

Carbon dynamics and stability between native Masson pine and exotic slash pine plantations in subtropical China

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Abstract Afforestation and ecological restoration have often been carried out with fast-growing exotic tree species because of their high apparent growth and yield. Moreover, fast-growing forest plantations have become an important component of mitigation measures to offset greenhouse gas emissions. However, information on the long-term performance of exotic and fast-growing species is often lacking especially with respect to their vulnerability to disturbance compared to native species. We compared carbon (C) storage and C accumulation rates in vegetation (above- and belowground) and soil in 21-year-old exotic slash pine (*Pinus elliottii* Engelm.) and native Masson pine (*Pinus massoniana* Lamb.) plantations, as well as their responses to a severe ice storm in 2008. Our results showed that mean C storage was $116.77 \pm 7.49 \text{ t C ha}^{-1}$ in slash pine plantation and

$117.89 \pm 8.27 \text{ t C ha}^{-1}$ in Masson pine plantation. The aboveground C increased at a rate of $2.18 \text{ t C ha}^{-1} \text{ year}^{-1}$ in Masson pine and $2.23 \text{ t C ha}^{-1} \text{ year}^{-1}$ in slash pine plantation, and there was no significant difference in C storage accumulation between the two plantation types. However, we observed significant differences in ice storm damage with nearly 7.5 % of aboveground biomass loss in slash pine plantation compared with only 0.3 % loss in Masson pine plantation. Our findings indicated that the native pine species was more resistant to ice storm because of their adaptive biological traits (tree shape, crown structure, and leaf surface area). Overall, the native pine species might be a safer choice for both afforestation and ecological restoration in our study region.

Keywords Carbon sequestration · Carbon concentration · Crown structure · Ice storm · *Pinus massoniana* · *Pinus elliottii*

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Introduction

Afforestation and ecological restoration have often been carried out with introduced species to achieve productivity gains (Del Lungo et al. 2006). Plantations have also been proposed as effective means for carbon (C) sequestration because of the rapid accumulation and potential for long-term storage of C in plant biomass and soil organic matter (Silver et al. 2004; Chazdon 2008; Paquette and Messier 2010; Jandl et al. 2007).

When developing restoration plans and managing forest plantations, two criteria are commonly considered (Candell and Raupach 2008). First, at stand scale, appropriate tree species selection (Kirby and Potvin 2007) is based on

the growth rate, self-thinning patterns, biomass accumulation, and valuable uses at the whole-tree or stand level. Fast-growing, short-lived species with low-density wood are favored in many afforestation projects (Chazdon 2008) because they provide a fast C offset, high wood volume, and high profits in a relatively short rotation. However, forest establishment and restoration are long-term processes, and the use of long-lived, slow-growing species seems to have greater long-term benefits for C sequestration (Chazdon 2008). For various reasons, exotic species (mainly *Eucalyptus* and pine) have often been used for afforestation in South America (Hall et al. 2012), Africa (Lemma et al. 2006), Europe (Engelmark et al. 2001; Finch and Szumelda 2007), Asia (Pan and Zheng 1990; Tian et al. 2004), and elsewhere around world (Lamb et al. 2005). In fact, these primarily monoculture plantations provide a large amount of timber and ecological services globally (Lamb et al. 2005).

The second criterion is the stability at the ecosystem or landscape level (Lamb et al. 2005) and considers how forests vary in total C accumulation, nutrient cycle, and water processes after taking disturbance into account. Given the profound implications for long-term ecosystem services such as soil organic matter management and sustainability of forest productivity, forest stability should receive greater attention in forest management though it is often only considered after species selection based on the growth rates (Jandl et al. 2007). Large-scale monocultures have been criticized in the past decades (Paquette and Messier 2010) in part because they are often more vulnerable to disturbances (such as storms, fire, and insect outbreaks) and can easily result in C leakage when compared with more diverse forests consisting of multiple tree species (Galik and Jackson 2009). For example, past insect outbreaks have caused some forests to change from C sinks to C sources (Kurz et al. 2008).

In addition to the uncertainty following reforestation regarding growth and stability of different forests, there are also large uncertainties in estimates of C storage and C dynamics in forest ecosystems (Brown 2002). Because C concentration of different plant tissues varies greatly (Bert and Danjon 2006), the generally applied conversion factor of 0.5 (dry biomass to C concentration) may be oversimplified, perhaps even leading to inaccurate estimates of ecosystem C storage. Additionally, long-term effects of disturbances on C dynamics are often not considered (Schulze et al. 2000).

China has seen a rapid growth in tree plantations in recent years (FAO 2010). This is particularly true in subtropical China where abundant precipitation, mild winters, and long-growing seasons make forest productivity particularly high (Chen et al. 2011). At the same

time, the combination of high precipitation and steep slopes makes this region vulnerable to soil erosion, and much of the top soil in southeastern China has been lost prior to major afforestation efforts starting in the 1980s (FAO 2010; Zhang and Song 2006). Thus, how to choose the proper species that optimizes tree growth, timber volume, and long-term ecosystem C accumulation on these impoverished soils has become a high-priority question (Wang et al. 2009; Wang et al. 2011; Zheng et al. 2008).

Forests in subtropical China are not heavily influenced by major hurricanes (or typhoons), but do suffer occasional large-scale disturbances such as ice storms. Indeed, ice storms and freezing caused extensive damages to forests throughout the region in 2008 (Stone 2008; Zhou et al. 2011). Forest plantations were severely disturbed during the event causing a significant increase in litterfall in most of the damaged forest (see Fig. 1, Ma et al. 2010). Furthermore, severe stand damages occurred in the area leading to further dieback, tree mortality, and loss of biomass, and different forest species recovered at different rates in the years following disturbance (Sun et al. 2012). Thus, understanding species differences in ice storm damage and biological traits underlying these differences has become an important area of research among forest scientists.

Masson pine (*Pinus massoniana* Lamb.), one of the dominant native tree species in southern China, covers an estimated area of 17.39 million ha, including plantation area of 5.83 million ha (SFA 2005). It is a pioneer tree species common in secondary forests and plays an important role in wood production, C sequestration, and provides various ecosystem services (Wilson 1993). Although this species was originally the target species for restoration in China, several exotic tree species have been introduced over past several decades because of their high growth rates (Xu 2011). For example, slash pine (*Pinus elliottii* Engelm.), native in southeastern USA, has been extensively planted in southern China because of its high growth rate and resin production, covering almost 2 million ha by 1995 (Chen et al. 1995). Non-native slash pine grew significantly faster than Masson pine in provenance test in mid-subtropical regions of China, but slash pine was vulnerable to low temperature and freezing if planted in northern subtropical regions (Pan and Zheng 1990). Slash pine was planted north of its native range due to its superior growth and form relative to the more hardy alternative loblolly pine (*Pinus taeda* L.) (Neary et al. 1990). However, in the decades following large-scale afforestation of slash pine, ice storms caused major damage to slash pine forests in the southeastern USA (Bragg et al. 2003; Hebb 1971), but there is lack of evidence about the vulnerability of slash pine to ice storms in



Fig. 1 Example of severely damaged slash pine plantations after the 2008 ice storm in Qianyanzhou, Jiangxi province, China. Shortly after the ice storm (*top panel*), examples of stem breakage (*mid panel*) and overall stand damage (*bottom panel*)

China. Moreover, some introduced species are known to degrade soil fertility and alter belowground biodiversity (Finch and Szumelda 2007; Kourtev et al. 2002; Zheng et al. 2005; Tian et al. 2004). They may also be susceptible to pest attacks (Haggard et al. 1998) and therefore

increase the risk of biological invasions (Dodet and Collet 2012).

