# Large, retained trees of *Cryptomeria japonica* functioned as refugia for canopy woody plants after logging 350 years ago in Yakushima, Japan

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## ARTICLE INFO

## ABSTRACT

Trees retained during green-tree retention forestry are expected to function as biological legacies that promote biodiversity and enhance ecosystem functions in plantation forests. Investigating how historically retained trees function as biological legacies could help predict the long-term ecological potential of current retention practices. Here, we investigated whether large, retained trees of *Cryptomeria japonica* D. Don (> 1000 years old) functioned as refugia for persistence of canopy woody plants after logging in a 350-year-old secondary forest in Yakushima, southern Japan. We climbed five each of retained and regenerated trees in a 1-ha research plot, measured trunk and crown structures, and tagged and measured every woody plant stem found on each tree. Compared to regenerated trees, retained trees had twice the surface area available for canopy plant colonization. Moreover, retained trees hosted disproportionately greater abundance of canopy woody plants. Together, the five retained trees hosted 22 species of woody plants comprising 1188 individuals, whereas regenerated trees hosted only 8 species (37 individuals). Combined with our ground-based measurement, canopy woody species contributed 16% of all woody plant species in the plot. Among the five retained trees, woody plant abundance increased markedly with increasing age of trunk breaks. This was because numerous epicormic branches had sprouted below trunk breaks creating large surface area upon which arboreal soil accumulated and woody plants established. Canopy woody plants on retained trees showed wide vertical distribution corresponding to complex crown structure, whereas those on regenerated trees occurred almost exclusively on the lower trunk. Maximum stem size of canopy woody plants was constrained by the volume of arboreal soil upon which they grew. Based on their size structures, we inferred that three species endemic to Yakushima (*Vaccinium yakushimense* Makino., *Viburnum urceolatum* Sieb. et Zucc., and *Rhododendron yakushimanum* Nakai), maintain stable populations in the retained trees by sprouting. Several other species scarcely found on the ground were also regenerating in the canopy. Our results demonstrate that retained trees of *Cryptomeria* functioned as refugia allowing canopy woody plants to persist after logging and give support to the importance of conserving large trees for enhancing biodiversity in forests where canopy plants contribute to species diversity.

## 1. Introduction

Biological legacies are organisms, organic matter, and structural features (e.g., standing trees, snags, logs, organic soil, etc.) that persist through a disturbance carrying over biological attributes to the re-covering ecosystem (Franklin et al., 2002). The concept of biological legacies has been applied to silviculture in the form of retention forestry to promote biodiversity and enhance ecosystem functions in plantation forests after logging (Rosenvald and Lohmus, 2008; Gustafsson et al., 2012). Retention forestry involves strategic maintenance of trees as biological legacies. Historically, trees have been retained purposively as

seed trees and shade trees to enhance regeneration after logging (Kohm and Franklin, 1997), or haphazardly left standing because they were too damaged or deformed to be useful (e.g., Takashima et al., 2017). Investigating how historically retained trees function as biological legacies can help predict the long-term potential of current retention forestry practices for conservation of biodiversity and ecosystem integrity (Root et al., 2007).

On Yakushima, a mountainous island in southern Japan, large *Cryptomeria japonica* D. Don. trees, which were too deformed to be used for timber, were left standing during a period of intensive logging in the Edo Era (1600–1800s, Takashima et al., 2017). There is speculation

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that the largest trees may have been retained for ethical reasons because the Islanders considered them sacred (Ohsawa et al., 2006). Such trees may have functioned as biological legacies during subsequent natural regeneration of the forest. Large trees are important for biodiversity because they provide various ecological functions such as providing food and habitat for arboreal animals, hosting diverse epiphytes, etc. (Lindenmayer et al., 2012). Yakushima is famous for its giant *Cryptomeria* trees, which are important structural features characterizing primary mixed conifer-broadleaved forest. For example, in a survey of 37 of the largest and oldest *Cryptomeria* trees on Yakushima, as many as 13 species of woody plants occurred in the crown of a single large tree reflecting the importance of such trees in hosting diverse plant communities (Yoshida, 1999).

Globally, canopy plants (including vascular epiphytes), representing approximately 9% of vascular plant species (Zotz, 2013), are an important component of biological diversity of forest ecosystems. In tropical rainforests vascular epiphytes contribute as much as 25% (Nieder et al., 2001) to 50% (Kelly et al., 1994) of vascular plant species. Canopy plants are abundant in forests with high precipitation, such as neotropical cloud forests (e.g., Nadkarni et al., 2004; Gotsch et al., 2015) and temperate rain forests (e.g., McCune et al., 2000; Ellyson and Sillett, 2003; Williams and Sillett, 2007) and contribute to various ecological functions such as providing food and habitat for canopy fauna (Yanoviak et al., 2003; Ellwood and Foster, 2004; Scheffers et al., 2014) and constitute an important part of the nutrient and water cycles in the forest canopy (Bohlman et al., 1995; Hölscher et al., 2004; Köhler et al., 2007; Gotsch et al., 2016). In forests with diverse canopy flora, plant species diversity and ecosystem functions cannot be understood without consideration of the canopy plant community (Díaz et al., 2010).

