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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

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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:

\[
W_s = 0.02644 \times (DBH_{0.1}^2 \times H)^{0.9688} \tag{1}
\]

\[
W_b = 0.01262 \times DBH_{0.1}^{2.364} \tag{2}
\]

\[
W_l = 0.005921 \times DBH_{0.1}^{2.288}, \tag{3}
\]

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

\[
1/H = 1/(a \times DBH^b) + 1/H_{max}, \tag{4}
\]

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):

\[
DBH_{0.1} = 0.941 \times DBH + 0.734. \tag{5}
\]

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

\[
W_{below} = 0.082 \times DBH^2. \tag{6}
\]
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:

\[ W = a \times \text{DBH}^b, \]

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 \(7.71 \times 10^{-2}\) 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*
occeded 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 &
McClougherty 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 & McClougherty 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 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


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


Cultures. Springer. pp. 211-220.


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).

<table>
<thead>
<tr>
<th>Organ</th>
<th>Age</th>
<th>Parameter</th>
<th>Coefficient</th>
<th>n</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>Current year</td>
<td>a</td>
<td>1.149×10⁻²</td>
<td>7</td>
<td>0.853</td>
</tr>
<tr>
<td></td>
<td>≥ 1 year</td>
<td>b</td>
<td>1.515</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Branch</td>
<td>Current year</td>
<td>a</td>
<td>1.045×10⁻¹</td>
<td>7</td>
<td>0.722</td>
</tr>
<tr>
<td></td>
<td>≥ 1 year</td>
<td>b</td>
<td>1.185</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culm</td>
<td>Current year</td>
<td>a</td>
<td>6.210×10⁻²</td>
<td>7</td>
<td>0.951</td>
</tr>
<tr>
<td></td>
<td>≥ 1 year</td>
<td>b</td>
<td>2.261</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>a</td>
<td>1.305×10⁻¹</td>
<td>8</td>
<td>0.915</td>
</tr>
</tbody>
</table>

A Self-archived copy in Kyoto University Research Information Repository [https://repository.kulib.kyoto-u.ac.jp](https://repository.kulib.kyoto-u.ac.jp)
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.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Stem density (No. ha⁻¹)</th>
<th>Culm density (No. ha⁻¹)</th>
<th>Mean DBH of woody trees (cm)</th>
<th>Mean DBH of bamboo (cm)</th>
<th>Total BA (m² ha⁻¹)</th>
<th>Percentage of bamboo in BA (%)</th>
<th>Number of Species (No. plot⁻¹)</th>
<th>Dominant tree speciesb</th>
</tr>
</thead>
<tbody>
<tr>
<td>SF</td>
<td>6600</td>
<td>0</td>
<td>7.29</td>
<td>n.a.</td>
<td>52.9</td>
<td>0</td>
<td>19</td>
<td>Quercus serrata (19.3), Myrica rubra (19.0), Q. variabilis (15.1), Ilex pedunculosa (12.3)</td>
</tr>
<tr>
<td>MF1</td>
<td>6225</td>
<td>1275</td>
<td>5.88</td>
<td>10.03</td>
<td>46.1</td>
<td>20.0</td>
<td>17</td>
<td>Q. serrata (27.2), I. pedunculosa (22.9), Chamaecyparis obtusa (16.8)</td>
</tr>
<tr>
<td>MF2</td>
<td>2375</td>
<td>5575</td>
<td>7.28</td>
<td>10.51</td>
<td>76.1</td>
<td>69.1</td>
<td>14</td>
<td>Q. variabilis (18.3), Q. serrata (5.4), Q. glauca (4.0)</td>
</tr>
<tr>
<td>BF</td>
<td>150</td>
<td>9675</td>
<td>1.97</td>
<td>10.52</td>
<td>88.3</td>
<td>99.9</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

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; diameter 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.

<table>
<thead>
<tr>
<th>Layer</th>
<th>SF</th>
<th>MF1</th>
<th>MF2</th>
<th>BF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oi (Mg ha⁻¹)</td>
<td>4.05 (0.767)</td>
<td>4.08 (0.874)</td>
<td>5.25 (2.32)</td>
<td>3.47 (1.69)</td>
</tr>
<tr>
<td>Oe+Oa (Mg ha⁻¹)</td>
<td>20.6 (6.05)ₐ</td>
<td>1.89 (0.598)ₜ</td>
<td>1.4 (0.984)ₜ</td>
<td>1.53 (0.291)ₜ</td>
</tr>
</tbody>
</table>

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 ($n = 2$).