In this study, we assessed C sequestration as the cumulative biomass increases since plantation establishment. The first objective was to compare C storage, partitioned in above- and belowground biomass and litter components between native Masson pine and exotic slash pine plantation. The second objective was to compare the C sequestration potential of the two plantations at different spatial scales and under the influence of disturbances. The main hypotheses were that: (1) fast-growing non-native slash pine would show greater C sequestration than the native Masson pine and that C distribution within trees would vary with species, but (2) exotic pines would have lower resistance to ice storm damage and hence reduced ecosystem stability.

Materials and methods

Study area

The study was carried out at the Qianyanzhou Ecological Research Station (Qianyanzhou), located in Taihe county, Jiangxi province (115°04'E, 26°44'N) in mid-subtropical China. The monsoon climate dominates in this region with a mean annual temperature of 17.9 °C and an average annual precipitation of 1,489 mm. The cloud-free duration per year is 1,306 h, and annual solar irradiation yields 4,349 MJ m⁻² on average. Soils are typical red soils commonly found in subtropical regions, classified as *aliudic cambosols* and derived from sandstone, sandy conglomerate, mudstone and alluvium (SITCAS 1989). The zonal vegetation of this region is subtropical evergreen broad-leaved forest.

As the primary forest had been destroyed before 1983, serious soil erosion caused severe land degradation and resulted in a landscape that dominated by mixed grasslands, shrub, and only 0.43 % of forest cover, and the total aboveground biomass was only ~2.56 t ha⁻¹ in this region (SITCAS 1989). In the 1980s, reforestation and sustainable land-use management projects were launched to improve ecosystem functioning and to meet economic needs of local residents. A wide variety of tree species were planted in this watershed (SITCAS 1989, see also “Appendix”). Because pines are tolerant to poor soil, both Masson pine and slash pine were planted across the study area in 1984 through 1986 (mean establishment year 1985) with an initial planting density of ~7,500 stem ha⁻¹ (SITCAS 1989). One-year-old saplings were planted in level trenches following site preparation. The plantations, which did not differ significantly in site conditions when they were established,

were neither fertilized nor thinned after establishment. The study area consisted of three watersheds covering 207 ha (Appendix Fig. 7).

Tree biomass allocation and C concentration

To assess tree-level biomass vertical distribution, 3 slash pine trees with mean diameter at breast height (DBH) of 15.6 cm (14.7–16.5) and mean height of 13.8 m (12.7–14.4), and 3 Masson pine trees with mean DBH of 14.4 cm (13.9–15.3) and mean height of 10.3 m (9.7–11.1) were cut, and the weights of branch, leaf, and stem were measured with the 1-m sectional method in March 2008. The tree crown was stratified into 3 parts: upper (uppermost 2 whorls), lower (lowest 2 whorls), and middle crown (in-between upper and lower crown). Samples of branch and foliage from each crown part were taken for organic C measurement with $K_2Cr_2O_7-H_2SO_4$ oxidation method (Zheng et al. 2008). Tree architecture characteristics (crown width, DBH, and height) were measured on a total of 775 Masson pines and 631 slash pines in the same 1-ha long-term forest plot.

Vegetation survey

To estimate aboveground stand biomass, a total of 30 plots (400 m² each) were selected as a representative, sufficiently replicated sample across topography and site conditions at the Qianyanzhou in 2005–2007 (Table 1, Appendix Fig. 7). Within these plots, the DBH of all trees

Table 1 Forest conditions of plantations in Qianyanzhou in 2005–2007 (mean ± SD)

Plantation type	Masson pine (MP)	Slash pine (SP)
Number of plots	13	17
DBH** (cm)	13.34 ± 0.91	16.03 ± 1.30
Individual DBH growth rate** (cm year ⁻¹)	0.64 ± 0.04	0.76 ± 0.06
Initial planting density around 1985 ^a (stem ha ⁻¹)	~7,500	~7,500
Stand density** (stem ha ⁻¹)	1,980 ± 359	1,439 ± 271
Basal area (m ² ha ⁻¹)	28.4 ± 3.4	30.0 ± 4.3
Dry wood density ^a (kg m ⁻³)	346.16	298.19
Leaf area index* (m ² m ⁻²)	3.73 ± 0.46	4.27 ± 0.63
Volume** (m ³ ha ⁻¹)	128 ± 17	158 ± 27

**, * Indicate a significant difference at $P < 0.01$, $P < 0.05$, respectively

^a SITCAS (1989)

>5 cm was measured. Empirically derived site- and species-specific allometric relationships were used to estimate overstory biomass (Li et al. 2006; Ma et al. 2008). The ratio of taproot to aboveground biomass (AGB) was assessed in a prior study as 0.239 for slash pine (Ma et al. 2008) and 0.163 for Masson pine (unpublished data). In both studies, main taproots and lateral roots were excavated (down to 60 cm below surface), rinsed, dried, and then weighed.

During the period from 2005 to 2007, twenty-six subplots (1 m² each) were established in the two pine plantations types; aboveground understory biomass was measured by destructively harvesting all herbaceous vegetation in August when annual herb biomass reached its maximum; and forest floor litter was collected. All these samples were taken to the laboratory and dried to constant weight at 70 °C.

In August 2007, fine root (<2 mm diameter) and coarse root (≥2 and <5 mm diameter) biomass was measured in 8 rectangular soil columns (25 cm length × 25 cm width × 40 cm depth), which were divided into four 10-cm layers. Roots were weighed after washing off soil and dried to constant weight at 70 °C. To assess normal litterfall in forests, freshly fallen leaf litter was collected monthly for 5 years with 22 l traps (1 m² each) and air-dried it at the experimental site.

Soil sampling and estimation of soil C storage

In August 2005 and 2006, 15 soil cores (4 cm in diameter and 40 cm in depth) were taken with soil augers in the understory subplots of the two pine plantations to measure soil C. For each 10-cm soil section, soil bulk densities were measured with a bulk density corer (Appendix Table 4).