Diversity and distribution of canopy plant communities are well documented for tropical and temperate rain forests of the Americas by directly accessing the canopy using rope-climbing techniques, observation towers, and canopy cranes (e.g. Pike et al., 1977; Nieder et al., 2000; Krömer et al., 2007; Sillett and Van Pelt, 2007; Gotsch et al., 2015). Population structure and dynamics of canopy plant communities, however, are less studied because it requires detailed measurement of plant abundance and sizes, which can be difficult to conduct with limited canopy access (Flores-Palacios and Garcia-Franco, 2001). Some plants are transient, ephemeral components of the canopy plant community (accidental epiphytes), while others are able to maintain stable populations (obligate and facultative epiphytes) (Benzing, 2004). In primary forests of Yakushima, *Vaccinium yakushimense* Makino., endemic to Yakushima, occurs almost exclusively on large trees and rocky outcrops and is rarely found on the forest floor (Tsutsumi, 2011). Consequently, in closed-canopy forests, *V. yakushimense* is an obligate epiphyte that can only regenerate in the canopy. Although rainforests of East Asia host rich and abundant canopy plant communities (Hsu et al., 2002; Chen et al., 2010; Nakanishi et al., 2016), past research on canopy plants in Japan, have been mostly limited to species inventories conducted from the ground using binoculars and telescoping pruners (e.g., Hattori et al., 2009). We are aware of only one study in Japan that observed canopy plants directly (Hirata et al., 2009). Because endemic species are ecologically important for biodiversity, direct, quantitative investigations in the canopy are needed to elucidate the demography and regeneration niche of unique canopy plants like *V. yakushimense*.

Because it can take many years for canopy plant communities to develop on trees, and because of their sensitivity to environmental change, canopy plants are often used as indicators of ecosystem integrity (McCune, 1993; Sillett, 1995; Köhler et al., 2007; Giordani et al., 2012). For example, epiphytic lichens and bryophytes in the crown of old-growth *Pseudotsuga menziesii* (Mirb.) Franco trees have a distinct vertical profile, which is not apparent in second-growth forests (McCune et al., 1997). In montane cloud forests of Costa Rica, biomass of epiphytic bryophytes and vascular plants on branches and trunks was 40 and 100 times greater in primary forest compared to secondary

forest (Nadkarni et al., 2004). Trees retained after logging may function as refugia to "life-boat" species over the forest regeneration stage (Rosenvald and Lohmus, 2008). For example, in a northern hardwood forest in New York, USA, community compositions of epiphytic lichen were indistinguishable among single-tree retention, reserve shelterwood, and old-growth forests (Root et al., 2007). Although retention practices are old, green-tree retention for conservation purposes is still a relatively new forestry practice. Thus, only short-term effects (< 6 years) have been documented scientifically (e.g., Hazell and Gustafsson, 1999; Perhans et al., 2009; Lohmus and Lohmus, 2010; Lobel et al., 2012) and the long-term outcome is uncertain. Long-term persistence of canopy plants have only been inferred retrospectively from research on remnant trees following natural disturbance (e.g., Peck and McCune, 1997; Sillett and Goslin, 1999).

Secondary forests of Yakushima and the retained trees therein, present a unique opportunity to investigate the long-term outcome of green-tree retention. Here, we compared species diversity and population structure of canopy woody plants on retained trees with those of regenerated trees in a 350-year-old secondary forest dominated by
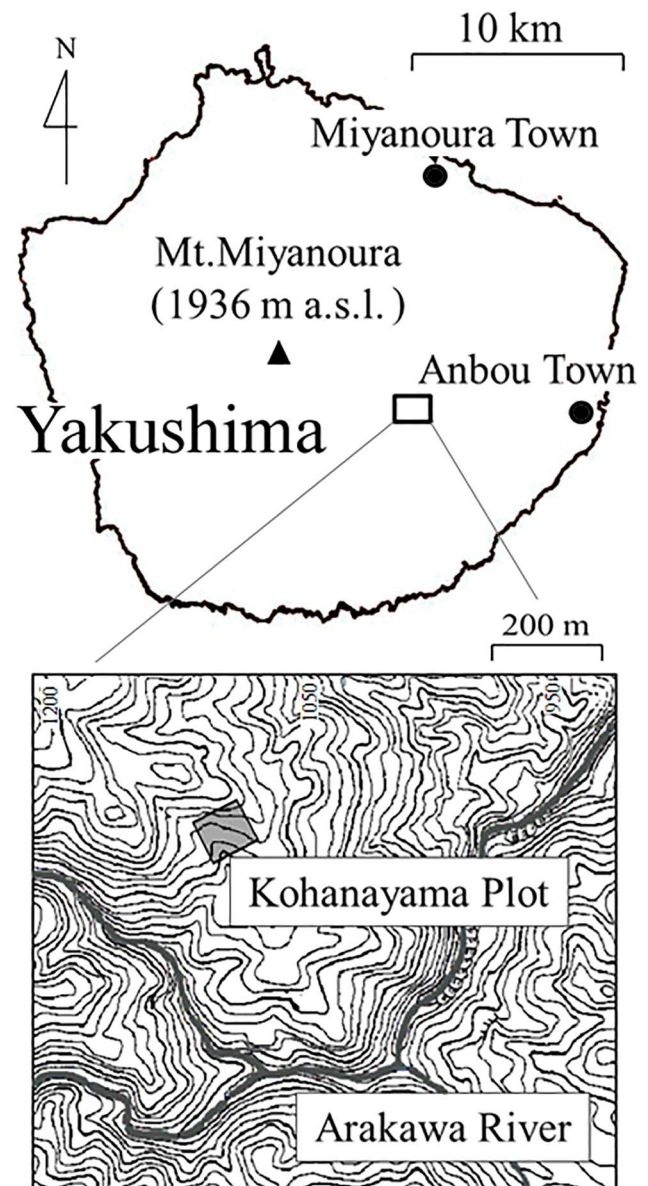


