mazel ex J. Houz.), one of the largest bamboo species in the world, was introduced from China into western Japan about 300 years ago for use as human food (young sprouts) and other products (adult culms) (Suzuki 1978; Shibata 2003). The species has been transplanted across a wide range of areas in western and central Japan, where well-managed plantation forests were established. Since the 1980s, most of these forests have been abandoned due to rapid declines in domestic bamboo industries.

Like other bamboo species, *P. pubescens* has active rhizomatous clonal growth. The belowground rhizome system is leptomorphic; it grows laterally, allowing rapid, widespread expansion of ramets (Makita 1998). Furthermore, young shoots quickly reach full heights of 10–20 m matching those of well-developed canopy trees. These growth capabilities probably facilitate invasions of neighboring secondary broad-leaved forests and/or coniferous plantations, whereby the bamboos rapidly become dominant components of the vegetation and often form pure stands in previously deciduous or coniferous vegetation (Isagi & Torii 1998; Suzuki & Nakagoshi 2011; Suzuki 2014). A clear risk of losing biodiversity and ecosystem functioning exists when exotic giant bamboos establish near-monospecific stands in previously diverse woodlands. Studies are urgently required to identify the relationships between growth characteristics of *P. pubescens*, its overwhelming invasion impacts, and ecosystem functioning.

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

Kisanuki 2006; Zhang *et al*. 2010; Akutsu *et al*. 2012; Bai *et al*. 2013). However, few studies have reported on the effects of invasion on the sizes of carbon (C) and nitrogen (N) stocks or their cycling. Information on these parameters is crucial for better understanding of ecosystem functioning before and after invasion. However, data on the biogeochemical characteristics of pure bamboo forests are available. For example, Isagi *et al*. (1997) showed that values of gross production and belowground C allocation in *P. pubescens* stands are higher than those in temperate broad-leaved and/or coniferous forest stands. The canopy of *P. pubescens* forest has higher N contents (Li *et al*. 1998) and elevated transpiration rates (Komatsu *et al*. 2010) in comparison with broad-leaved and/or coniferous forest, suggesting that the canopy photosynthetic rate may be higher in *P. pubescens* stands than in native forest vegetation (Yen & Lee 2011). These characteristics are likely common to other bamboo species under various climatic conditions (Isagi 1994; Tripathi & Singh 1996; Tu *et al.* 2013).

Previous research on the impacts of bamboo invasions and/or range expansions on C and N biogeochemistry in Japan have focused on the understory dwarf species *Sasa kurilensis* (Rupr.) Makino & Shibata, which has growth traits similar to those of *P. pubescens* with the exception of culm height (Tripathi *et al*. 2005; Watanabe *et al*. 2013; Fukuzawa *et al*. 2014). These works have shown that *S. kurilensis* contributes greatly to C and N retention and their cycling in broad-leaved forest biomass and soils, but bamboo invasion and replacement of vegetation in native forests were not included in the scope of these studies.

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

pubescens, into secondary broad-leaved forest on (i) dry matter mass, (ii) C stocks, and (iii) N stocks in both plants and soils. We measured these parameters in above- and belowground plant parts, and in soil horizons of a secondary forest, in a pure *P. pubescens* stand, and in two mixed forest stands that differed in the degree of bamboo invasion.

Materials and methods

Study site

Fieldwork was conducted on Mt. Tennozan located on the boundary between Kyoto and Osaka prefectures in western Japan (34°54′N, 135°46′E; Fig. 1). Mean annual temperature and precipitation at the nearest weather station (AMeDAS) were 15.3°C (2001–2010, AMeDAS Kyotanabe, 34°50′N, 135°46′E) and 1459 mm (2001–2010, AMeDAS Nagaokakyo, 34°56′N, 135°41′E), respectively. The bedrock geology of our study area comprised Mesozoic sedimentary sandstone, shale, and chert belonging to Tamba terrane.

The native forest we studied was dominated by broad-leaved trees, including *Quercus serrata* Thunb. and *Quercus variabilis* Blume, which are typical of Japanese temperate secondary woodlands. *P. pubescens* was introduced a few hundred years ago in a patchy distribution pattern through the region. The stands were well managed for the production of young bamboo sprouts as human food. Broad-leaved secondary forests were established and cut for fuel. Broad-leaved trees were harvested in our study area until the 1950s, but no anthropogenic disturbance has occurred for at least 60 years (Tokuchi *et al*. 2010). *P. pubescens* plantations in this region have been abandoned since the 1970s, and invading bamboo shoots were still expanding into neighboring broad-leaved forests at the time of our study (Torii & Isagi 1997; Torii 1998). According to a vegetation census by aerial photography in 2003, 46% of the areas around Mt. Tennozan (238.5 ha) are covered by secondary broad-leaved forests, 41% by *P. pubescens* stands, and 7% by mixed broad-leaved/bamboo stands (Tokuchi *et al*. 2010).

We selected vegetation stands dominated by (i) broad-leaved trees, (ii) *P. pubescens*, and (iii) mixed stands of trees and bamboo along a ridge located on Mt. Tennozan. We established one square plot (20 × 20 m) in broad-leaved tree forest stand (SF), one in a moso bamboo stand (BF), and two plots containing mixed forest stands (MF1, MF2). According to the earlier aerial photographs (1961, 1974, and 2003), BF had been dominated by *P. pubescens* prior to 1974. The bamboo has been invading MF1 since 1974 and MF2 since 1961. In plots MF1, MF2, and BF, expanding and overcrowding bamboo shoots have not been cut or managed during recent decades. Thus, plots SF, MF1, MF2, and BF represent a stage with no *P. pubescens* invasion, an early stage of invasion, a mid-stage of invasion, and a last stage of invasion, respectively.

Vegetation censuses and biomass estimation

We measured diameters at breast height (DBHs; cm) and identified all trees and bamboo shoots exceeding 1 cm in DBH.

Above- and belowground biomasses of broad-leaved trees in all plots were estimated using allometric equations relating DBH and height developed by different author earlier (Nishioka *et al.* 1982; Goto *et al.* 2006; Ogawa & Kira 1977; Nagano & Kira 1978; Ogino 1977). Broad-leaved tree biomasses allocated to stems (main trunks, W_s; kg), branches (W_b; kg), and leaves (W_l; kg) were calculated thus:

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

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

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

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

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

where a and b are constants, and H_{max} is the asymptotic maximum height (m; Ogawa & Kira 1977). $DBH_{0.1}$ is stem diameter (cm) for a position located one-tenth of the way along the maximum trunk length; $DBH_{0.1}$ was estimated from the measured DBH using the following empirical equation, which was developed for a warm–temperate secondary oak forest by Nagano and Kira (1978):

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

We calculated the biomass of broad-leaved tree coarse roots (≧2 mm in diameter) (W_{below}; kg) using the following extended allometric equation:

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

Eq. 6 was developed for a cool–temperate beech forest by Ogino (1977). We estimated the biomass of broad-leaved tree fine roots (<2 mm in diameter) by soil block sampling (see below).

To estimate the aboveground biomass of *P. pubescens* shoots, we applied the allometric equation developed for a site close to one of our study plots (BF) by Abe and Shibata (2009) in June 2006:

$$W = a \times \mathrm{DBH}^{b}, \tag{7}$$

where parameters a and b were estimated individually for culms, branches, and leaves. The allometric relationship between the dry weight of each component and culm DBH was calculated separately for current-year shoots and shoots older than 1 year (Abe & Shibata 2009). The parameters are summarized in Table 1.

We used two methods of soil-block sampling to estimate the belowground biomass of *P. pubescens* shoots. One method estimated the "stump," which we define here as the culm between the soil surface and rhizome (stump-block); the second method was used for root estimation (root-block). In the first procedure, we carefully excavated three soil blocks (each 50 × 50 cm to 50 cm depth) centered around bamboo shoots by using a shovel and saw within the pure *P. pubescens* stand located outside plot BF in August 2006. We cut free the aboveground part, dug into the soil, and carefully excavated the subterranean parts of the shoot. The stump-blocks were washed with tap water to remove mineral soils. The remaining root systems were separated into the stump and other components. The stumps were dried at 40°C for 1 week and then weighed. We constructed an allometric equation from the relationship between the dry weight of stump per shoot and culm DBH (see Eq. 7), and subsequently estimated the total bamboo stump biomass within our plots as a portion of the belowground biomass components.

In the second procedure, we collected two soil blocks (50 × 50 cm to 30 cm depth) inside each plot in the period from February to April 2006 for our calculations of root biomass per unit area and the extent of bamboo rhizome lateral extension. These root-block samples were divided into vertical portions 0–5, 5–10, 10–20, and 20–30 cm downward from the soil surface.