Soil samples were taken from each depth increment, and soil organic C (SOC) was measured with the dichromate method (Zheng et al. 2008) (Appendix Table 4). Soil nitrogen (N) concentration was estimated with the Kjeldahl method (Scheiner 1976) (Appendix Table 4). C densities of the upper 40 cm were calculated from soil depth, soil bulk density, and the corresponding SOC values with the following Eq. (2.1):

$$C_s = B_d \times C_c \times D/10 \times (1 - G) \quad (2.1)$$

where C_s is soil C storage (t C ha⁻¹), B_d is soil bulk density g cm⁻³, C_c is soil C concentration (g kg⁻¹), G is gravel content (%), and D is the soil sampling depth (cm). Given the relatively low gravel content (0.36–2.3 %) and the relative homogeneity of soils in the study area, the gravel component had little impact on the comparison between plantation types. Information on gravel content

(G) for the two plantations was taken from historical site data for the Qianyanzhou research station (Yuan 1999).

Soil C storage in the deeper soil horizons (41–100 cm) was inferred from this study using an empirical relationship between soil C concentration in deeper (below 40 cm) and shallow soil layer (0–40 cm) derived previously for this site (Yang 2005).

C sequestration baseline

As a baseline for net C sequestration rates of the reforestation project, we used biomass estimates (1983–1986) for grassland ecosystems at Qianyanzhou taken from the literature (SITCAS 1989). We also measured aboveground biomass and soil C concentration in two grassland plots within the same study area in 2006. Values measured for grasslands within the site were generally similar to those reported in the literature.

The impact of ice storm on C storage in plantations

We estimated C losses due to ice storm at both stand and region scale. First, forest damage from ice storms was assessed with a global positioning system (GPS) and by mapping all damaged sites in the study area. Areas with different damage levels (no damage, low damage, immediate damage, and heavy damage) were assessed for the two plantation types using a geographical information system (GIS), validated by field surveys.

Within these areas, plots were selected according to the level of damage. Since slash pine showed a large range of damage levels and widely dispersed damaged area, which required more plots and different plot size to survey, a total of 22 plots (total area = 2,325 m²) were established for slash pine with apparently damaged and undamaged plantations (Fig. 1, Appendix Fig. 7). Conversely, ice storm caused no damage or low damage in Masson pine and therefore required less plots to estimate C loss. Hence, five plots (total area = 2,300 m²) were established to assess damage to Masson pine in April 2008.

In these plots, we measured DBH and damage level of every tree and estimated branch and stem breakage (i.e., the number of broken branches or stems (or uprooted stems)/total number of trees). Theoretical tree biomass of different components was calculated based on the species-specific allometric relationships (Li et al. 2006; Ma et al. 2008). Then, we quantified C losses in these plots at stand level (Ma et al. 2010) with the following Eq. (2.2):

$$\text{Aboveground C storage loss} = (B_f \times C_f + B_b \times C_b) \times P_b + B_a \times P_s \quad (2.2)$$

where B_f and B_b are foliage and branch biomass (t ha⁻¹), respectively, C_f and C_b are C concentration in foliage and branches (%), P_b and P_s are the percentage of branch breakage and stem breakage, and B_a is the expected AGB of undamaged stands (t ha⁻¹).

Using forest area for each damage level, and corresponding C losses at the stand scale, aboveground C losses of the two pine plantations at the regional scale were estimated. Note that we avoided double-counting branch breakage in the estimations of stem breakage.

Additionally, we simulated tree crown ice load, using crown dimension and leaf traits and assuming layers of 0.6, 1.3, and 2.5 cm of ice in the following Eq. (2.3):

$$\text{Crown ice load} = L \times D \times T \quad (2.3)$$

where L was of total leaf surface area (m²), D was the density of ice (916.7 kg m⁻³), and T is the thickness of ice (m). Ice accumulation between 0.6 and 1.3 cm will cause small branches breakage; ice accumulations greater 2.5 cm in thickness may result in extensive damage (Van Dyke 1999). Please note that these estimations do not account for differences in ice load due to different crown architectures, e.g., greater ice accumulation on broader canopy.

Statistical analysis

Statistical analysis was performed using the R software, version 2.15.0 (R development core team 2012). For aboveground C storage, each forest canopy plot was treated as an experimental unit. To examine statistical significance in differences in basal area, C components, and soil conditions between two plantations, *t* tests were used. The least significant differences (LSD) was used for pairwise comparisons when comparing C components. Unless otherwise stated, $P < 0.05$ was the accepted probability level.

Results

Tree canopy structure and biomass allocation in Masson pine and slash pine

Masson pine biomass showed a greater taper along tree stem (yielding a cone-like shape) than slash pine. Slash pine allocated relatively more biomass to the stem and less biomass into the crown (Fig. 2), at the individual tree level. On the other hand, Masson pine had more live branch biomass than slash pine and foliage distribution was more even across the live crown (Fig. 2). Crown biomass ranged from ~28 % of total aboveground biomass in slash pine to ~51 % in Masson pine. The proportion of stem to total aboveground biomass was ~70 % in Masson pine and ~80 % in slash pine (Fig. 2).

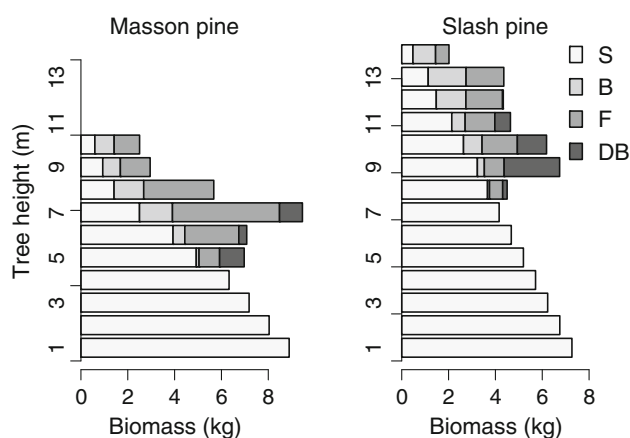


Fig. 2 Tree-level aboveground biomass (kg) vertical distribution in Masson pine and slash pine by tree compartment (*S* stem; *B* branches; *F* foliage; *DB* dead branches)

Fine and coarse root biomass in the two plantation types decreased with increasing soil depth (Table 2). Most of the roots were located in the upper 10 cm and accounted for 53.6–67.6 % of total root biomass in the upper 40 cm (Table 2). Fine root biomass was 12.5 % larger and coarse root biomass was 6.3 % lower in Masson pine than in slash pine (Table 2).

C storage and distribution at ecosystem level

Mean ecosystem (vegetation + litter + soil) C storage ranged from 117.89 t C ha⁻¹ in Masson pine to 116.77 t C ha⁻¹ in slash pine 20–22 years after afforestation (Table 2). The total living vegetation C pool was 51.39 ± 6.15 t C ha⁻¹ (mean ± SD) in Masson pine and 51.48 ± 6.89 t C ha⁻¹ in slash pine, while mean soil C was ~60 t ha⁻¹ (ranging from 45 to 80 t ha⁻¹, Table 2). Because of high stand density, canopy biomass of Masson pine was larger than that of slash pine (Table 2). The shoot/root ratio of C storage was 4.3:1 in Masson pine and 3.2:1 in slash pine, which means that more biomass was allocated to roots in slash pine than in Masson pine (Table 2).