**Fig. 1.** Location of the study plot in Yakushima Island, Kagoshima, Japan. Contours are drawn at 10-m intervals.

**Table 1**

Tree ID, structural attributes and number of woody plants on retained and regenerated trees of *Cryptomeria japonica*. Trees are listed in order of increasing diameter at breast height (DBH, 1.3 m above ground level).

| Tree ID (number) | Structural attributes | | | | Number of woody plants | | | |
|---|---|---|---|---|---|---|---|---|
| | DBH (cm) | Height (m) | Effective surface area (m$^2$) | Age of trunk break (yrs) | Species | Individuals | Stems | Stem density (m$^{-2}$) |
| *Retained trees* | | | | | | | | |
| Tak (040008) | 124.8 | 26.2 | 126.3 | 155 | 9 | 92 | 173 | 1.37 |
| Nad (040018) | 129.5 | 32.7 | 127.5 | 191 | 10 | 90 | 231 | 1.81 |
| P1 | 157.4 | 32.6 | 167.6 | 412 | 12 | 391 | 733 | 4.37 |
| P2 | 173.2 | 33.4 | 201.4 | | 7 | 45 | 50 | 0.25 |
| NK | 179.8 | 21.3 | 163.5 | 566 | 20 | 570 | 1200 | 7.34 |
| **Total/mean**[*] | | | 786.3 | | **22** | **1188** | **2387** | **3.04 ± 2.84** |
| *Regenerated trees* | | | | | | | | |
| Ash (220032) | 82.5 | 28.4 | 67.8 | | 3 | 8 | 13 | 0.19 |
| Tok (230012) | 87.7 | 28.4 | 82.9 | | 2 | 5 | 5 | 0.06 |
| San (050097) | 88.5 | 22.4 | 78.1 | | 4 | 11 | 14 | 0.18 |
| Ebo (230022) | 97.7 | 28.8 | 98.3 | | 3 | 9 | 9 | 0.09 |
| Koh (230011) | 103.0 | 28.0 | 93.7 | | 4 | 4 | 4 | 0.04 |
| **Total/mean**[*] | | | 420.8 | | **8** | **37** | **45** | **0.11 ± 0.07** |

Tree NK had a broken top.

Numbers in ( ) indicate tree tag number from the ground survey in 2005 (Takashima et al., 2017).

  [*] Mean ± s.d. is given for stem density (number of stems/effective surface area).

*Cryptomeria.* Our main objective was to infer whether the retained trees functioned as refugia for woody plant communities to persist after logging. In addition, we inferred demography of canopy species from their size structure to understand community dynamics of canopy woody plants.

## 2. Study site and methods

The study was conducted on Yakushima (30°18′N, 130°34′E), an island on the southern coast of Kyushu, Japan. Yakushima is a mountainous island (0–1936 m elevation) with an area of 504 km$^2$ located in the warm-temperate zone of East Asia. Mean annual temperature below 100 m elevation is 15.4 °C (ranging from 5.4 °C in January to 24.8 °C in July) and annual precipitation ranges 2,400–5900 mm. Vegetation of Yakushima spans from warm-temperate, evergreen broadleaf forest in the lowland area to timberline above 1800 elevation. Mixed conifer-broadleaf forests dominated by *Cryptomeria* occur from 1000 to 1700 m elevation (Ohsawa, 1995). Frequent typhoons and monsoon rain storms may bring as much as 7400 mm of annual precipitation in mid- to high-elevation zones where *Cryptomeria* forests are found (Aiba et al., 2007).