Within plots MF1, MF2, and BF, we found several centimeter-thick layers of live fine- and coarse-roots between the mineral and organic layers (see below). We termed this layer the “root mat” (RM) and separated it out from the other layers in the root-blocks. The living roots in the RM and mineral soil layers were divided into those from broad-leaved trees and those from *P. pubescens*, and sorted by hand into categories of fine roots, coarse roots, and bamboo rhizomes in the laboratory. Each component was carefully separated according to illustrations in Suzuki (1978) and Makita (1998). We distinguished rhizomes from roots by the presence of nodes in the former. The various components were dried at 40°C for 72 h and weighed. The area-based biomasses of these components were determined by calculation for these soil blocks.

Finally, we used the predictions of our allometric regressions for stand-level integration of the biomasses of stems, branches, leaves, and coarse roots of broad-leaved trees, and the biomasses of culms, branches, leaves, and stumps of *P. pubescens*. We used the root-block predictions to integrate area-based biomasses of tree fine roots, and bamboo coarse roots, fine roots, and rhizomes in the RM and mineral soil layers.

Soil sampling

We estimated the dry masses of organic matter in the organic soil layers of the four plots. Four frames (20 × 20 cm) were deployed haphazardly on the surface soils in the period February–April 2006, and from these, we collected all forest-floor organic matter in the litter (Oi) and humus layers (Oe+Oa). Samples of this organic matter were dried at 40°C for 1 week and weighed.

We used soils collected in the root-blocks to determine soil bulk density. After removing roots and rhizomes, we divided the dry weight of fine mineral soil that passed through a 2-mm sieve by the total dry weight of bulk soil for each soil layer. Organic matter and mineral soils were also present in the RM layer. Consequently, we used a 4-mm mesh to sieve the RM samples collected from the root-blocks in preparation for soil analysis.

Chemical analysis

Bamboo organs (leaves, branches, culms, fine and coarse roots, and rhizomes), forest-floor organic matter, and mineral soils were ground in a mill prior to measurements of C and N contents with a NC analyzer (NC-22A; Sumigraph, Osaka, Japan). We assumed that the C and N contents of bamboo stumps were the same as those in bamboo rhizomes. Reports have indicated that the C and N contents of *P. pubescens* leaves vary significantly by culm age (Li *et al*. 1998). Thus, we made separate measurements of aboveground compartments of *P. pubescens* on current-year shoots and those older than 1 year. We obtained C and N contents of most broad-leaved tree organs from previous reports (Tsutsumi *et al*. 1968; Katagiri & Tsutsumi 1975), but our data on fine and coarse roots were obtained by the analyses described above. By multiplying the dry weights of plant organs or soil organic matter in the soil layers by the respective C and N contents and summing, we were able to estimate the total area-based C and N stocks in each plot.

Data analysis

We used paired *t*-tests to detect significant differences in the C and N contents of *P. pubescens* leaves, branches, and culms between current-year shoots and those older than 1 year. The Kruskal-Wallis test was used to test the effect of stand characteristics on the mean C and N contents in coarse and fine roots of bamboo and broad-leaved trees, and in bamboo rhizomes and stumps. We also used the Stell-Dwass post hoc test for multiple comparisons to detect differences in the mean C and N contents in these components between pairs of stand types. Significant differences in the mean C and N contents in the soil organic matter within each layer (forest floor, RM, and 0–10-cm and 10–30-cm layers) among stand types were also analyzed by the Kruskal-Wallis test followed by the Steel-Dwass post hoc test. Statistical analyses were performed using R software (R Development Core Team 2010).

Results

Stand structure

Stem and culm densities, mean DBH, total basal area (BA), proportion of *P. pubescens* in BA, numbers of species, and dominant broad-leaved tree species in SF, MF1, MF2, and BF are summarized in Table 2. As the proportions of *P. pubescens* in BA increased, the numbers of plant species in the plots decreased (Table 2). Patterns of DBH frequency distribution differed dramatically among plots (Fig. 2). Thus, DBH distributions of broad-leaved trees were positively skewed in plots SF, MF1, and MF2, while DBH distributions of bamboo shoots showed a normal curve in plots MF1, MF2, and BF. In mixed stands (plots MF1 and MF2), distributions showed a bimodal curve with one smaller mode comprising the DBH distribution of broad-leaved trees and the larger mode comprising that of bamboo shoots. Mean DBH values of bamboo culms were similar among the plots regardless of differences in culm density (Table 2). As bamboo culm densities increased, the frequencies of broad-leaved trees with DBH values <12 cm decreased dramatically (e.g., in plot MF2); we found no trees with DBH values >12 cm in plot BF (Fig. 2).

Above- and belowground biomasses

We used an allometric equation (Eq. 7) describing the relationship between culm DBH and stump dry weight to predict biomasses of belowground stumps of *P. pubescens* shoots; the calculated values of parameters a and b were 7.71×10^{-2} and 1.434 ($r^2 = 0.954$), respectively.

Figure 3 depicts the vertical distribution of belowground biomasses of coarse and fine roots, and rhizomes of *P. pubescens* shoots per unit area in plots MF1, MF2, and BF. Fine roots of *P. pubescens* occurred most densely in the 0–5-cm mineral soil layer; coarse roots and rhizomes occurred most densely below 5 cm soil depth (Fig. 3).

Details of aboveground and belowground biomasses of each compartment, and total biomasses are presented in Fig. 4 and Appendix A. No increasing or decreasing trends were observed in aboveground and total biomasses. However, belowground biomass increases were associated with *P. pubescens* invasions (Fig. 4). At the stand level, the dry mass ratio of non-photosynthetic organs to photosynthetic organs (culm/foliage ratio, C/F; Iwaki 1958) increased from 22.7 to 35.8 (Fig. 5a), while the dry mass ratio of aboveground organs to belowground organs (top/root ratio, T/R) decreased from 3.41 to 1.39 as the proportion of bamboo increased in BA (Fig. 5b). The C/F ratio of broad-leaved trees remained constant among plots other than BF (Fig. 5a), in which all large canopy trees had disappeared as a result of the bamboo invasion (Fig. 2). No differences were detected in the C/F ratio of *P. pubescens* shoots across our plots (Fig. 5a). Among plots, the T/R ratio of broad-leaved trees was lowest in BF; the T/R ratio of *P. pubescens* tended to increase with increasing proportions of bamboo in BA (Fig. 5b).

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

Values of forest-floor organic matter mass in the Oi layer were not significantly different among plots (Kruskal-Wallis test, $P > 0.05$), but those in the Oe+Oa layer were significantly larger in plot SF than in the other plots (Kruskal-Wallis and Steel-Dwass tests, $P < 0.05$; Table 3).

The bulk density of mineral soil that passed through a 2-mm sieve tended to increase with depth and decrease with the proportion of bamboo in BA (Table 4). The RM layer, which appeared to have developed between the organic and the mineral soil layers in the presence of *P. pubescens*, included a small amount of mineral soil (Table 4).

C and N contents and stocks in plants and soils

Details of the mean C and N contents in each compartment of *P. pubescens* and broad-leaved trees are listed in Table 5. In *P. pubescens*, the C contents in leaves, branches, and culms were not significantly different between current shoots and shoots older than 1 year (paired *t*-test, $P > 0.05$; Table 5), and the N contents in leaves, branches, and culms did not vary between the two age classes of shoots (paired *t*-test, $P > 0.05$; Table 5). The leaves and the branches of *P. pubescens* contained less C and more N than equivalent organs of broad-leaved trees. The culms of *P. pubescens* contained less C than the stems of broad-leaved trees; the N contents in bamboo culms and tree stems were closely similar (Table 5). The coarse and fine roots of *P. pubescens* contained less C and N than those of the broad-leaved trees (Table 5). C and N contents in the rhizomes, stumps, and coarse roots of *P. pubescens* were closely similar.

C and N contents of each soil layer in the four plots are detailed in Table 6. C and N contents in the Oi layer differed significantly among plots (Kruskal-Wallis and Steel-Dwass tests, $P < 0.05$). As the proportion of bamboo BA increased in the stands, the C and N contents in this layer decreased (Table 6).

Values of C stocks in plants and soils in the stands ranged from 83.4 to 108.2 MgC ha^{-1} in aboveground parts, from 28.7 to 64.6 MgC ha^{-1} in belowground parts, and from 45.0 to 54.0 MgC ha^{-1} in soils (Fig. 6a, Appendix B). The values of N stocks ranged from 0.44 to 0.57 MgN ha^{-1} in aboveground parts, from 0.38 to 0.60 MgN ha^{-1} in belowground parts, and from 2.13 to 2.98 MgN ha^{-1} in soils (Fig. 6b). Forty to sixty percent of C was stored in aboveground parts, but >70% of the stand N stock was stored in the soils (Fig. 7). The proportion of total stand C stored in belowground parts increased with increasing proportions of bamboo BA, but the proportions of N shifted little in response to increasing bamboo BA (Fig. 7).

Discussion

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

The dominant tree species in our stands were *Q. serrata* and/or *Q. variabilis*, which are typical of the secondary forest around Mt. Tennozan (Table 2). The above- and belowground biomasses in a pure stand of broad-leaved trees (SF) were 211.8 and 62.1 Mg ha^{-1}, respectively (Fig. 4, Appendix A); these values exceed those previously reported for forests with similar tree species composition in the other areas (Table 7). The differences between studies is likely attributable the greater stand age (~60 years) and a higher density of trees with DBH >5 cm in our data set. Surviving large trees with DBH values exceeding 30 cm on Mt. Tennozan also contributed significantly to the large biomass values we calculated.