We found no significant differences in aboveground C concentrations (total C in total biomass of a given component) between the two tree species except for dead branches, which was greater in Masson pine than in slash pine ($P < 0.05$, Table 2). C concentration in stems was 49.7 and 51.5 %, in branches 51.9 and 51.1 % and in foliage 52.5 and 52.0 % in Masson pine and slash pine, respectively (Table 2). Biomass-weighted mean C concentration in the canopy was 50.29 and 51.53 %, in roots 43.83 and 44.06 % in Masson and slash pine, respectively (Table 2). C concentrations in roots were consistently lower than those in other tree components. There was no consistent trend in C concentration of foliage or branches with crown position or

between species, but C concentration in branches showed less variation in contrast with foliage (Appendix Fig. 8). Carbon concentration ranged from 41.8 to 57.1 % leading to an underestimation of C stocks of 0.6–3.0 % when assuming 50 % C content to convert AGB to C stock.

Understory biomass C storage in shrubs was larger in slash pine than that in Masson pine (t test, $P < 0.05$; Table 2.), it accounted for 1.65 and 2.41 % of total ecosystem C in Masson pine and slash pine, respectively. Forest floor litter C ranged from 6.19 to 9.24 t C ha⁻¹ and took 5.19 and 7.84 % of total ecosystem C for Masson pine and slash pine, respectively (Table 2).

Soil C pool accounted for most of ecosystem C storage and was significantly larger in shallow soil (0–20 cm) than in deep horizons (20–40 cm). Soil C storage in the uppermost 40 cm was 37.35 t C ha⁻¹ in slash pine and 41.71 t C ha⁻¹ in Masson pine, but the difference was not statistically significant ($P > 0.05$) (Table 2).

Slash pine had greater bole diameter, was taller and had deeper crowns than Masson pine but had also lower wood density (Fig. 3). While above-ground biomass was greater in Masson pine than in slash pine (92.28 t and 89.05 t ha⁻¹, respectively) belowground biomass was greater in slash pine than in Masson pine (17.18 and 13.3 t ha⁻¹, respectively, Fig. 3).

C accumulation rate in different components

During forest development from 1985 to 2006, C storage in these ecosystems increased significantly (Fig. 4), mainly due to biomass accumulations. C storage in non-afforested grasslands decreased somewhat during the 21-year period because of a slight decline in soil C resulted from soil erosion (Fig. 4). Before reforestation (1983–1985), the watershed was dominated by grassland communities with an average total C storage of ~68 t ha⁻¹ of which nearly 97 % were stored in soils (Fig. 4).

Average C storage in two pine plantations was ~106 t C ha⁻¹, not accounting for root C storage (Fig. 4). With respect to different C pools, aboveground vegetation C increased remarkably while there was no significant change in soil C. Litter C storage was smaller in grassland (0.02 t C ha⁻¹) and shrubs (0.44 t C ha⁻¹) (SITCAS 1989), and much greater in Masson pine (6.19 t C ha⁻¹) and slash pine (9.24 t C ha⁻¹). During the past 21 years, aboveground overstory C in pine plantations increased at a mean rate of 2.18 t C ha⁻¹ year⁻¹ in slash pine and 2.23 t C ha⁻¹ year⁻¹ in Masson pine, and the mean total ecosystem C accumulation rates were 2.25 t C ha⁻¹ year⁻¹ in slash pine and 2.31 t C ha⁻¹ year⁻¹ in Masson pine. Compared with the initial grassland soil C storage of 68.2 t ha⁻¹ in 1984 (Huang et al. 2007), there was a mean reduction of 16 % in soil C storage in slash pine and Masson pine plantations.

Table 2 Biomass, C concentration, and C storage distributions in Masson pine and slash pine plantations measured in Qianyanzhou in 2005–2007 (mean ± SD)

Types	Masson pine			Slash pine				
	Biomass (t ha ⁻¹)	C concentration (%)	C storage (t C ha ⁻¹)	Proportion (%)	Biomass (t ha ⁻¹)	C concentration (%)	C storage (t C ha ⁻¹)	Proportion (%)
<i>Vegetation</i>								
Stem	53.15 ± 7.78*	49.69 ± 0.61	26.41 ± 3.87*	22.40	46.3 ± 7.37*	51.52 ± 2.93	23.85 ± 3.8*	20.42
Branch	15.99 ± 2.32	51.91 ± 2.00	8.30 ± 1.2	7.04	15.94 ± 2.38	51.10 ± 0.94	8.15 ± 1.22	6.98
Foliage	5.02 ± 0.72**	52.48 ± 1.10	2.63 ± 0.38**	2.23	6.96 ± 1.04**	52.04 ± 2.52	3.62 ± 0.54**	3.10
Dead wood	4.82 ± 1.24**	49.42 ± 0.77*	2.38 ± 0.61**	2.02	2.67 ± 0.81**	52.68 ± 0.61*	1.40 ± 0.43**	1.20
Taproot	13.3 ± 2.23**	48.28 ^a	6.41 ± 1.07**	5.44	17.18 ± 2.68**	49.97 ^a	8.57 ± 1.34**	7.34
Coarse root	3.03 ± 0.66	44.78 ± 1.55	1.36 ± 0.3	1.15	3.23 ± 1.63	45.34 ± 2.40	1.46 ± 0.74	1.25
Fine root	4.44 ± 1.46	43.18 ± 0.80	1.92 ± 0.63	1.63	3.95 ± 1.96	43.01 ± 1.30	1.70 ± 0.84	1.46
Understory in herb	1.58 ± 0.95	45.47 ± 2.87	0.72 ± 0.43	0.61	1.71 ± 1.27	45.47 ± 2.87	0.78 ± 0.58	0.67
Understory in shrub	0.94 ± 1.95*	45.47 ± 2.87	0.43 ± 0.89	0.36	2.23 ± 3.27*	45.47 ± 2.87	1.01 ± 1.49*	0.86
Understory root	1.86 ± 1.13	43.91 ^a	0.82 ± 0.5	0.70	2.33 ± 1.42	44.97 ^a	1.05 ± 0.64	0.90
Total living	104.13 ± 12.46	49.36	51.39 ± 6.15	43.59	102.80 ± 13.75	50.08	51.48 ± 6.89	44.09
<i>Detritus</i>								
Litter	12.38 ± 6.20*	50.04 ^a	6.19 ± 3.10	5.25	18.21 ± 5.41*	50.14 ± 2.58	9.24 ± 2.71	7.91
Soil 0–10 cm		1.26 ± 0.24	16.74 ± 3.91	14.17		1.22 ± 0.38	16.78 ± 5.01	14.37
Soil 11–20 cm		0.74 ± 0.14	10.94 ± 2.51	9.25		0.63 ± 0.16	9.25 ± 2.18	7.92
Soil 21–30 cm		0.55 ± 0.14	8.17 ± 2.43	6.93		0.43 ± 0.12	6.61 ± 1.68	5.66
Soil 31–40 cm		0.39 ± 0.06	5.86 ± 1.09	4.97		0.30 ± 0.11	4.71 ± 1.24	4.03
Soil 41–100 cm			18.68 ± 4.05 ^b	15.85			18.70 ± 5.37 ^b	16.01
Total mineral soil			60.31 ± 13.98	51.16			56.05 ± 15.48	48.00
Total ecosystem			117.89 ± 8.27				116.77 ± 7.49	