We measured the canopy woody plant community on *Cryptomeria* trees in the Kohanayama area of Yakushima, where a permanent plot (100 × 100 m) was established by the Kumamoto Regional Forest Office in 1973 (Fig. 1). The plot is located in a mixed conifer-broadleaf forest at 1050 m elevation. *Cryptomeria* is the dominant tree species and tree-ring records from a near-by stand (800 m away) indicated that Kohanayama area was logged around 1650 (Ushijima et al., 2006). Size distribution of the *Cryptomeria* trees in the plot is bimodal suggesting that trees with diameter at breast height (DBH, 1.3 m above ground level) < 110 cm regenerated naturally after logging, while larger trees are those that were retained (Itaka et al. 2013; Takashima et al., 2017). Based on this distinction, density of retained *Cryptomeria* in the plot is 15 trees ha$^{-1}$, while that of regenerated trees is 181 trees ha$^{-1}$. Dendrochronological analyses indicate that retained trees in the stand exceed 1000 years in age (Ushijima et al., 2006). Other tree species in the plot include (in order of decreasing basal area): *Trochodendron aralioides* Sieb. et Zucc., *Stewartia monadelpha* Sieb. et Zucc., *Cleyera japonica* Thunb., *Illicium anisatum* L., and *Lindera erythrocarpa* Makino. (Ishii et al., 2010).

### 2.1. Field measurements

We used single-rope climbing technique for access and double-rope technique to maneuver in the crown of five each of retained and regenerated *Cryptomeria* trees (Table 1. Hereafter, we refer to the trees by their ID). The five retained trees were chosen based on their size to represent trees in the plot > 110 cm DBH and location away from trails for overhead safety. The regenerated trees were chosen randomly from those growing near the retained trees. To calculate trunk surface area, we measured trunk circumference at 2-m height intervals using a tape measure. We also measured diameter of each branch/limb attached to the trunk just outside its collar. Length of each branch/limb was measured by stretching a tape measure along its length to farthest foliage away from the trunk. Rope installation and structural measurements were conducted during 2008–2010 field seasons. There were no major crown disturbances in our study trees during this period.

Four of the five retained trees had evidence of major trunk breaks, as indicated by a sudden decrease in trunk diameter. To determine the age of the trunk break, we used an increment borer (400 mm × 4.3 mm, Haglöf Sweden AB, Långsele, Västernorrland, Sweden) to extract core samples at the base of reiterated trunks in July 2013. For tree NK, which had a broken top, a core was extracted from the largest reiterated limb. The extracted core samples were glued to wooden mounts and polished with progressively finer grit sandpaper. Individual growth rings were counted using a microscope mounted on a sliding stage. Although we did not cross-date cores, all cores reached near the pith so ring counts represent minimum trunk/limb age (discounting missing rings).

We put temporary tags (masking tape) on all woody plant stems in the crown of each tree to keep track of stems during measurement. A tape measure was stretched vertically from treetop to ground to determine height above ground of each stem. Diameter of each stem was measured with a digital caliper and length was measured by stretching a tape measure along the stem to farthest foliage away from its base. We then dug the litter layer to confirm whether or not stems were connected to each other. Connected stems were defined as ramets of a single individual plant.

Canopy plants were found on three types of substrate: trunk, branches, and arboreal soil. To contrast the trunk with appendages, we included limbs (*sensu* Sillett and Van Pelt, 2007) with branches because

only tree NK had significantly large limbs and almost all woody plants occurred on its horizontal surface (usually on moss mats), whereas those on trunks occurred on vertical surfaces (on top of bark irregularities, burls, etc.). Arboreal soil consists of decomposed organic matter that accumulate in the crown at base of live and dead branches, on crotches, or on irregularities on the trunk (Enloe et al., 2010; Gotsch et al., 2016). We measured length, width, and depth of each location where measureable amounts of arboreal soil had accumulated to roughly estimate its volume and distinguished these locations from trunk and branches. The canopy measurements were labor-intensive and had to be spread across three field seasons (2011–2013). There were no major crown disturbances in our study trees during this period.

We also measured woody plants on the ground for comparison with the canopy. In previous surveys, only trees > 4 cm DBH were measured (Ishii et al., 2010). To obtain data on smaller individuals and compare species composition at similar spatial resolution between canopy and ground, we randomly selected five of the 20 × 20 m sub-plots (0.2 ha total) within the permanent plot and measured all woody plants > 1.3 m tall and < 4 cm DBH. Within each of the selected sub-plots, we established four 5 × 5 m survey plots along the sub-plot diagonal (0.05 ha total). In each survey plot, we counted all woody plants shorter than 1.3 m DBH, including seedlings, and identified them to species. The ground survey was conducted during 2013–2014 field seasons.

In July of 2013, we set circular litter traps with 1-m$^2$ openings on the ground and in the crown of the study trees. One ground trap was set at the center of each randomly chosen sub-plot. The crown traps were hung near the trunk of each study tree at three heights: below the lowest branch (crown base), at one-third (mid-crown), and two-thirds (upper-crown) of the distance to treetop from crown base. The litter traps were collected in July 2014 and contents were sorted and weighed after oven-drying to constant weight. Seeds of woody plants were separated and identified to species.