Culm density (9675 ha^{-1}; Table 2) and aboveground biomass (182.1 Mg ha^{-1}; Fig. 4, Appendix A) in the abandoned pure *P. pubescens* stand (BF) were within the range of previously reported values for equivalent vegetation, but belowground biomass we measured (127.1 Mg ha^{-1}; Fig. 4, Appendix A) exceeded previously reported values (Table 8). *P. pubescens* biomass surveys in various regions of Japan have detected an exponential relationship between BA and above- or belowground biomasses (FFPRI 2009). Using this regression relationship, we calculated biomasses 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 ha^{-1} below ground, which fit our empirical estimates for aboveground biomass but not those for belowground biomass. The discrepancy between estimates is likely due to the difficulty in accurately defining the belowground compartment of bamboo species, especially for the leptomorph types like *P. pubescens*. Comprehensive inclusion of all belowground compartments requires estimation of the spatial extent of rhizome and root system biomasses in addition to stump estimates derived from the allometric relationship with DBH. Previous studies may not have implemented this inclusive procedure and therefore underestimated belowground biomass. We believe that our comprehensive approach provides reliable values.

We calculated T/R values of 3.41 and 1.39 in the secondary broad-leaved (SF) and *P. pubescens* stands (BF; Fig. 5b), respectively. According to Saito (1989), T/R falls within the range of 3–7 and is close to unity in broad-leaved/coniferous forest stands and grasslands. Thus, our measure of stand structure in *P. pubescens* vegetation was close to that of grassland meadows, but bamboo biomass was comparable to that of a well-developed secondary forest.

Changes in stand structure and biomass as bamboo invasion proceeds

In our study sites, bamboo density and percentage of bamboo in total BA was higher in the plot where the number of years passed after *P. pubescens* invasion was longer (Table 2), indicating that the dominance of *P. pubescens* in the plot represents a stage of invasion.

As *P. pubescens* invaded our secondary forest sites, numbers of plant species decreased and total basal area increased. Okutomi *et al*. (1996) observed similar shifts in the vegetation during a study of plant spatial distributions and canopy structures in a mixed broad-leaved tree/bamboo forest, although they did not determine biomasses. At our study site, the above- and belowground biomasses of broad-leaved trees decreased as those of *P. pubescens* increased, but no monotonous trends were apparent in the summed biomass data (Table 5c). These relationships might be explainable as follows. In the early stages of invasion, smaller trees are replaced by small numbers of bamboo culms, with consequent decreases in whole stand biomass (plot MF1). Only large trees survive as the invasion proceeds. During the mid-stages of the invasion process, bamboo density increases and stand biomass reaches a maximum (as in plot MF2). Finally, whole stand biomass decreases when high densities of bamboo cause the deaths of large broad-leaved trees (perhaps due to competition for light, water, and/or mineral nutrients), as in plot BF.

An increase in the C/F ratio as bamboo dominance increased indicates that the proportion of photosynthetic organs in the aboveground biomass increased at the stand level (Fig. 5a). *P. pubescens* is a highly productive plant that produces more leaves on fewer culms (stems) than woody species (Isagi *et al.* 1997; Yen & Lee 2011). In addition, the leaf N contents of *P. pubescens* exceeded those of woody plants (Table 5, Li *et al.* 1998), suggesting that *P. pubescens* has a higher photosynthetic capacity (Reich *et al.* 1997). Isagi *et al.* (1997) measured high gross production rates in a *P. pubescens* stand. They also pointed out that a large proportion of the photosynthetic products was allocated to belowground systems and then transported to newly developing bamboo shoots (Isagi *et al.* 1997).

In stands where bamboo had invaded secondary forest (plots MF1 and MF2), the belowground biomass of *P. pubescens* exceeded aboveground biomass (Fig. 4c, Appendix A), and the stand T/R ratio declined dramatically (Fig. 5b). These trends indicate that the ramet population of *P. pubescens* initially expands its root system into adjacent forest stands, a process that results in rapid changes in stand biomass distribution.

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

Although aboveground compartments of *P. pubescens* had lower C and higher N contents than those of broad-leaved trees (Table 5), total aboveground C and N stocks did not change monotonically following *P. pubescens* invasion of secondary forest stands (Fig. 6) due to an aboveground biomass buildup during invasion. The C and N contents in the belowground compartments of broad-leaved trees exceeded those of bamboo (Table 5). C stocks per unit area in belowground compartments and total belowground biomass approximately doubled during *P. pubescens* invasions (Fig. 6a, Appendix B), but N stocks did not change (Fig. 6b, Appendix B). This indicates that the difference of not only the dry matter mass but also the chemical content of each plant compartment between broad-leaved tree and *P. pubescens* can largely affect the element stock and distribution in the forest stand. These physiological characteristics of *P. pubescens* including higher productivity, greater belowground allocation, and lower C and/or higher N contents in leaves rather than those of trees are partly reported in cases of some other bamboo species, such as *P. bambusoides* Sieb. et Zucc. in western Japan (Isagi *et al.* 1993), *Bambusa* spp. in Puerto Lico (O'Connor et al. 2000), and *Dendrocalamus strictus* (Roxb.) Nees in India (Tripathi & Singh 1996). Because these studies only described the stand structure and/or nutrient dynamics in bamboo forest, further researches are necessary to elucidate their changes by bamboo invasion into the native forest in each area.

When total values were calculated by summing the stocks for plants and soil organic matter in each plot, the ratio of belowground C in total C stocks increased during bamboo invasion of secondary forest (Fig. 7a). Thus, the development of *P. pubescens* root systems may greatly change the C distribution in forest stands.

More than 70% of N was stored in the soils (Fig. 7b). In general, microbial decomposition of organic matter in forest soils releases C as gaseous CO_2 into the atmosphere, but N is largely immobilized and retained underground (e.g., Vitousek et al. 1979; Johnson *et al.* 2000; Berg & McClaugherty 2014). This results in little effect of invasions by *P. pubescens* on N stock size or its distribution.

The C/N ratio of organic matter in the surface soil layer (on a weight basis) is a useful indicator of the degree of decomposition (Berg & McClaugherty 2014), net nitrification rate (Goodale & Aber 2001; Fukushima *et al.* 2011) and leaching of mineralized N from forest soils (Lovett *et al*. 2004). When forest-floor organic matter with a relatively high C/N ratio decomposes, organic N is generally mineralized but then rapidly immobilized by heterotrophic soil microbes. When the C/N ratio of soil organic matters decreases as decomposition progresses, microbe demand for mineral N becomes satiated; inorganic N is then nitrified by autotrophic nitrifiers and subsequently leached from the soil. The C/N ratio of the forest-floor organic matter at our study site increased monotonically with bamboo shoot density (Table 9). Previous studies revealed that understorey dwarf bamboo like *S. kurilensis* in a broad-leaved secondary forest in northern Japan (Tripathi *et al.* 2005; Watanabe *et al.* 2013) and *Chusquea culeou* E. Desv. in an old-growth broad-leaved forest in Patagonia (Austin & Marchesini 2012) plays a key role in retaining mineral N in soil through N uptake by bamboo and N immobilization during bamboo litter decomposition. The giant bamboo has greater biomass, litter fall, and productivity than dwarf bamboo. Hence, the process of *P. pubescens* invasion into secondary forest may depress the rate of N cycling and prevent the loss of inorganic N from soils.

Moreover, Umemura & Takenaka (2014a) demonstrated that soil pH increases as *P. pubescens* invades surrounding evergreen coniferous forests, which may greatly affect the net nitrification rates in soil because some groups of ammonia-oxidizing bacteria can deactivate and some groups of ammonia-oxidizing archaea can activate under low pH (Nicol *et al.* 2008). Overall, *P. pubescens* invasion into forest stands clearly alters N cycling between plants and soil due to changes in soil organic matter quality (e.g., the C/N ratio) and physicochemical parameters (e.g., pH). The details of these processes should be studied by examining changes in soil N dynamics during invasion.

Conclusion

In our secondary forest located in western Japan, stand structure and the distribution of plant biomass were affected by *P. pubescens* dominance, which is almost equal to the degree of *P. pubescens* invasion. The changes in (i) standing biomass, (ii) C and N stocks in plants and soil, and (iii) their distributions during bamboo invasion were likely triggered by the rapid bamboo rhizomatous clonal growth and the deaths of large(L412-414) broad-leaved trees. Nevertheless, few differences in biomass or C and N stock sizes were observed between a broad-leaved forest stand and a pure *P. pubescens* stand, suggesting that the capabilities for storing C and N in plants and soil are comparable in broad-leaved and bamboo forests. In contrast, the allocation of C into belowground biomass (T/R ratio), the N content of leaves, the C/F ratio in aboveground vegetation, and the C/N ratio in forest-floor organic matter shifted markedly in response to invasion. These shifts are likely driven by the physiological attributes of invading *P. pubescens*, and may have large effects on the rates of C and N cycling and loss in forest ecosystems during early invasion. To better understand the effects of *P. pubescens* invasion on ecosystem functions, future studies on soil N dynamics and N retention will be required.