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

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).

<table>
<thead>
<tr>
<th></th>
<th>Total C (%)</th>
<th>Total N (%)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Phyllostachys pubescens</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current</td>
<td>41.9 (1.72)</td>
<td>2.43 (0.30)</td>
<td>3</td>
</tr>
<tr>
<td>≥ 1 year</td>
<td>43.2 (0.46)</td>
<td>2.03 (0.19)</td>
<td>3</td>
</tr>
<tr>
<td>Branch</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current</td>
<td>46.4 (0.23)</td>
<td>0.55 (0.17)</td>
<td>3</td>
</tr>
<tr>
<td>≥ 1 year</td>
<td>45.8 (1.11)</td>
<td>0.51 (0.25)</td>
<td>3</td>
</tr>
<tr>
<td>Culm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current</td>
<td>46.3 (0.69)</td>
<td>0.18 (0.043)</td>
<td>3</td>
</tr>
<tr>
<td>≥ 1 year</td>
<td>46.8 (1.22)</td>
<td>0.19 (0.050)</td>
<td>3</td>
</tr>
<tr>
<td>Coarse root</td>
<td>44.2 (0.32)</td>
<td>0.23 (0.015)</td>
<td>9</td>
</tr>
<tr>
<td>Fine root</td>
<td>43.2 (0.50)</td>
<td>0.51 (0.044)</td>
<td>9</td>
</tr>
<tr>
<td>Rhizome and stump</td>
<td>44.3 (0.15)</td>
<td>0.26 (0.029)</td>
<td>9</td>
</tr>
</tbody>
</table>

**Broad-leaved tree**

<table>
<thead>
<tr>
<th></th>
<th>Total C (%)</th>
<th>Total N (%)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>52.6 †</td>
<td>1.57 ‡</td>
<td></td>
</tr>
<tr>
<td>Branch</td>
<td>51.8 †</td>
<td>0.38 ‡</td>
<td></td>
</tr>
<tr>
<td>Stem</td>
<td>50.9 †</td>
<td>0.19 ‡</td>
<td></td>
</tr>
<tr>
<td>Coarse root</td>
<td>46.1 (0.48)</td>
<td>0.59 (0.049)</td>
<td>9</td>
</tr>
<tr>
<td>Fine root</td>
<td>46.7 (0.54)</td>
<td>0.77 (0.040)</td>
<td>8</td>
</tr>
</tbody>
</table>

†; 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).

<table>
<thead>
<tr>
<th>Soil layer</th>
<th>SF</th>
<th>MF1</th>
<th>MF2</th>
<th>BF</th>
</tr>
</thead>
<tbody>
<tr>
<td>C(%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oi</td>
<td>46.2</td>
<td>(0.36)</td>
<td>a</td>
<td>43.5</td>
</tr>
<tr>
<td>Oe+Oa</td>
<td>28.7</td>
<td>(7.91)</td>
<td>ab</td>
<td>39.3</td>
</tr>
<tr>
<td>RM</td>
<td>n.a.</td>
<td></td>
<td></td>
<td>26.6</td>
</tr>
<tr>
<td>0-10 cm</td>
<td>2.92</td>
<td>(0.99)</td>
<td></td>
<td>3.25</td>
</tr>
<tr>
<td>10-30 cm</td>
<td>0.69</td>
<td>(0.13)</td>
<td></td>
<td>1.57</td>
</tr>
<tr>
<td>N(%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oi</td>
<td>1.02</td>
<td>(0.17)</td>
<td>a</td>
<td>0.85</td>
</tr>
<tr>
<td>Oe+Oa</td>
<td>1.59</td>
<td>(0.21)</td>
<td>a</td>
<td>1.61</td>
</tr>
<tr>
<td>RM</td>
<td>n.a.</td>
<td></td>
<td></td>
<td>1.36</td>
</tr>
<tr>
<td>0-10 cm</td>
<td>0.16</td>
<td>(0.058)</td>
<td></td>
<td>0.18</td>
</tr>
<tr>
<td>10-30 cm</td>
<td>0.042</td>
<td>(0.001)</td>
<td></td>
<td>0.099</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>Site</th>
<th>Age (year)</th>
<th>Aboveground biomass (Mg ha$^{-1}$)</th>
<th>Belowground biomass (Mg ha$^{-1}$)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shimane Prefecture</td>
<td>40</td>
<td>96.3 - 218.0</td>
<td>n.a.</td>
<td>Katagiri (1988)</td>
</tr>
<tr>
<td>Kyoto Prefecture</td>
<td>n.a.</td>
<td>102</td>
<td>23.4</td>
<td>Goto <em>et al.</em> (2003); Dannoura <em>et al.</em> (2006)</td>
</tr>
<tr>
<td>Miyazaki Prefecture</td>
<td>60 - 62</td>
<td>118.5 - 127.4</td>
<td>n.a.</td>
<td>Kai (1984)</td>
</tr>
<tr>
<td>Nagano Prefecture</td>
<td>16</td>
<td>132.2</td>
<td>24.1</td>
<td>Katakura <em>et al.</em> (2007)</td>
</tr>
<tr>
<td>Kyoto Prefecture</td>
<td>60 ~</td>
<td>211.8</td>
<td>62.1</td>
<td>This study (plot SF)</td>
</tr>
</tbody>
</table>