***, * Indicated a significant difference between two plantations at $P < 0.01$, $P < 0.05$, respectively

^a C concentration data were from the (Yuan 1999)

^b Soil C storage at the depth of 41–100 cm was indirectly inferred (Yang 2005)

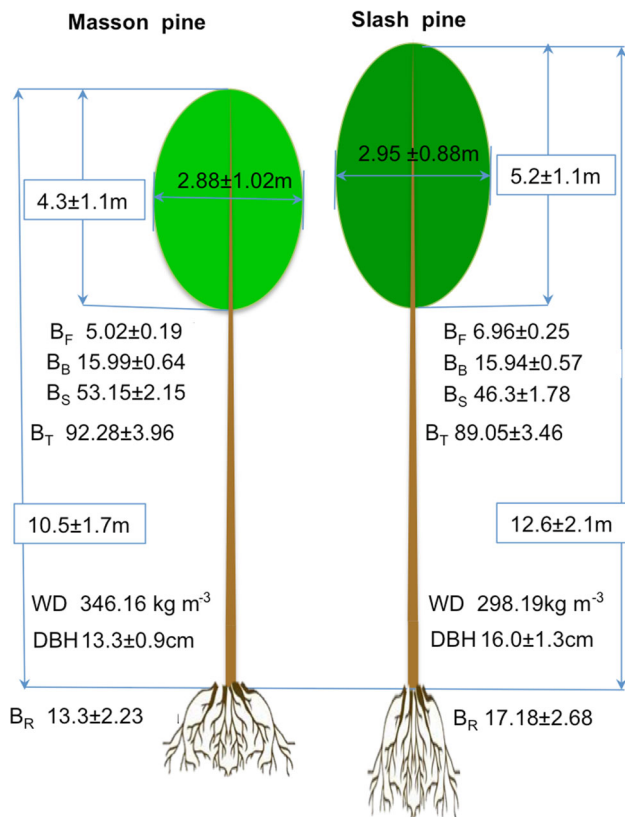


Fig. 3 Tree shape and crown structure in Masson pine and slash pine at the stand level (mean ± SE) (B_T total biomass ($t\ ha^{-1}$); B_S stem biomass ($t\ ha^{-1}$); B_B branches biomass ($t\ ha^{-1}$); B_F foliage biomass ($t\ ha^{-1}$); B_R taproot biomass ($t\ ha^{-1}$); WD wood density)

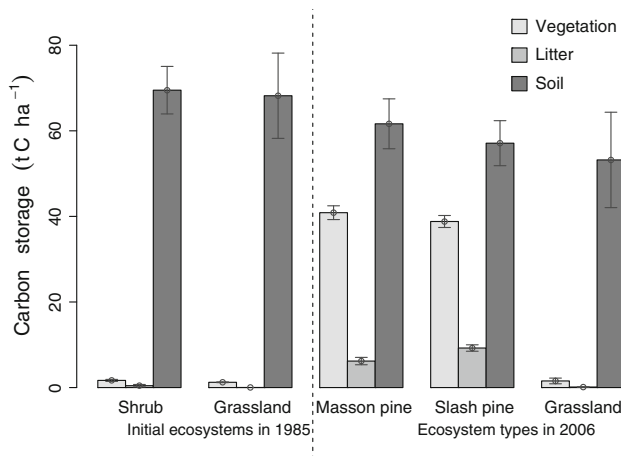


Fig. 4 C storage in 1985 and in 2006, 21 years after reforestation. The transition from grassland to forest increased C sequestration through considerable C accumulation in vegetation but not in soils

C losses due to ice storm disturbance

Slash pine plantations were more vulnerable to ice storm damage than Masson pine plantations (Table 3; Fig. 5).

Table 3 The impact of the 2008 ice storm on aboveground C storage in slash pine and Masson pine plantations in Qianyanzhou, Jiangxi province, China

	Slash pine (SP)		Masson pine (MP)
	Branch breakage only	Severe damage ^a (stem and branch breakage)	Branch breakage only
Total planted area in station (ha)	38.6		62.3
Ice stormed stricken area investigated (m^2)	8,906	20,704	–
Sample area (m^2)	900	1,425	2,300
Stand densities (stem ha^{-1})	1,289 ± 518	1,490 ± 504	2,100 ± 491
Branches breakage rates (%)	16 ± 15	33 ± 21	1 ± 4
Stem breakage rate (%)	–	37 ± 25	–
Overstory C loss from ice storm ($t\ C\ ha^{-1}$) ^b	1.98 ± 1.65	20.63 ± 13.59	0.12 ± 0.31

^a Severe damage assessed in April and October 2008

^b Ice storm impact on biomass investigated by Ma et al. (2010) C concentration from this study

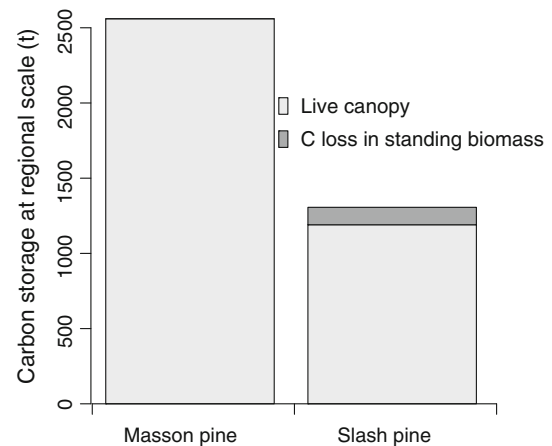


Fig. 5 Overstory C storage at the watershed scale (207 ha) and C loss in standing pine plantations due to the 2008 ice storm in Qianyanzhou, China. There was a substantial aboveground tree C loss (7.5 %) in slash pine but not in Masson pine plantations

Nearly 20 % of slash pine stand area was severely damaged (Fig. 5), while there was little substantial damage to Masson pine stand, only a few isolated individual tree crowns were damaged (Appendix Fig. 7; Table 3). The total area affected by severe damage (branch and stem

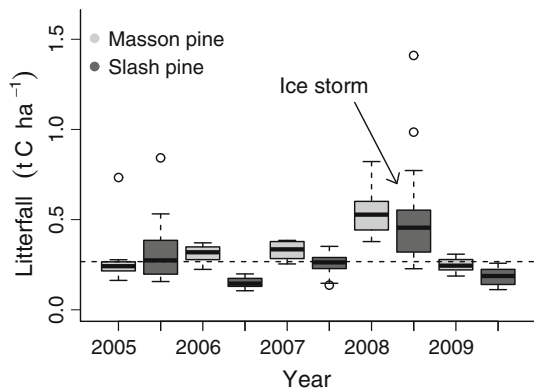


Fig. 6 Litterfall in January and February in undamaged Masson pine and slash pine plantations during 2005–2009. The litterfall was extremely increased by the 2008 ice storm event

breakage + stem uprooting + crown loss) in slash pine was about 7.72 ha and the mean overstory C loss was $\sim 15 \text{ t ha}^{-1}$ (Table 3) in the damaged area. At the watershed scale (207 ha), nearly 7.5 % of the AGB in slash pine plantations was transferred to dead organic matter and subsequent decomposition, compared to <0.3 % in Masson pine plantations (Fig. 5; Table 3).