Acknowledgments

We thank Ms. Satomi Yoneda, Ms. Momoko Sakai, and Dr. Shuhei Matsuyama (Kyoto University) for their assistance in data collection. We also thank Dr. Yuhei Abe (Kagawa Prefecture) for sharing data and Dr. Takahito Yoshioka (Kyoto University) for helpful comments. Funding was provided by a Sasakawa Scientific Research Grant from The Japan Science Society, ESPEC Foundation for Global Environment Research and Technology (ESPEC Prize for the Encouragement of Environmental Studies), a Grant-in-Aid for Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology, Japan (no. 22780145 and 26660127), to KF, and a grant from Suntory Holdings Limited, Japan, to NT.

References

Abe Y. & Shibata S. (2009) Stand structure of non-management *Phyllostachys pubescens* forest and dynamics for 3 years after improvement management in Mt. Tennozan. *Journal of the Japanese Society of Revegetation Technology* 35: 57-62. (in Japanese with English abstract)

Akutsu H., Aizawa M., Matsue K. & Ohkubo T. (2012) Distribution and invasion of *Phyllostachys pubescens* stands into neighboring forests in Nasukarasuyama, Tochigi Prefecture. *Bulletin of Utsunomiya University Forest* 48: 139-152. (in Japanese with English abstract)

Austin A. T. & Marchesini V. A. (2012) Gregarious flowering and death of understorey bamboo slow litter decomposition and nitrogen turnover in a southern temperate forest in Patagonia, Argentina. *Functional Ecology* 26: 265-273.

Bai S., Zhou G., Wang Y., Liang Q., Chen J., Cheng Y. & Shen R. (2013) Plant species diversity and dynamics in forests invaded by Moso bamboo (*Phyllostachys edulis*) in Tianmu Mountain Nature Reserve. *Biodiversity Science* 21: 288-295.

Berg B. & McClaugherty C. (2014) *Plant litter: Decomposition, humus formation, carbon sequestration.* Third Edition. Springer-Verlag, Berlin Heidelberg.

Dannoura M., Suzuki M., Kominami Y., Goto Y. & Kanazawa Y. (2006) Estimation of root biomass and root surface area in a broad-leaved secondary forest in the southern part of Kyoto Prefecture. *Journal of the Japanese Forest Society* 88: 120-125. (in Japanese with English summary)

FFPRI. (2009) Development of a method of estimating carbon accumulation and absorption in

Japanese bamboo forests. *Kenkyu Seika Senshu, Forestry and Forest Products Research Institute 2009*. pp. 4-5. (in Japanese)

Fukushima K., Tateno, R. & Tokuchi N. (2011) Soil nitrogen dynamics during stand development after clear-cutting of Japanese cedar (*Cryptomeria japonica*) plantations. *Journal of Forest Research* 16: 394-404.

Fukuzawa K., Shibata H., Takagi K., Satoh F., Koike T. & Sasa K. (2014) Role of dominant understory *Sasa* bamboo in carbon and nitrogen dynamics following selective tree cutting in cool-temperate forest in northern Japan. *Plant Species Biology* (in press)

Goodale C. L. & Aber J. D. (2001) The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecological Applications* 11: 253-267.

Goto S., Bagana, Kawai H., Zhang F., Jia S., Saijoh Y. & Akiyama T. (2008) Estimation of biomass and carbon storage in abandoned bamboo stands ecosystem. *Journal of the Japanese Agriculture Systems Society* 24: 243-252. (in Japanese with English abstract)

Goto Y., Kominami Y., Miyama T., Tamai K. & Kanazawa Y. (2003) Aboveground biomass and net primary production of a broad-leaved secondary forest in the southern part of Kyoto Prefecture, Central Japan. *Bulletin of Forestry and Forest Products Research Institute* 2: 115-147. (in Japanese with English abstract)

Goto Y., Tamai K., Miyama T., Kominami Y. & Hosoda I. (2006) Effects of disturbance on vertical stratification of broad-leaved secondary forests in Tatsunokuchi-yama Experimental Forest. *Bulletin of Forestry and Forest Products Research Institute* 5: 215-225. (in Japanese with

English abstract)

Hasegawa M. (1989) Productivity of the oak coppice forests. *Journal of the Toyama Forestry and Forest Products Research Center* 2: 5-12. (in Japanese)

Isagi Y. (1994) Carbon stock and cycling in a bamboo *Phyllostachys bambusoides* stand. *Ecological Research* 9: 47-55.

Isagi Y., Kawahara K. & Ito H. (1997) Net production and carbon cycling in a bamboo *Phyllostachys pubescens* stand. *Plant Ecology* 130: 41-52.

Isagi Y., Kawahara K. & Kamo K. (1993) Biomass and net production in a bamboo *Phyllostachys bambusoides* stand. *Ecological Research* 8: 123-133.

Isagi Y. & Torii, A. (1998) Range expansion and its mechanism in a naturalized bamboo species, *Phyllostachys pubescens*. *Journal of Sustainable Forestry* 6: 127-142.

Iwaki H. (1958) The influence of density on the dry matter production of *Fagopyrum esculentum*. *Japanese Journal of Botany* 16: 210-226.

Johnson D. W., Cheng W. & Burke I. C. (2000) Biotic and abiotic nitrogen retention in a variety of forest soils. *Soil Science Society of America Journal* 64: 1503-1514.

Kai S. (1984) Studies on characteristics and management of warm-temperate deciduous broad-leaved forest. *Bulletin of the Miyazaki University Forests* 10: 1-124. (in Japanese with English abstract)

Katagiri S. (1988) Position related differences in mineral cycling in a mountain side deciduous broad-leaved secondary forest. *Japanese Journal of Ecology* 38: 135-145. (in Japanese with

English summary)

Katagiri S. & Tsutsumi T. (1975) The relationship between site condition and circulation of nutrients in forest ecosystem (III): Above ground biomass and nutrient contents of stands. *Journal of the Japanese Forest Society* 57: 412-419. (in Japanese with English abstract)

Katakura M., Yamauchi N. & Koyama Y. (2007) Aboveground and belowground biomass and C stock in *Quercus serrata*, *Pinus densiflora*, and *Larix kaempferi* forests, and their changes after *P. densiflora* cutting in Nagano. *Research Bulletin of the Nagano Prefecture Forestry Research Center* 22: 33-55. (in Japanese)

Komatsu H., Onozawa, Y., Kume T., Tsuruta K., Kumagai T., Shinohara Y. & Otsuki K. (2010) Stand-scale transpiration estimates in a Moso bamboo forest: II. Comparison with coniferous forests. *Forest Ecology and Management* 260: 1295-1302.

Kumemura A., Teraoka Y. & Takeuchi I. (2009) The above-ground biomass and stand structure of unmanaged Moso bamboo (*Phyllostachys pubescens*) stands in Kagoshima Prefecture. *Research Bulletin of the Kagoshima University Forests* 36: 1-8. (in Japanese with English summary)

Li R, Werger M. J. A., During H. J. & Zhong Z. C. (1998) Carbon and nutrient dynamics in relation to growth rhythm in the giant bamboo *Phyllostachys pubescens*. *Plant and Soil* 201: 113-123.

Lovett G. M., Weathers K. C., Arthur M. A. & Schultz J. C. (2004) Nitrogen cycling in a northern hardwood forest: Do species matter? *Biogeochemistry* 67: 289-308.

Makita A. (1998) The significance of the mode of clonal growth in the life history of bamboos. *Plant*

Species Biology 13: 85-92.

Nagano M. & Kira T. (1978) Aboveground biomass. In *Biological production in a warm-temperate evergreen oak forest of Japan. JIBP Synthesis vol. 18*. Kira T., Ono Y., Hosokawa T. (eds). University of Tokyo Press, Tokyo, pp.69-82.

Nakai A. & Kisanuki H. (2006) Effect of bamboo culm density on the tree species diversity and density of understory at a forest stand on a major bed along Miya River downstream. *Bulletin of the Faculty of Bioresources, Mie University* 33: 21-28. (in Japanese with English abstract)

Nicol G. W., Leininger S., Schleper C. & Prosser J. I. (2008) The influence of soil pH on the diversity, abundance and transcriptional activity of ammonia oxidizing archaea and bacteria. *Environmental Microbiology* 10: 2966-2978.

Nishioka M., Umehara T. & Nagano M. (1982) Aboveground biomass in Minohyama, the habitat of monkey. Bulletin report of monkeys in Minohyama. *The Minoh City board of education*. pp.117-139. (in Japanese)

O’Connor P. J., Covich A. P., Scatena F. & Loope L. L. (2000) Non-indigenous bamboo along headwater streams of the Luquillo Mountains, Puerto Rico: Leaf fall, aquatic leaf decay and patterns of invasion. *Journal of Tropical Ecology* 16: 499-516.