n.a.; not available.
Table 8. Above- and belowground biomass in un-managed *Phyllostachys pubescens* forest from previous studies and this study.

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

n.a.; not available
Table 9 C/N ratios of aboveground and belowground compartments and soil layers, their respective subtotals, and total values.

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

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)
Fig. 3

Biomass (Mg ha\(^{-1}\))

<table>
<thead>
<tr>
<th>Depth</th>
<th>Coarse root</th>
<th>Fine root</th>
<th>Rhizome</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-5 cm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-10 cm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-20 cm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20-30 cm</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

MF1

RM*

MF2

RM*

BF

RM*
Fig. 4

(a) 

(b) 

(c) 

Biomass (Mg ha⁻¹)

Biomass (Mg ha⁻¹)

Biomass (Mg ha⁻¹)

SF MF1 MF2 BF

SF MF1 MF2 BF

SF MF1 MF2 BF

Bamboo leaf
Bamboo branch
Bamboo culm
Tree leaf
Tree branch
Tree stem
Bamboo rhizome
Bamboo fine root
Bamboo coarse root
Bamboo stump
Tree fine root
Tree coarse root
Aboveground bamboo
Aboveground tree
Belowground bamboo
Belowground tree
Fig. 6

(a) Carbon stock

(b) Nitrogen stock

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

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

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

<table>
<thead>
<tr>
<th>Mg ha⁻¹</th>
<th>Broad-leaved tree</th>
<th>Bamboo</th>
<th>Total biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Aboveground</td>
<td>Belowground</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leaf</td>
<td>Branch</td>
<td>Stem</td>
</tr>
<tr>
<td>SF</td>
<td>8.95</td>
<td>23.8</td>
<td>179.1</td>
</tr>
<tr>
<td>MF1</td>
<td>6.21</td>
<td>16.4</td>
<td>122.4</td>
</tr>
<tr>
<td>MF2</td>
<td>4.16</td>
<td>11.2</td>
<td>84.6</td>
</tr>
<tr>
<td>BF</td>
<td>0.01</td>
<td>0.02</td>
<td>0.07</td>
</tr>
</tbody>
</table>
Appendix B. Carbon and nitrogen stocks in aboveground and belowground compartments and in each soil layer, their respective subtotals, and total values.