According to our estimations, slash pine shows an ice load nearly twice as high as Masson pine, indicating that long and more needles in broader crown are the major reasons for the different ice storm vulnerability (Appendix Table 5).

Even in forests with no obvious damage, ice storms caused abundant fresh leaf litterfall (Fig. 6). This storm-induced litterfall was roughly twice the amount of litterfall normally observed for the two-month period around the storm (1.83-fold for Masson pine; 2.13-fold for slash pine, Fig. 6). The amount of litterfall during the two-month storm period was estimated to be $\sim 0.54 \text{ t ha}^{-1}$ (Fig. 6). There was no significant difference in the amount of fresh litterfall between two tree species following the ice storm (t test, $P > 0.05$), while litterfall in Masson pine was higher than that in slash pine in observed normal years (e.g., 2006, 2007, 2009, $P < 0.01$) except for 2005. Moreover, litterfall variability was increased by the disturbance event (Fig. 6).

Discussion

C storage and distribution at the ecosystem scale

There was no significant difference in C storage between two plantation ecosystems at the same subtropical climate, age, and site quality after 20 years of growth. This may be due to several reasons, anchored in the different

biological traits and ecological strategies of slash pine and Masson pine. First, canopy biomass was higher for Masson pine than for slash pine, but slash pine allocated more biomass to coarse roots. Second, there is a period of rapid growth rate at the early stage of slash pine plantation (Tian et al. 2004), for instance, in an 8-year experiment, the timber volume of slash pine plantation was five times greater than that in a Masson pine plantation (Pan and Zheng 1990). However, as forests matured, these high rates for slash pine disappeared. Third, even though slash pine is superior to Masson pine in terms of short-term timber production, Masson pine has higher stand densities and thus shows similar levels of aboveground C storage. However, slash pine is more prone to ice storm damage than Masson pine at the ecosystem scale, and C losses and the potential threat to ecosystem stability due to ice storm must be considered when taking management decisions.

C accumulation rate during forest development

Forest restoration sequestered significantly more C than the original grassland community, though the potential C sequestration by the two species studied here was tempered by disturbance. Overall, the rate of C accumulation was similar between our site and others within the region. In another site ~ 300 km from ours but at the same latitude (red soil region of the Hunan province), aboveground C accumulation rates during a 14-year period were $2.66 \text{ t C ha}^{-1} \text{ year}^{-1}$ in slash pine plantation and $1.97 \text{ t C ha}^{-1} \text{ year}^{-1}$ in Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) and C storage between 104.07 and $141.99 \text{ t C ha}^{-1}$ (Zheng et al. 2008). In another 15-year-old plantation dominated by pure Chinese fir, C storage ranged between 123 and 142 t C ha^{-1} (Wang et al. 2009) and were about $101.4 \text{ t C ha}^{-1}$ in an 18-year-old and $260.2 \text{ t C ha}^{-1}$ in a premature stand of subtropical evergreen broad-leaved forest (age >60 years (Zhang et al. 2010). Results from Zhang et al. (2010) show that there is a period of rapid C accumulation during the early stages of reforestation. However, over time, these high rates can be expected to decrease toward forest maturation. For example, 55–61 years after converting abandoned pastures to forest plantations or secondary forest, C sequestration rates in tropical regions were not more than $1.4 \text{ t C ha}^{-1} \text{ year}^{-1}$ (Silver et al. 2004).

Some studies (Zheng et al. 2005; Pan and Zheng 1990; Tian et al. 2004) have been carried out investigating whether exotic slash pine is well adapted to Chinese subtropical monsoon climate. While our research site was considered of fairly good climate for slash pine

growth, the studied plantations did not perform as well as American slash pine forests (Clark et al. 2004; Gholz and Fisher 1982). This may be due to differences in climate; while mean July temperature and annual precipitation are very similar, mean January temperature is about 14 °C in Florida (Clark et al. 2004) but only 6.4 °C at our sites.

Our results indicated that pine plantations might not transfer organic C into long-term soil C pools. These results are consistent with other studies that have also shown relatively low accumulation of soil C under pine plantations (Wang et al. 2011; Guo et al. 2007). Similarly, Paul et al. (2002) found that soil C may be lost rapidly in softwood plantations and especially in pine plantations, which can show decreases in soil C storage by 12–15 % (Guo and Gifford 2002). However, Richter et al. (1999) found that soil C increased by 1.00 t C ha⁻¹ year⁻¹ in pine ecosystems in South Carolina, USA, 40 years after establishment. The different results here may have been due to the prior site use and degradation from intensive cotton production depleting soil C storage in the South Carolina site.

Due to methodological limitations, there are still large uncertainties in estimations of fine root C components. Average fine root C storage in our plantations (1.81 t C ha⁻¹) was higher than in plantations of Chinese fir (~0.75 t C ha⁻¹) but less than fine root biomass in natural forest of *Castanopsis kawakamii* (Hayata) (~2.5 t C ha⁻¹) (Yang et al. 2004). Fine root C storage in 14-year-old slash pine plantations was ~0.2 t C ha⁻¹ in Hunan province (Zheng et al. 2008) and 4.4 t C ha⁻¹ in 17-year-old slash pine plantations in Florida, USA (Shan et al. 2001).

A large proportion of soil C accumulates in deeper soil horizons (>20 cm) in a wide range of ecosystems (Jobbagy and Jackson 2000), and root traits such as rooting depth exert a strong influence on soil C (Jobbagy and Jackson 2000; Jandl et al. 2007). In this study, the taproots of slash pine were deeper than those of Masson pine, which may lead to a greater C transfer into deeper soil horizons in slash pine plantations. However, lacking data for root respiration and, turnover, the absolute rate of C transfer remain unknown.

Assuming an initial soil C storage of 68.2 t C ha⁻¹ in 1984 (Huang et al. 2007), soil C storage was reduced in slash pine plantations by 19.7 % by 2006, seemingly due to forest establishment (Paul et al. 2002). However, model simulations for our sites indicate that soil C decreased during the initial 7 years after afforestation, followed by an annual increase of ~0.74 t C ha⁻¹ year⁻¹ (Huang et al. 2007).