Ogawa H. & Kira T. (1977) Methods of estimating forest biomass. In *Primary productivity of Japanese forests*. *JIBP Synthesis vol. 16*. Shidei T., and Kira T. (eds.) University of Tokyo Press, Tokyo, pp.15-25.

Ogino K. (1977) A beech forest in Ashiu - biomass, its increment and net production. In *Primary*

Productivity of Japanese Forest. JIBP Synthesis vol. 16. Shidei T., Kira T. (eds.) University of Tokyo Press, Tokyo, pp 172-186.

Okutomi K., Shinoda S. & Fukuda H. (1996) Causal analysis of invasion of broad-leaved forest by bamboo in Japan. *Journal of Vegetation Science* 7: 723-728.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reich P. B., Walters M. B. & Ellsworth D. S. (1997) From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94: 13730-13734.

Saito H. (1989) Forest Production. In: *Forest Ecology.* Tsutsumi T. (ed.) Asakurasyoten, Tokyo, pp. 43-95. (in Japanese)

Segawa Y. & Kato R. (1970) The growth of coppice forest of *Quercus serrate* Thunb. at the Koma experiment forests. *Annual Report of the Tohoku Branch, Forest Experiment Station* 11: 188-198. (in Japanese)

Shibata S. (2003) *Phyllostachys pubescens* and Japanese. *Journal of the Japanese Society of Revegetation and Technology* 28: 406-411. (in Japanese)

Suzuki S. (1978) Index to Japanese Bambusaceae. Gakken. Tokyo (in Japanese)

Suzuki S. (2014) Chronological location analyses of bamboo groves and their expansion in Japanese satoyama landscapes. *Plant Species Biology* (in press)

Suzuki S. & Nakagoshi N. (2011) Sustainable Management of Satoyama Bamboo Landscapes in Japan. *In* Hong S.-K., Wu J., Kim J.-E. & Nakagoshi N. (eds.), Landscape Ecology in Asian

Cultures. Springer. pp. 211-220.

Tokuchi N., Usui N., Ueda M. & Fukushima K. (2010) Vegetation change and nutrient cycling in satoyama: Case study of bamboo invasion in Tennou-zan. *Water Science* 54 (1): 90-103. (in Japanese)

Torii A. (1998) Estimation of range expansion rate of bamboo stands using aerial photographs: Case study on Mt. Hachiman, Shiga Prefecture, and Mt. Otoko, Kyoto Prefecture, Japan. *Japanese Journal of Ecology* 48: 37-47. (in Japanese with English abstract)

Torii A. & Isagi Y. (1997) Range expansion of bamboo species in southern areas of Kyoto Prefecture, Japan. *Japanese Journal of Ecology* 47: 31-41. (in Japanese with English abstract)

Tripathi S. K. & Singh K. P. (1996) Culm recruitment, dry matter dynamics and carbon flux in recently harvested and mature bamboo savannas in the Indian dry tropics. *Ecological Research* 11: 149-164.

Tripathi S. K., Sumida A., Shibata H., Uemura S., Ono K. & Hara T. (2005) Growth and substrate quality of fine root and soil nitrogen availability in a young *Betula ermanii* forest of northern Japan: Effects of the removal of understory dwarf bamboo (*Sasa kurilensis*). *Forest Ecology and Management* 212: 278-290.

Tsutsumi T., Kawahara T. & Shidei T. (1968) The circulation of nutrients in forest ecosystem (I): On the amount of nutrients contained in the above-ground parts of single tree and of stand. *Journal of the Japanese Forest Society* 50: 66-74. (in Japanese with English abstract)

Tu L., Hu T., Zhang J., Huang L., Xiao Y., Chen G., Hu H., Liu L., Zheng J., Xu Z. & Chen L.

(2013) Nitrogen distribution and cycling through water flows in a subtropical bamboo forest under high level of atmospheric deposition. *PLoS ONE* 8: e75862. Doi: 10.1371/journal.pone.0075862.

Umemura M. & Takenaka C. (2014a) Changes in chemical characteristics of surface soils in hinoki cypress (*Chamaecyparis obtusa*) forests induced by the invasion of exotic Moso bamboo (*Phyllostachys pubescens*) in central Japan. *Plant Species Biology* (in press)

Umemura M. & Takenaka C. (2014b) Biological cycle of silicon in moso bamboo (*Phyllostachys pubescens*) forests in central Japan. *Ecological Research* 29: 501-510.

Vitousek P. M., Gosz J. R., Grier C. C., Melillo J. M., Reiners W. A. & Todd R. L. (1979) Nitrate losses from disturbed ecosystems. *Science* 204: 469-474.

Watanabe T., Fukuzawa K. & Shibata H. (2013) Temporal changes in litterfall, litter decomposition and their chemical composition in Sasa dwarf bamboo in a natural forest ecosystem of northern Japan. *Journal of Forest Research* 18: 129-138.

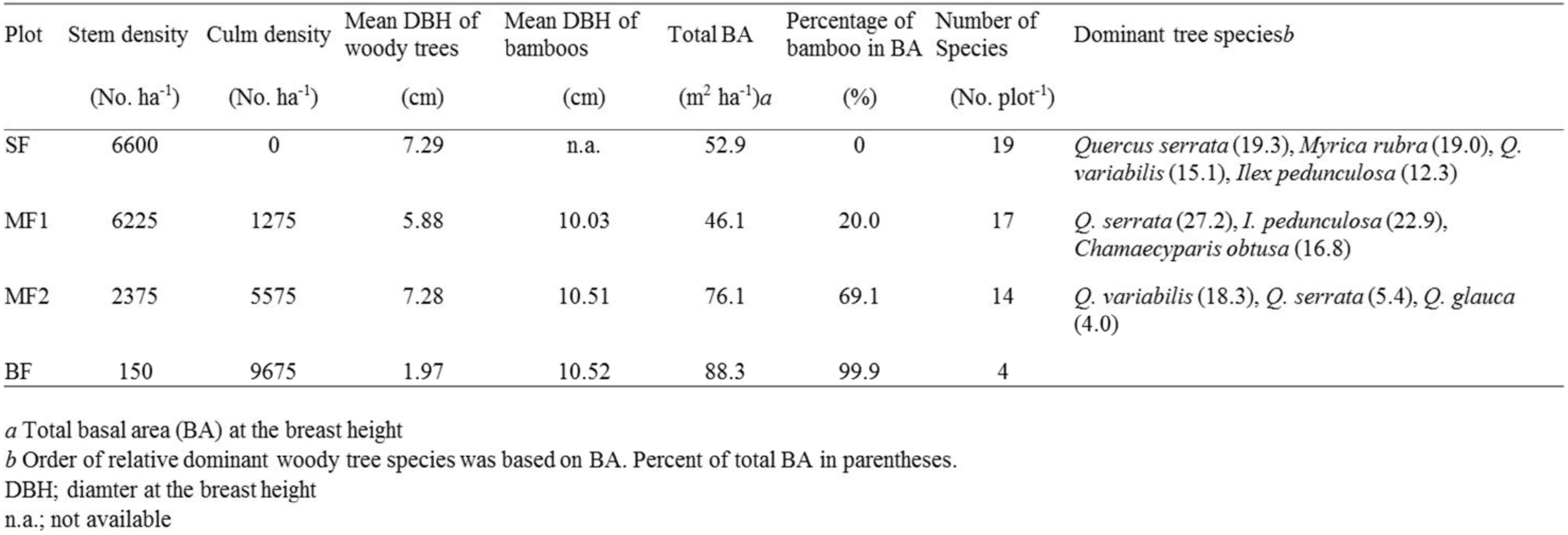
Yen T.-M. & Lee J.-S. (2011) Comparing aboveground carbon sequestration between moso bamboo (*Phyllostachys heterocycla*) and China fir (*Cunninghamia lanceolata*) forests based on the allometric model. *Forest Ecology and Management* 261: 995-1002.

Zhang C., Xie G., Fan S. & Zen L. (2010) Variation in vegetation structure and soil properties, and the relation between understory plants and environmental variables under different *Phyllostachys pubescens* forests in southeastern China. *Environmental Management* 45: 779-792.

Table 1. The parameters of regression equations predicting biomasses of each *P. pubescens* organ from diameters at breast height (DBH). Data are from Abe and Shibata (2009).