### 2.2. Data analysis

Structural measurements of each tree were used to calculate surface area available for plant colonization (hereafter: effective surface area). Using trunk circumference measurements, we calculated effective surface area (m$^2$) of trunks as sum of surface areas of 2-m-long columns:

$$\text{Trunk surface area} = \sum \pi (r_a + r_b) \sqrt{(r_a - r_b)^2 + 4}$$

where $r_a$ and $r_b$ are lower and upper radii of each section, respectively. We approximated effective surface area of branches as that of a cone using branch diameter and length measurements. Although our estimates of branch surface area underestimate true surface area because it ignores higher order axes, most canopy woody plants in this study were found near the trunk on lower-order axes. Therefore, we believe this is a fair approximation of "effective surface area" available for colonization by woody plants. Effective surface areas of trunk and branches were summed for each tree to obtain estimates of total effective surface area. To roughly estimate the amount of arboreal soil at each location, we multiplied the length, width, and depth of each soil accumulation.

To investigate whether canopy woody plants are growth-limited, we used boundary-line analysis to estimate potential pattern of stem growth for the six most abundant species. To define the boundary line (maximum growth curve), a set of maximum points were selected incrementally assuming that stem length ($L$) should increase with increasing stem diameter ($D$) (Ishii et al., 2000). We fit exponential generalization of the allometric equation to the selected set of maximum points:

$$L = L_{\max}\{1 - \exp(aD^b)\}$$

where $a$, $b$, and $L_{\max}$ are parameters estimated using nonlinear least squares regression function in JMP (version 12, SAS Institute, USA). $L_{\max}$ is the model estimate of maximum stem length. We also analyzed



**Fig. 2.** Example of numerous epicormic branches (directly above climber) sprouted beneath the trunk break in a retained tree of *Cryptomeria japonica*.

vertical distribution and size structure of species with more than two individuals (six individuals per ha). Because plant size and age are correlated, dynamics of plant populations are often reflected in their size structure (Silvertown and Charlesworth, 2001). For example, positive-skewed size distribution having numerous small individuals reflects continuous regeneration, while unimodal distribution reflects a cohort originating from a single regeneration event.

### 3. Results

#### 3.1. Host-tree structure and distribution of arboreal soil

Together, the five retained trees hosted 22 species of woody plants comprised of 1188 individuals, whereas regenerated trees hosted only 8 species and 37 individuals (Table 1, 2). Retained trees were larger and had approximately twice the effective surface area of regenerated trees. Relative to their surface area, retained trees hosted disproportionately more woody plants than regenerated trees. On average, there were more than three stems per m$^2$ (3.04 m$^{-2}$) of surface area on retained trees compared to 0.11 m$^{-2}$ (approximately one stem per 10 m$^2$) on regenerated trees. Among the retained trees, abundance of woody plants was highest on tree NK, which had the largest DBH and oldest trunk break (566 years). On the other hand, abundance was lowest on tree P2, which had the second largest DBH but no evidence of a trunk break. Woody plant abundance on retained trees increased markedly with increasing age of the trunk break.