C enters the soil system through the incorporation of aboveground litterfall, dissolved organic C, fine root

turnover, and via root exudates and symbiotic fungi (Trumbore and Czimeczik 2008). A recent study found that litter decomposition rates had little effect on upper-soil SOC storage in the same pine ecosystem (Liu et al. 2011), which is corroborated by the fact that recent leaf litter was not a major source of microbial C in temperate forest mineral soil (Kramer et al. 2010). Thus, we assume that changes in fine root dynamics and an overall reduction in root production is a likely cause of the soil C reduction after land-use change from pasture to conifer plantation (Guo et al. 2007).

Damage and C loss due to ice storm

With global climate change, extreme weather events are likely to become more frequent (IPCC 2007). Monoculture pine plantations may be especially vulnerable to climate change and extreme weather events such as drought (Allen et al. 2010). Other disturbances like the severe ice storm that occurred in southern China in 2008 (Zhou et al. 2011) highlighted the importance of understanding species responses to disturbance in forest management. Recently, the negative impact of non-native tree species used in China's new forests has sparked concerns and public discussion (Xu 2011). Tree species such as slash pine, loblolly pine, or *Eucalyptus* (spp.) showed a poor resistance to snow and ice load and suffered severe whole-stand damage, while Masson pine plantations were severely affected only in some areas (Zhou et al. 2011). During the ice storm event, most of the damage occurred in slash pine plantations, with approximately 15 t C ha⁻¹ of aboveground C lost in severely damaged areas, that accounted for ~20 % of the overall slash pine plantation area (Fig. 5). Moreover, regional root C storage would be further decreased due to taproot mortality following stem breakage and uprooting.

The larger canopy, greater height, and the larger leaf surface area of slash pine (Figs. 2, 3) explain its vulnerability to heavy ice loading. Another reason may be the lower dry wood density in slash pine (298.19 kg m⁻³) than in Masson pine (346.16 kg m⁻³) (Li et al. 2006) and may be due to rapid growth rates of slash pine (~20 % faster in DBH growth rate, see Table 1). Additionally, slash pine was much taller than Masson pine with greater foliage biomass (Fig. 3), which makes it mechanically more susceptible to breakage. Following stem and branch breakage, damage may then propagate as limbs fall and damage neighboring trees. Slash pine needles are thick and long with a large leaf surface area, which can result in greater ice accumulation (Appendix Table 5), exacerbating subsequent tree damage. Together, these factors may contribute to greater sensitivity of slash pine to ice storm damage.

Our study confirms slash pine's general vulnerability to ice storms whether in China or in the USA (Bragg et al. 2003), mainly due to the biological traits of this species. Except for the natural factors, human disturbances are a complex and inevitable issue in plantations. For example, resin collection can have an influence on the resistance to ice storm. That would be unlikely the major cause of tree collapse in our study area. But, there still need work to quantify the damaged degree and human disturbances. Given that slash pine is usually planted at large spatial scales, there is a high risk of large-scale losses in ecosystem function as well as in service provisions over longer time scales.

Exotic slash pine in ecological restoration: C dynamics and ecological services

Our study demonstrates that landscape C dynamics were substantially altered by the ice storm event. We could also show that the native Masson pine species seemed better adapted for ice storms and that this advantage will likely lead to more C accumulation and to less variation in ecological function and service over time.

According to our long-term observation, slash pine is not likely to become an invasive plant species due to little regeneration success observed under slash pine plantations; however, the use of slash pine may facilitate the introduction of exotic organisms. Biological invasive species of pine-feeding mealybug, *Oracella acuta* (Lobdell), accidentally introduced and established in Guangdong province in 1988, spread rapidly through these plantations, and caused a large loss of timber volume of both native and non-native forest ecosystems (Sun et al. 1996). Moreover, it has been shown that slash pine is also vulnerable to native pests (Zhao et al. 2007; Wen et al. 2004).

From the perspective of forest management, native tree species have a greater potential to meet a variety of objectives of afforestation (Butterfield 1995) and are better suited for use in low-input forestry (Haggar et al. 1998). A growing body of theories and evidence suggests that native species have considerable advantages over exotic species in a variety of ecological functions (Hartley 2002). For example, they offer habitats for countless invertebrates and microorganisms and are thus essential for maintaining biodiversity and the long-term integrity of vegetation communities (Hartley 2002; Carnus et al. 2006). However, forest managers should not only consider direct impacts of plantation forestry on biodiversity but also envision multiple perspectives across scales. Using highly productive exotic tree species can be a valuable tool for reducing

harvest pressure on natural forests and, as such, can be a means for conserving native plant and animal communities (Hartmann et al. 2010). In our study, the exotic tree species, although commonly thought to be of higher apparent growth yield, did not seem to be a better choice for sequestering C, and hence, enhancing the native tree species is an ecologically safer option.

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Appendix

Land-use history and ecosystem characteristics in research site

Natural vegetation in the study area is broadleaf forest. However, deforestation and other human disturbances caused massive soil erosion in the past and prevented successful natural regeneration. In the 1970s, residual Masson pine forests were cut and replaced with sugar cane (*Saccharum sinense* Roxb.) cultures, but this kind of vegetation was not well suited for the site conditions and the cultures failed completely and were abandoned (SIT-CAS 1989).

A lot of land became barren and grasslands until, in the 1980s, projects of reforestation and sustainable land-use management were initiated to restore ecosystem functioning and to meet the economic needs of the population. A wide variety of tree species were planted in this watershed (SITCAS 1989), some of them crop species (e.g., *Citrus reticulata* Blanco., *Castanea mollissima* Blume.) but mostly forest species such as Slash pine (*P. elliottii* Engelm.), Masson pine (*P. massoniana* Lamb.), and Chinese fir [*C. lanceolata* (Lamb.) Hook.] in either monocultures or mixed plantations. The understory shrub vegetation is dominated by *Quercus fabric* Hance., *Loropetalum chinense* (R. Br.) Oliver., *Lespedeza formosa* (Vog.) Koehne., and the herbal layer is composed of about 20–30 species, mainly *Adiantum flabellulatum* Linn., *Woodwardia japonica* (L. F.) Sm., *Dicranopteris dichotoma* (Thunb.) Bernh., *Dryopteris championi* (Benth.) C. Chr. apud Ching (Liu et al. 2005) (Figs. 7, 8; Tables 4, 5).