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

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



Plot	Stem density (No. ha^{-1})	Culm density (No. ha^{-1})	Mean DBH of woody trees (cm)	Mean DBH of bamboos (cm)	Total BA (m^2 ha^{-1})*a*	Percentage of bamboo in BA (%)	Number of Species (No. plot^{-1})	Dominant tree species*b*
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

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

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*

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

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

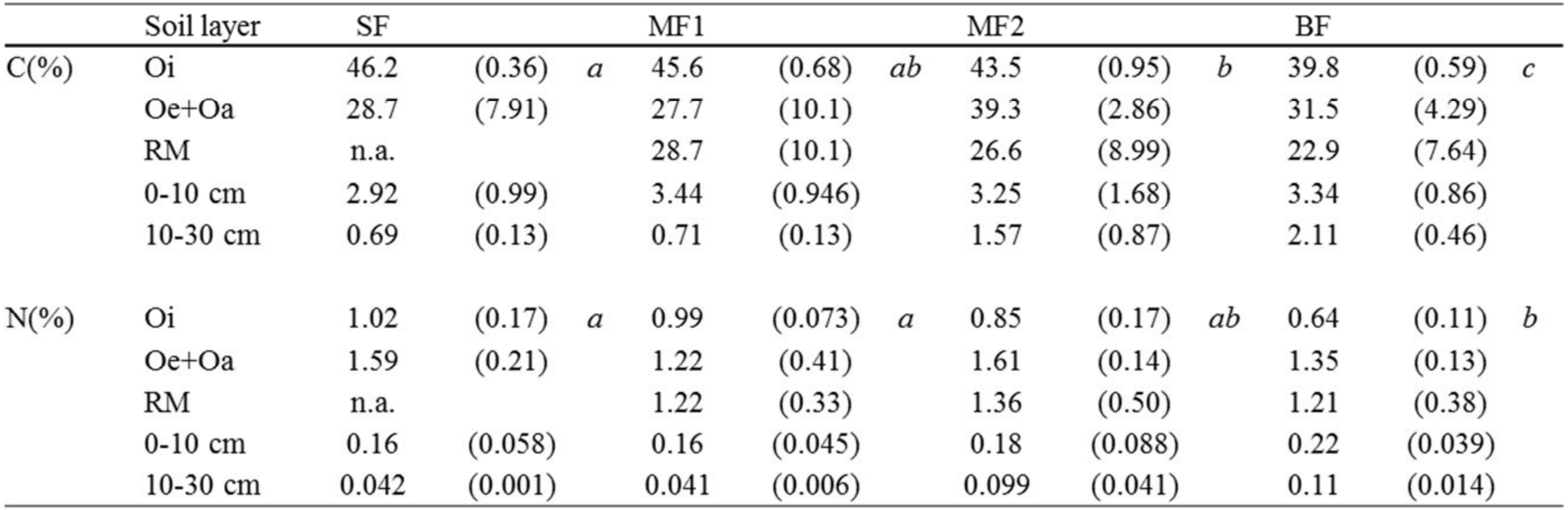
n.a.; not available

Table 5 Mean C and N contents in each organ of *P. pubescens* and broad-leaved trees. SD in parentheses. Both C and N contents in leaves, branches, and culms of bamboo shoots were not 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

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

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)	

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

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

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)

n.a.; not available.

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

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)

n.a.; not available

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

n.a.; not available.

Figure legends

Fig. 1 Location of the study site.

Fig. 2 Diameter at breast height (DBH) frequency distributions of *P. pubescens* (■) and other plants (□) in the study plots: (a) plot dominated by secondary broad-leaved forest (SF), (b) mixed bamboo/broad-leaved forest plot subjected to bamboo invasion since 1974 (MF1), (c) mixed bamboo/broad-leaved forest plot subjected to bamboo invasion since 1961 (MF2), (d) plot dominated by bamboo (BF).

Fig. 3 Vertical distributions of biomass in *P. pubescens* roots (*n* = 2 for the root mat layer, *n* = 4 for each mineral soil layer in the 0–30 cm depth range, and *n* = 2 for rhizomes). Error bars are standard deviation (SDs).

* RM; root mat

Fig. 4 (a) Aboveground and (b) belowground biomasses of broad-leaved trees and *P. pubescens* organs; (c) total biomass.

Fig. 5 (a) Ratios of non-photosynthetic organ to photosynthetic organ dry weights (C/F); (b) ratios of aerial organ to root dry weights (T/R) for whole plants, broad-leaved trees, and *P. pubescens*.

Fig. 6 (a) Carbon and (b) nitrogen stocks in all aboveground and belowground compartments and in each soil layer.

Fig. 7 The proportion of above- and belowground compartments and soils to total (a) carbon and (b) nitrogen stocks for four plots.

Fig. 1

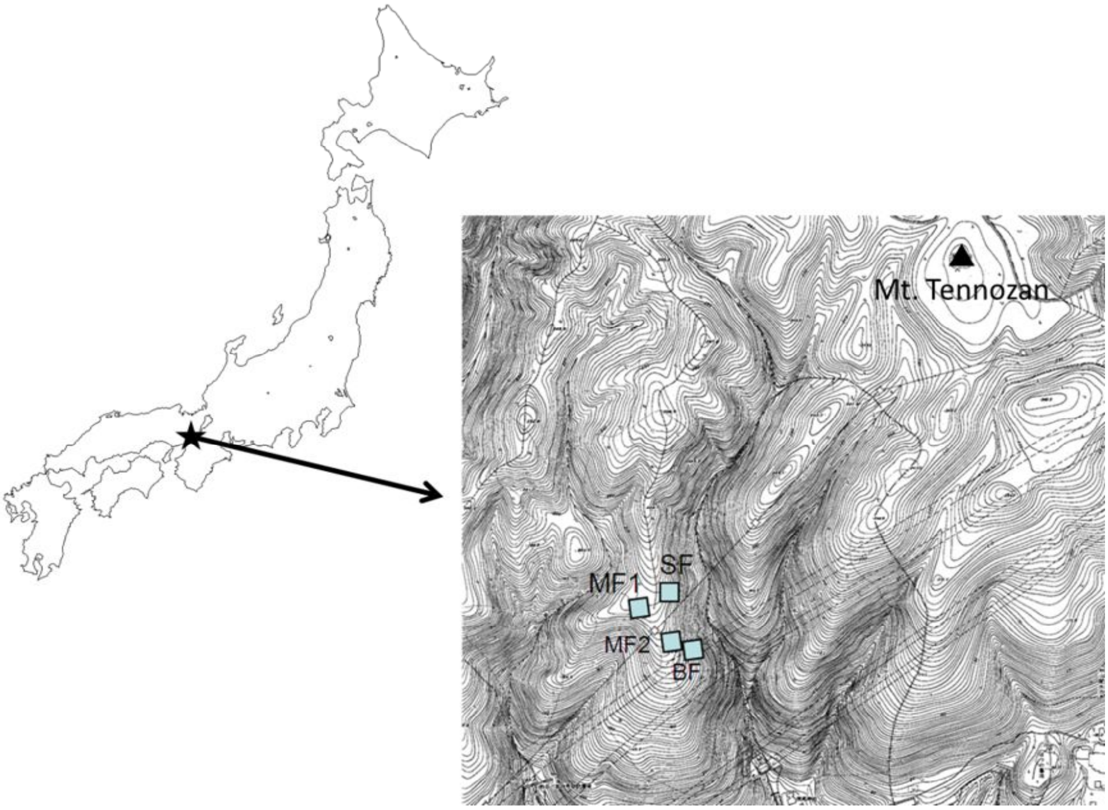


Fig. 2

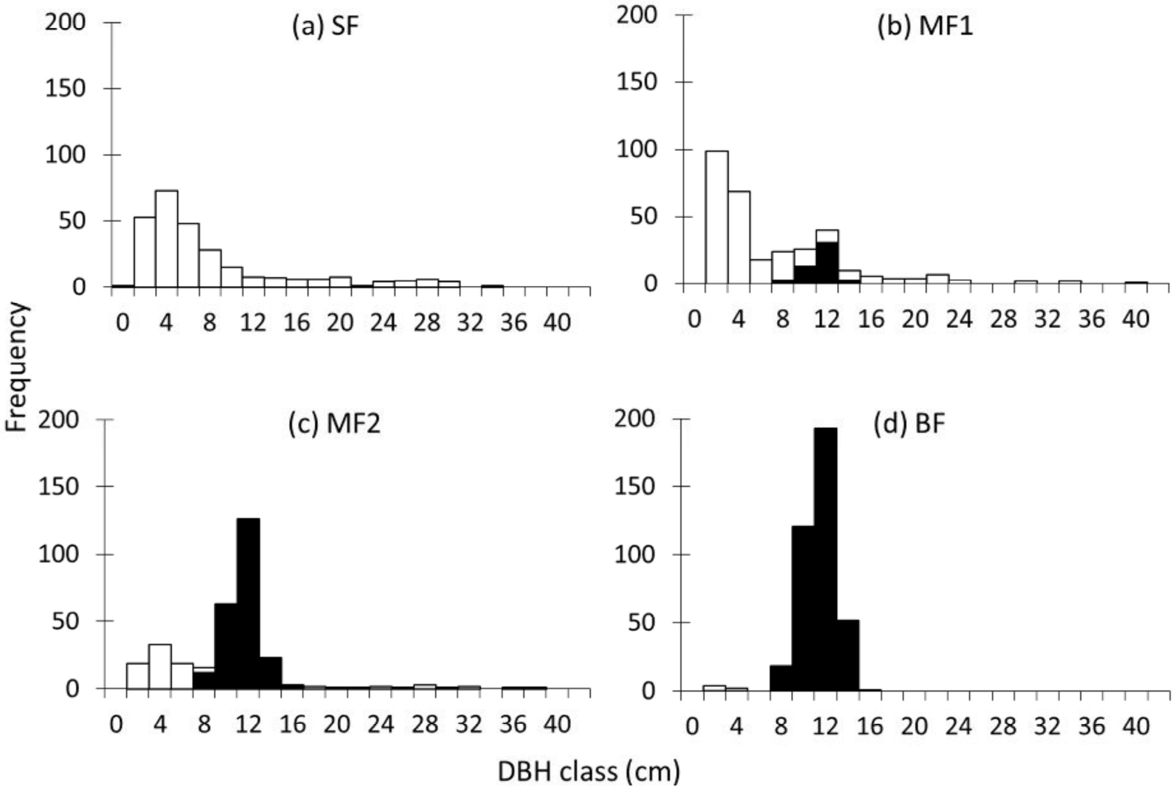

(a) SF
(b) MF1
(c) MF2
(d) BF
Frequency
DBH class (cm)
0
50
100
150
200
0 4 8 12 16 20 24 28 32 36 40