In three of the retained trees with trunk breaks (Tak, Nad, and P1), numerous epicormic branches had sprouted below the reiterated trunk (Fig. 2). In these trees, effective surface areas of branches were markedly high just below trunk breaks (Fig. 3). Tree NK had a discontinuous vertical distribution of branch surface area. This tree had a broken top and only four branches/limbs growing out of the main stem: two at 9 m (diameter, length = 88 cm, 8.9 m and 90 cm, 9.1 m) and two at 16 m
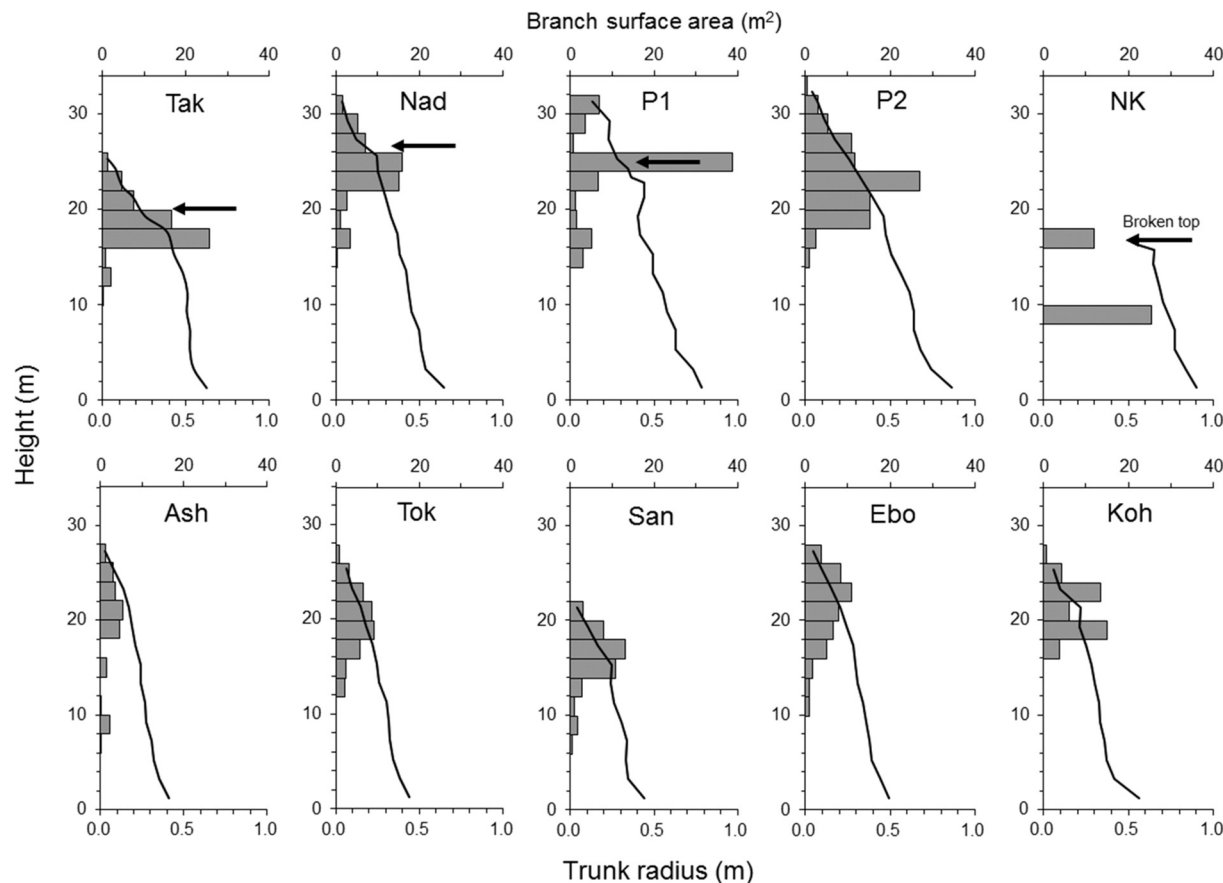
Fig. 3. Vertical change in trunk diameter (lines) and distribution of effective surface area of branches (bars) of retained and regenerated trees of *Cryptomeria japonica* in Yakushima Island, Japan. Arrows indicate heights of major trunk breaks where core samples were taken. The effective surface area of each branch is assigned at the height of branch attachment to trunk.

(44 cm, 6.5 m and 66 cm, 7.2 m). In contrast to the retained trees, effective surface area of branches on regenerated trees was more continuously distributed.

Vertical distribution of arboreal soil on retained trees showed two distinct peaks at 12–18 and 22–26 m (Fig. 4a). These peaks represented soil accumulations on epicormic branches of trees Tak, Nad, and P1. For the regenerated trees, there was only one incidence of arboreal soil (volume = 0.0014 m³) on tree Koh. A total of 728 g m⁻² of litter was collected in traps on the ground, of which about half were *Cryptomeria* leaves (Fig. 4b). A total of 2771 and 1757 g m⁻² of litter was collected in the crown of retained and regenerated trees, respectively. This reflected the difference in the amount of *Cryptomeria* leaf litter between

retained and regenerated trees. While the amount of leaf litter decreased with increasing height in the crown of regenerated trees, there was no such trend for retained trees.

### 3.2. Distribution and regeneration of canopy woody plants

Woody plants on retained trees showed wide vertical distribution with three distinct peaks (Fig. 5). Peaks at 22–26 and 16–18 m represented stems on epicormic branches of trees Tak, Nad, and P1, while the peak at 8–14 m represented stems on lower branches of tree NK. Woody plants on retained trees were also found on various types of substrate, with 52% occurring on branches and 23 and 25% on the
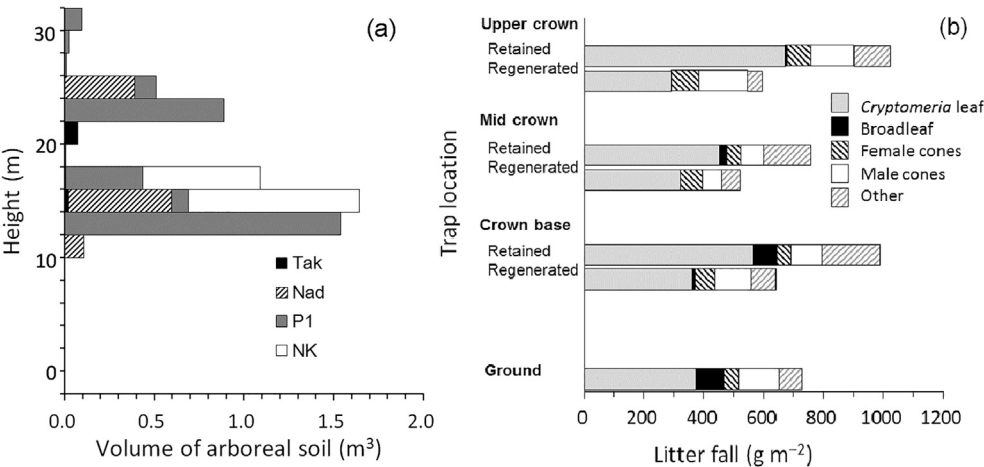