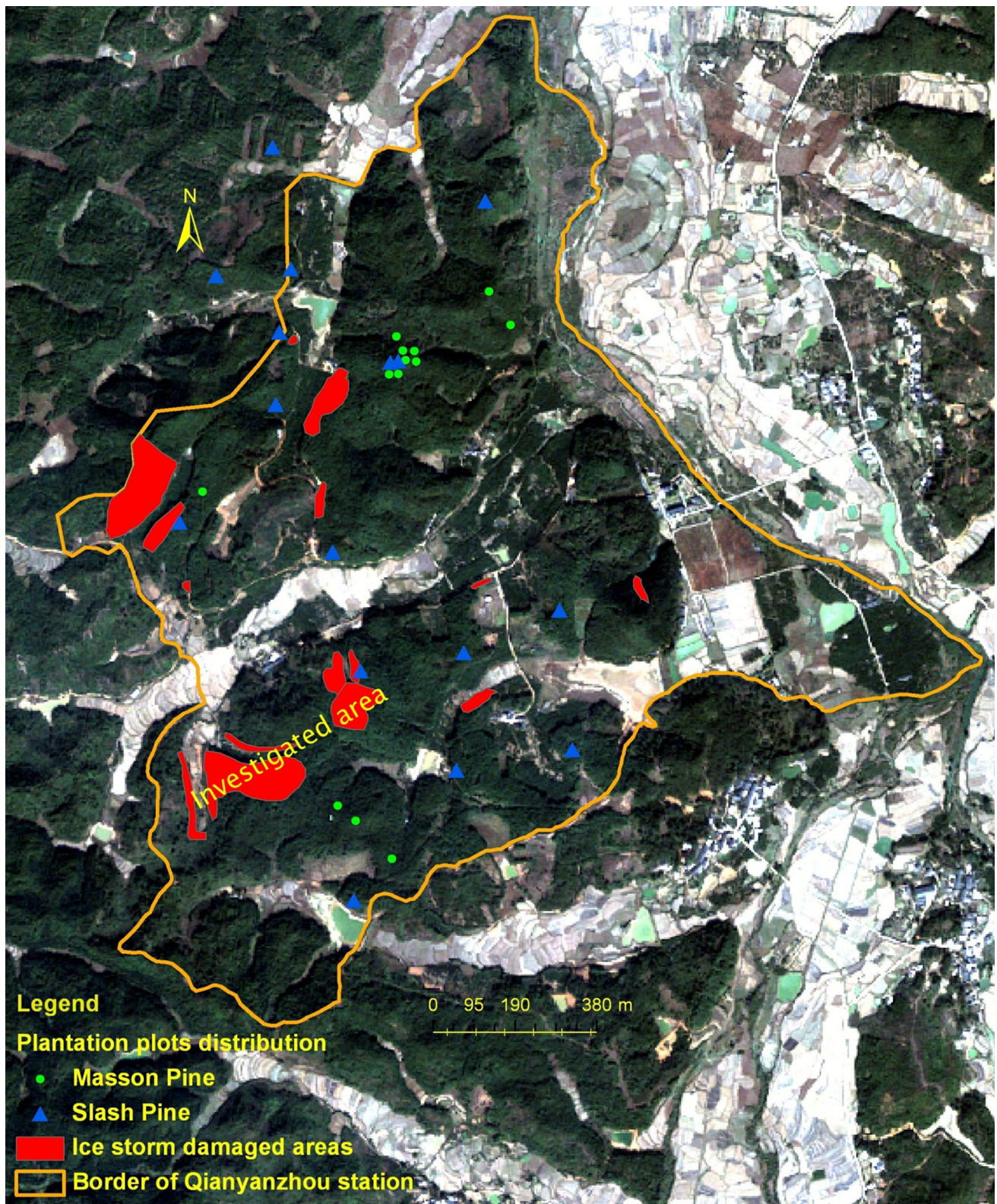


Fig. 7 Forest survey plots spatial distribution and ice-damaged areas in slash pine plantations in Qianyanzhou Ecological Research Station, Jiangxi province, China (the ice-damaged map cited from Ma et al. 2010)

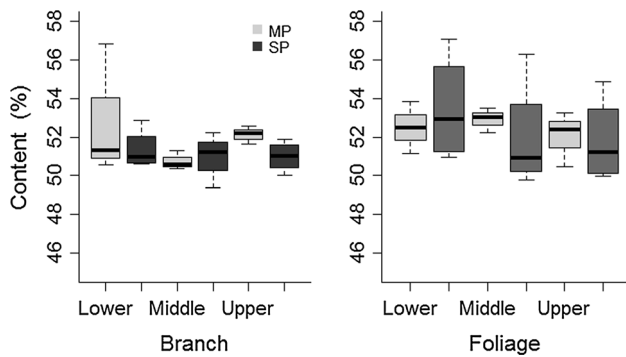


Fig. 8 Carbon content of branch (*left panel*) and foliage (*right panel*) biomass in different crown sections of the two plantation types (*MP* Masson pine; *SP* slash pine). There was no consistent trend in carbon content in relation to crown position (*t* test, $P > 0.05$) or between branches and foliage of the two species (*t* tests, branch: $P = 0.288$; foliage: $P = 0.929$)

Table 4 Chemical and physical characteristics of upper 40-cm soil in pine plantation as measured in Qianyanzhou in 2006

	Depth (cm)	Masson pine	Slash pine
Bulk density (g m^{-3})	0–10	1.36 ± 0.10	1.42 ± 0.08
	10–20*	1.50 ± 0.16	1.49 ± 0.09
	20–30	1.48 ± 0.11	1.57 ± 0.10
	30–40	1.52 ± 0.12	1.64 ± 0.24
Soil organic C (mg g^{-1})	0–10	12.6 ± 2.4	12.2 ± 3.8
	0–20	7.4 ± 1.4	6.3 ± 1.6
	20–30	5.5 ± 1.4	4.3 ± 1.2
	30–40	3.9 ± 0.6	3.0 ± 1.1
Total nitrogen (mg g^{-1})	0–10	0.80 ± 0.18	0.91 ± 0.25
	0–20	0.59 ± 0.09	0.57 ± 0.11
	20–30	0.52 ± 0.14	0.46 ± 0.09
	30–40	0.43 ± 0.06	0.39 ± 0.13

* Indicated a significant difference between two plantations at $P < 0.05$

Table 5 The simulation of Masson pine (MP) and slash pine (SP) when ice weight loaded on crown

	MP	SP
Mean DBH in typical tree (cm)	13.3	16.0
Mean height in typical tree (m)	10.5	12.6
Crown width (m)	2.9	3.0
Crown height (m)	4.3	5.2
Specific leaf area ^a ($\text{m}^2 \text{kg}^{-2}$)	8.6	6.0
Total leaf surface area (m^2)	35.6	64.9
Foliage biomass (kg)	2.1	4.7
Foliage water content (%)	0.57	0.59
Foliage fresh weight (kg)	4.8	11.5
Branch biomass (kg)	7.5	10.5

Table 5 continued

	MP	SP
Branch water content (%)	0.55	0.53
Branch fresh weight (kg)	16.5	22.4
Ice weight loaded on crown (kg)		
0.6 cm	195.8	356.7
1.3 cm	424.3	772.9
2.5 cm	815.9	1,486.3
Crown weight (kg)	21.3	33.8
Crown weight when ice loaded (kg)		
0.6 cm	217.1	390.6
1.3 cm	445.6	806.7
2.5 cm	849.8	1,520.2
The ratio ice load/crown weight		
0.6 cm	9.2	16.8
1.3 cm	19.9	36.3
2.5 cm	38.4	69.9

^a Mean specific hemisurface leaf area, data from (Li et al. 2007)

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