Fig. 3

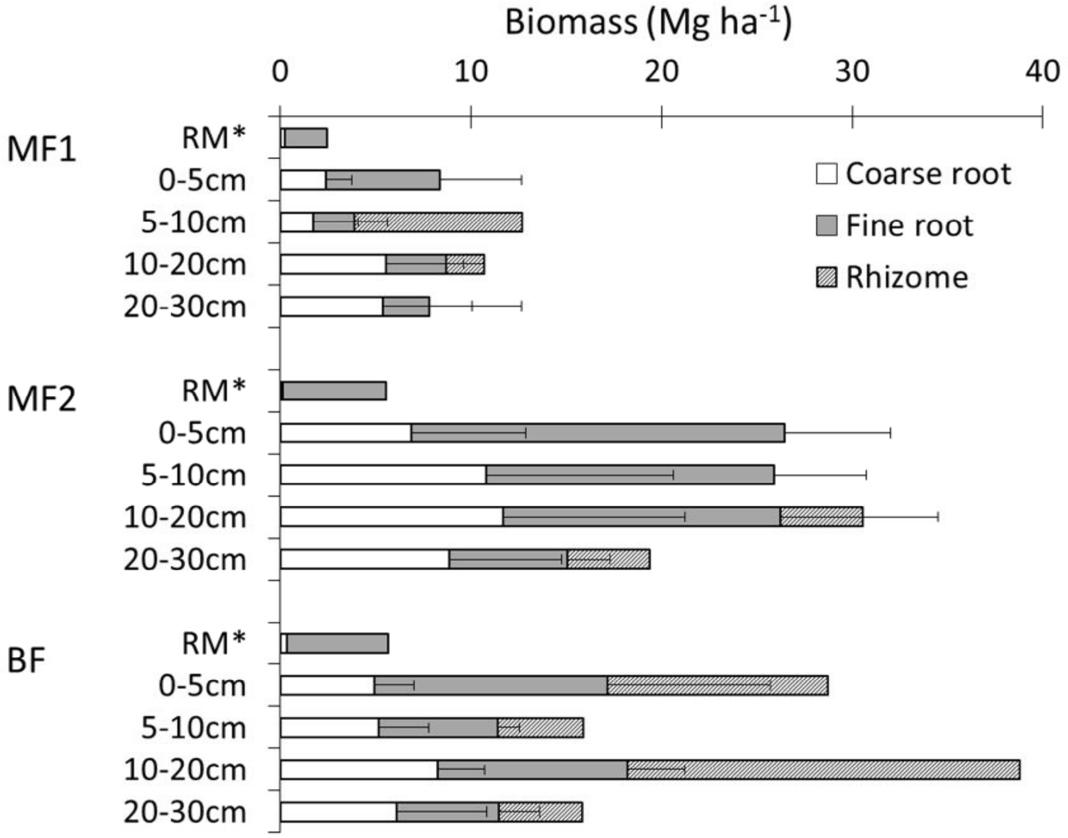

Biomass (Mg ha-1)
0
10
20
30
40
MF1
RM*
0-5cm
5-10cm
10-20cm
20-30cm
MF2
RM*
0-5cm
5-10cm
10-20cm
20-30cm
BF
RM*
0-5cm
5-10cm
10-20cm
20-30cm
☐ Coarse root
▩ Fine root
▨ Rhizome

Fig. 4

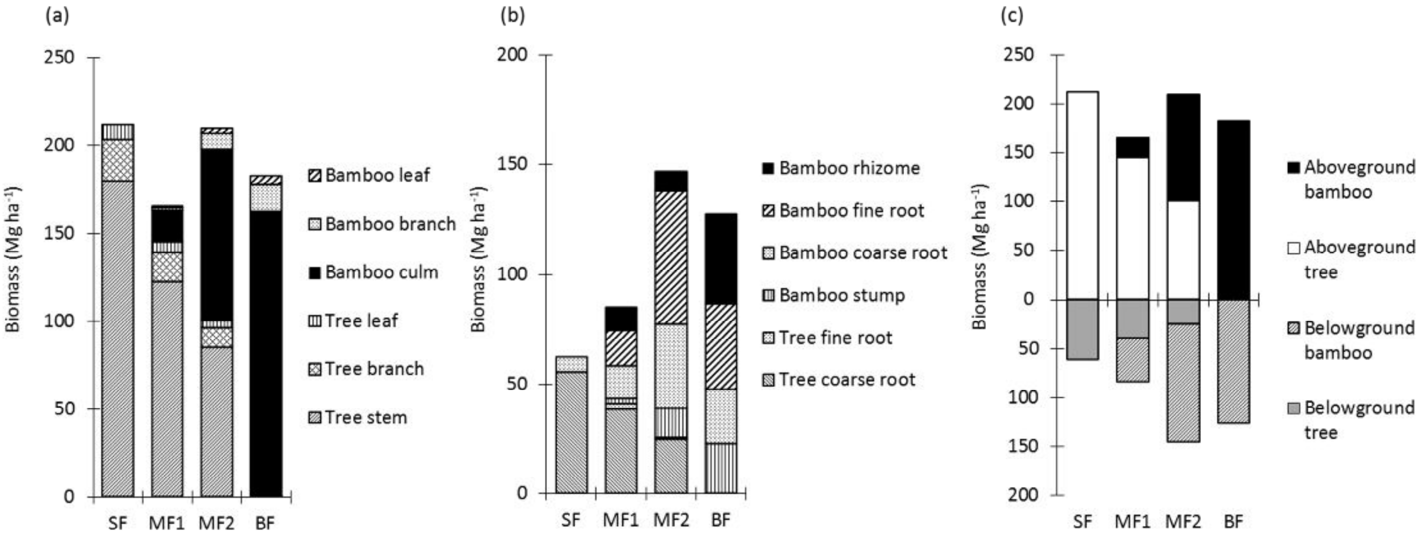

(a)
Biomass (Mg ha^{-1})
250
200
150
100
50
0
SF
MF1
MF2
BF
▨ Bamboo leaf
▨ Bamboo branch
■ Bamboo culm
▥ Tree leaf
▨ Tree branch
▨ Tree stem
(b)
Biomass (Mg ha^{-1})
200
150
100
50
0
SF
MF1
MF2
BF
■ Bamboo rhizome
▨ Bamboo fine root
▨ Bamboo coarse root
▥ Bamboo stump
▨ Tree fine root
▨ Tree coarse root
(c)
Biomass (Mg ha^{-1})
250
200
150
100
50
0
50
100
150
200
SF
MF1
MF2
BF
■ Aboveground bamboo
☐ Aboveground tree
▨ Belowground bamboo
■ Belowground tree