Fig. 4. (a) Vertical distribution of arboreal soil in retained trees of *Cryptomeria japonica* in Yakushima Island, Japan and (b) amount and type of litter collected from traps set on the ground and in the canopy of retained and regenerated trees.
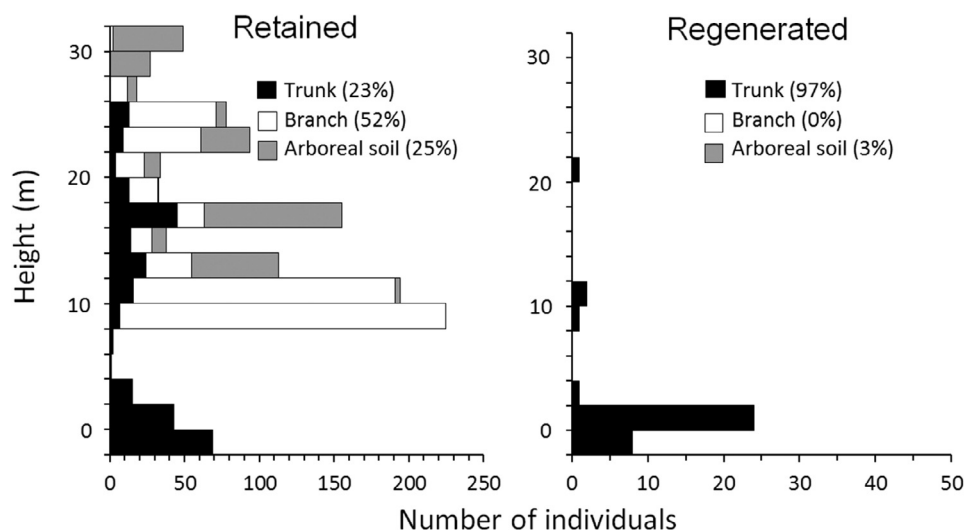
Fig. 5. Vertical distribution of woody plant stems and their occurrence on different substrates on retained and regenerated trees of *Cryptomeria japonica* in Yakushima Island, Japan. Negative height reflects woody plants on the trunk below average ground level for trees standing on slopes. Numbers in () indicate percentage of individuals occurring on each substrate. Note varied x-axis ranges.

trunk and arboreal soil, respectively. On regenerated trees, all woody plants were found on the lower trunk, except for one *I. anisatum* found on a small soil accumulation at 20 m on tree Koh.

On retained trees, maximum stem size (basal area and length) on arboreal soil, increased exponentially with increasing soil volume (Fig. S1, $r^2$ = 0.941 and 0.955, respectively). Stem length of the six most abundant species found on retained trees showed asymptotic growth patterns in relation to stem diameter (Fig. 6). Many of the stems were much shorter than the estimated maximum growth curve suggesting growth limitation (including those due to stem injury).

Estimates of maximum stem length of the six species ranged 142–357 cm.

*V. yakushimense*, *Sorbus commixta* Hendl., and *Rhododendron keiskei* Miq. were the most abundant species on retained trees (Table 2). These and several other species on retained trees were scarcely found on the ground, whereas species found on regenerated trees were generally abundant on the ground. Of the species on retained trees, seven were found only in the canopy, contributing an additional 16% (7/44) of total number of woody plant species in the plot.