<table>
<thead>
<tr>
<th></th>
<th>SF</th>
<th>MF1</th>
<th>MF2</th>
<th>BF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C (MgC ha⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aboveground biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td>4.7</td>
<td>3.5</td>
<td>3.5</td>
<td>2.1</td>
</tr>
<tr>
<td>Branch</td>
<td>12.3</td>
<td>9.3</td>
<td>10.0</td>
<td>6.9</td>
</tr>
<tr>
<td>Stem and Culm</td>
<td>91.2</td>
<td>70.6</td>
<td>88.7</td>
<td>75.9</td>
</tr>
<tr>
<td>Subtotal</td>
<td>108.2</td>
<td>83.4</td>
<td>102.2</td>
<td>85.0</td>
</tr>
<tr>
<td>Belowground biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coarse root</td>
<td>25.5</td>
<td>24.4</td>
<td>28.1</td>
<td>10.9</td>
</tr>
<tr>
<td>Fine root</td>
<td>3.2</td>
<td>7.9</td>
<td>26.7</td>
<td>16.9</td>
</tr>
<tr>
<td>Rhizome</td>
<td>n.a.</td>
<td>4.8</td>
<td>3.8</td>
<td>18.2</td>
</tr>
<tr>
<td>Stump</td>
<td>n.a.</td>
<td>1.1</td>
<td>3.9</td>
<td>9.9</td>
</tr>
<tr>
<td>Subtotal</td>
<td>28.7</td>
<td>38.1</td>
<td>64.6</td>
<td>55.9</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oi</td>
<td>1.9</td>
<td>1.9</td>
<td>2.3</td>
<td>1.4</td>
</tr>
<tr>
<td>Oe+Oa</td>
<td>5.9</td>
<td>0.5</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>RM</td>
<td>n.a.</td>
<td>5.5</td>
<td>3.9</td>
<td>4.4</td>
</tr>
<tr>
<td>0-10</td>
<td>29.1</td>
<td>25.3</td>
<td>23.3</td>
<td>16.9</td>
</tr>
<tr>
<td>10-30</td>
<td>12.8</td>
<td>11.8</td>
<td>22.8</td>
<td>30.9</td>
</tr>
<tr>
<td>Subtotal</td>
<td>49.7</td>
<td>45.0</td>
<td>53.0</td>
<td>54.0</td>
</tr>
<tr>
<td>Total</td>
<td>186.6</td>
<td>166.5</td>
<td>219.8</td>
<td>194.9</td>
</tr>
<tr>
<td><strong>N (MgN ha⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aboveground biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td>0.14</td>
<td>0.11</td>
<td>0.13</td>
<td>0.10</td>
</tr>
<tr>
<td>Branch</td>
<td>0.090</td>
<td>0.071</td>
<td>0.089</td>
<td>0.078</td>
</tr>
<tr>
<td>Stem and Culm</td>
<td>0.34</td>
<td>0.27</td>
<td>0.35</td>
<td>0.31</td>
</tr>
<tr>
<td>Subtotal</td>
<td>0.57</td>
<td>0.44</td>
<td>0.56</td>
<td>0.49</td>
</tr>
<tr>
<td>Belowground biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coarse root</td>
<td>0.32</td>
<td>0.26</td>
<td>0.23</td>
<td>0.087</td>
</tr>
<tr>
<td>Fine root</td>
<td>0.053</td>
<td>0.098</td>
<td>0.32</td>
<td>0.20</td>
</tr>
<tr>
<td>Rhizome</td>
<td>n.a.</td>
<td>0.028</td>
<td>0.023</td>
<td>0.11</td>
</tr>
<tr>
<td>Stump</td>
<td>n.a.</td>
<td>0.006</td>
<td>0.035</td>
<td>0.058</td>
</tr>
<tr>
<td>Subtotal</td>
<td>0.38</td>
<td>0.39</td>
<td>0.60</td>
<td>0.42</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Oi</td>
<td>0.041</td>
<td>0.040</td>
<td>0.045</td>
<td>0.022</td>
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<tr>
<td>Oe+Oa</td>
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<td>0.023</td>
<td>0.023</td>
<td>0.021</td>
</tr>
<tr>
<td>RM</td>
<td>n.a.</td>
<td>0.24</td>
<td>0.20</td>
<td>0.23</td>
</tr>
<tr>
<td>0-10</td>
<td>1.63</td>
<td>1.15</td>
<td>1.28</td>
<td>1.10</td>
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<tr>
<td>10-30</td>
<td>0.77</td>
<td>0.67</td>
<td>1.44</td>
<td>1.58</td>
</tr>
<tr>
<td>Subtotal</td>
<td>2.77</td>
<td>2.13</td>
<td>2.98</td>
<td>2.96</td>
</tr>
<tr>
<td>Total</td>
<td>3.72</td>
<td>2.96</td>
<td>4.15</td>
<td>3.86</td>
</tr>
</tbody>
</table>

n.a.: not available.