Fig. 5

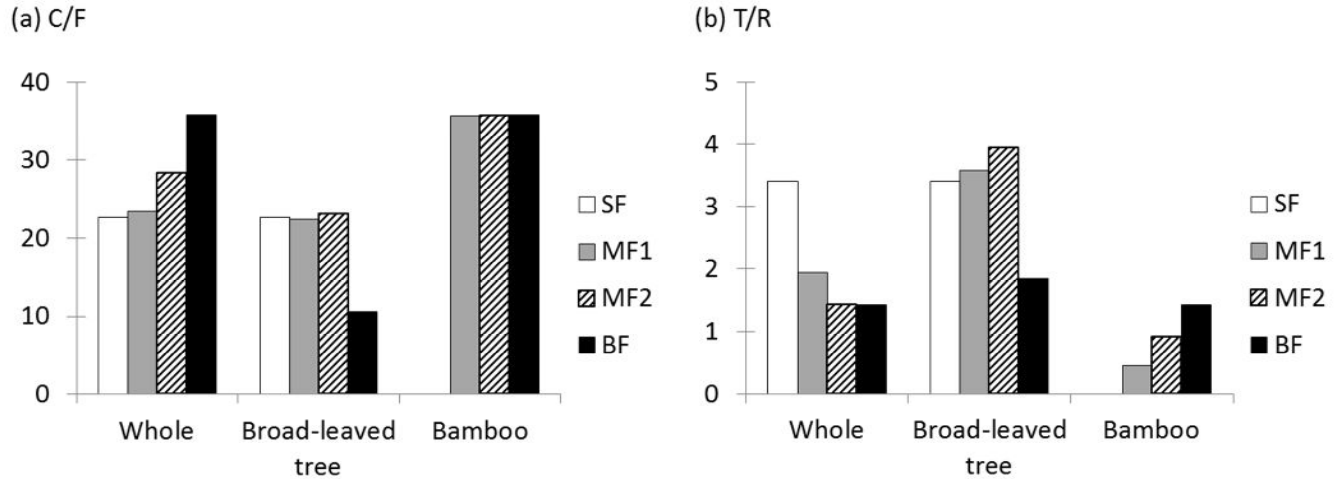

(a) C/F
40
30
20
10
0
Whole
Broad-leaved tree
Bamboo
☐ SF
■ MF1
▨ MF2
■ BF
(b) T/R
5
4
3
2
1
0
Whole
Broad-leaved tree
Bamboo
☐ SF
■ MF1
▨ MF2
■ BF

Fig. 6

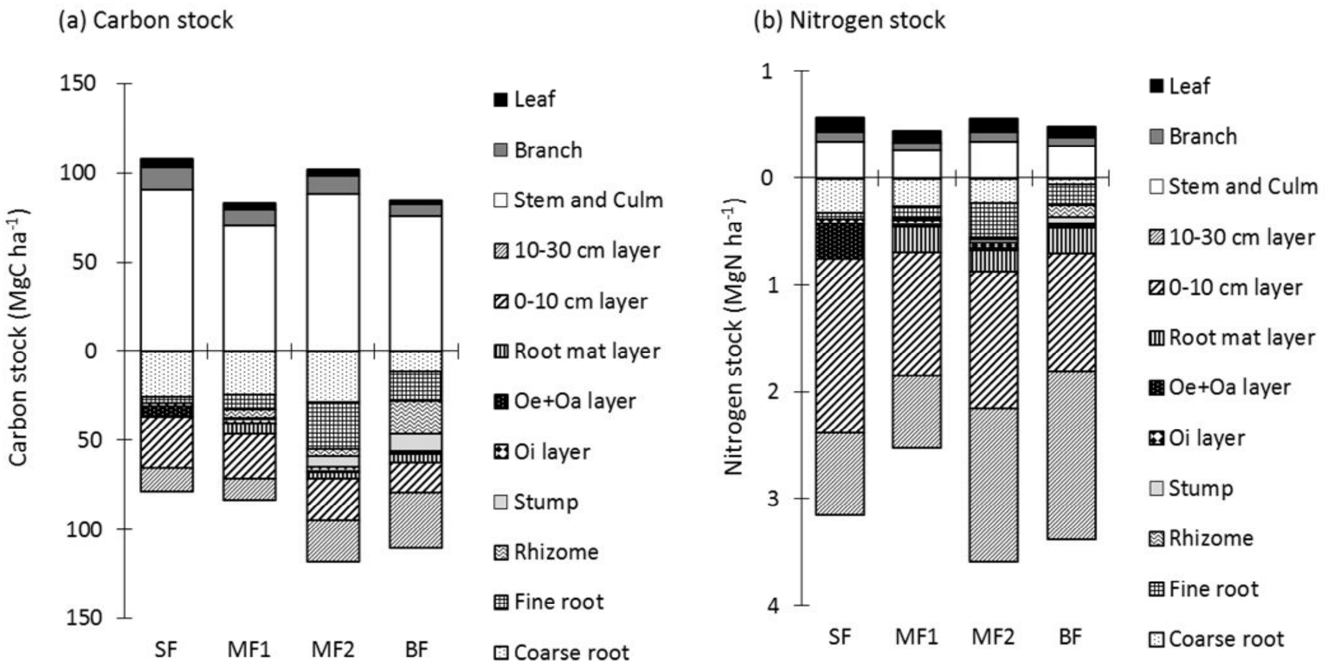
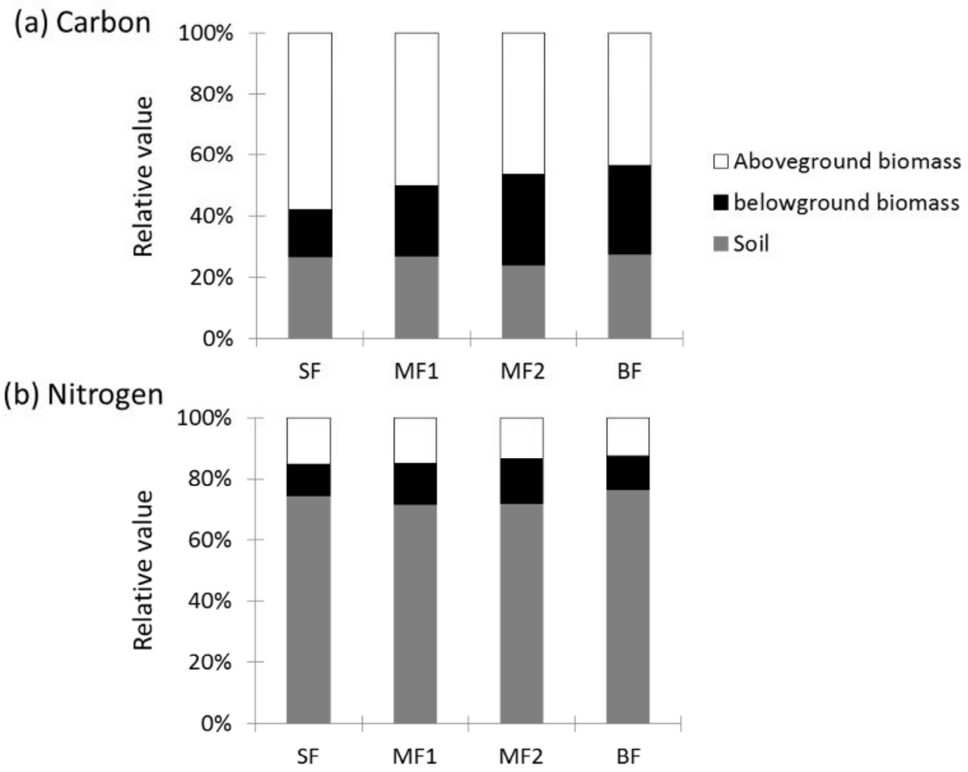
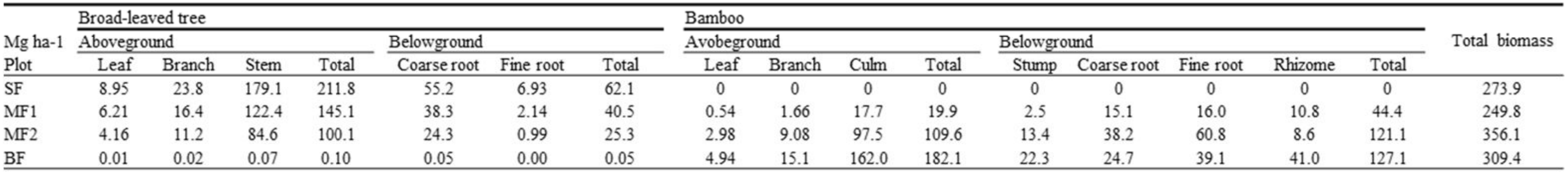

(a) Carbon stock
Carbon stock (MgC ha^{-1})
150
100
50
0
50
100
150
SF
MF1
MF2
BF
■ Leaf
■ Branch
□ Stem and Culm
▨ 10-30 cm layer
▨ 0-10 cm layer
▥ Root mat layer
■ Oe+Oa layer
▣ Oi layer
□ Stump
▨ Rhizome
▦ Fine root
▣ Coarse root
(b) Nitrogen stock
Nitrogen stock (MgN ha^{-1})
1
0
1
2
3
4
SF
MF1
MF2
BF
■ Leaf
■ Branch
□ Stem and Culm
▨ 10-30 cm layer
▨ 0-10 cm layer
▥ Root mat layer
■ Oe+Oa layer
▣ Oi layer
□ Stump
▨ Rhizome
▦ Fine root
▣ Coarse root

Fig. 7


(a) Carbon
Relative value
100%
80%
60%
40%
20%
0%
SF
MF1
MF2
BF
☐ Aboveground biomass
■ belowground biomass
■ Soil
(b) Nitrogen
Relative value
100%
80%
60%
40%
20%
0%
SF
MF1
MF2
BF

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



	Broad-leaved tree							Bamboo									Total biomass
Mg ha-1	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

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

n.a.: not available.