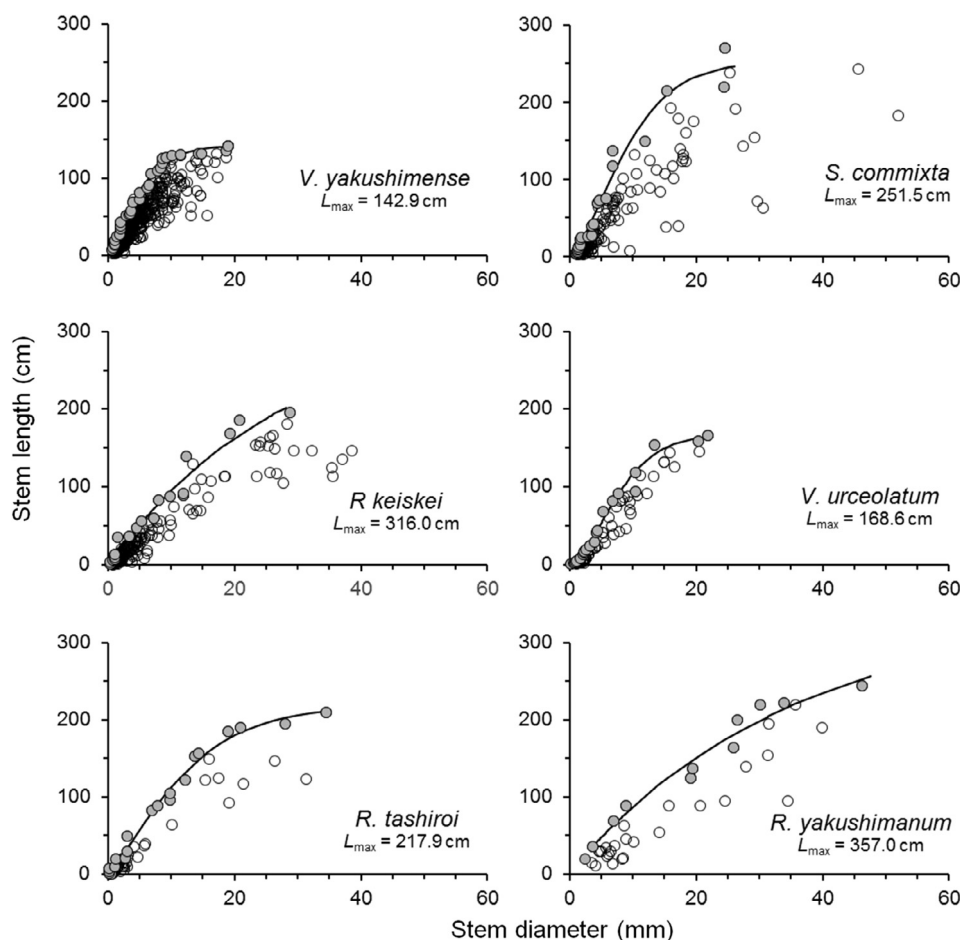Vertical distributions of canopy woody species with more than two



Fig. 6. Relationship between stem diameter and length for the six most abundant woody plant species found on retained trees of *Cryptomeria japonica* in Yakushima Island, Japan. Filled symbols indicate maximum points selected incrementally in order of increasing diameter and length. Lines indicate non-linear regressions for estimating maximum stem length ($L_{max}$) using the selected maximum points.

**Table 2**

List of woody plants found on retained and regenerated trees of *Cryptomeria japonica* and on the ground in Yakushima Island, southern Japan. Species are listed in order of decreasing abundance on retained trees.

| Species | Number of individuals (ha$^{-1}$) | | |
|---|---|---|---|
| | Retained* | Regenerated* | Ground |
| *Vaccinium yakushimense* | 1293 | – | – |
| *Sorbus commixta* | 570 | – | 1 |
| *Rhododendron keiskei* | 540 | 36 | 5 |
| *Viburnum urceolatum* | 249 | – | 40 |
| *Rhododendron tashiroi* | 237 | 615 | 2982 |
| *Cryptomeria japonica* | 129 | – | 378 |
| *Ilex pedunculosa* | 114 | – | 23 |
| *Rhododendron yakushimanum* | 114 | – | – |
| *Trochodendron aralioides* | 69 | 109 | 103 |
| *Symplocos myrtacea* | 66 | 181 | 7974 |
| *Illicium anisatum* | 57 | 290 | 3633 |
| *Skimmia japonica* var. *japonica* | 48 | – | 20 |
| *Eurya japonica* | 27 | 36 | 430 |
| *Stewartia monadelpha* | 12 | – | 185 |
| *Pieris japonica* | 6 | 36 | 1284 |
| *Skimmia japonica* **var.** *intermedia* | 6 | – | – |
| *Ilex rotunda* | 6 | – | – |
| *Tsuga sieboldii* | 6 | – | – |
| *Ilex crenata* var. *fukasawana* | 6 | – | 40 |
| *Cleyera japonica* | 3 | – | 255 |
| *Abies firma* | 3 | – | – |
| *Clematis pierotii* | 3 | – | – |
| *Camellia sasanqua* | – | – | 760 |
| *Neolitsea aciculata* | – | 36 | 384 |
| *Lindera erythrocarpa* | – | – | 13 |
| *Neolitsea sericea* | – | – | 13 |
| *Cinnamomum japonicum* | – | – | 7 |
| *Zanthoxylum ailanthoides* | – | – | 5 |
| *Clethra barbinervis* | – | – | 4 |
| *Dendropanax trifidus* | – | – | 2 |
| *Styrax japonicus* | – | – | 2 |
| *Kalopanax septemlobus* | – | – | 141 |
| *Camellia japonica* var.*macrocarpa* | – | – | 1 |
| *Daphniphyllum macropodum* var. *macropodum* | – | – | 1 |
| *Eurya japonica* var. *yakushimensis* | – | – | 1 |
| *Sarcandra glabra* | – | – | 280 |
| *Daphne kiusiana* | – | – | 40 |
| Total individuals | 3564 | 1339 | 19007 |
| Total species | 22 | 8 | 37 |

Species in bold did not occur on the ground.

* Calculated as mean number of individuals per study tree multiplied by tree density.
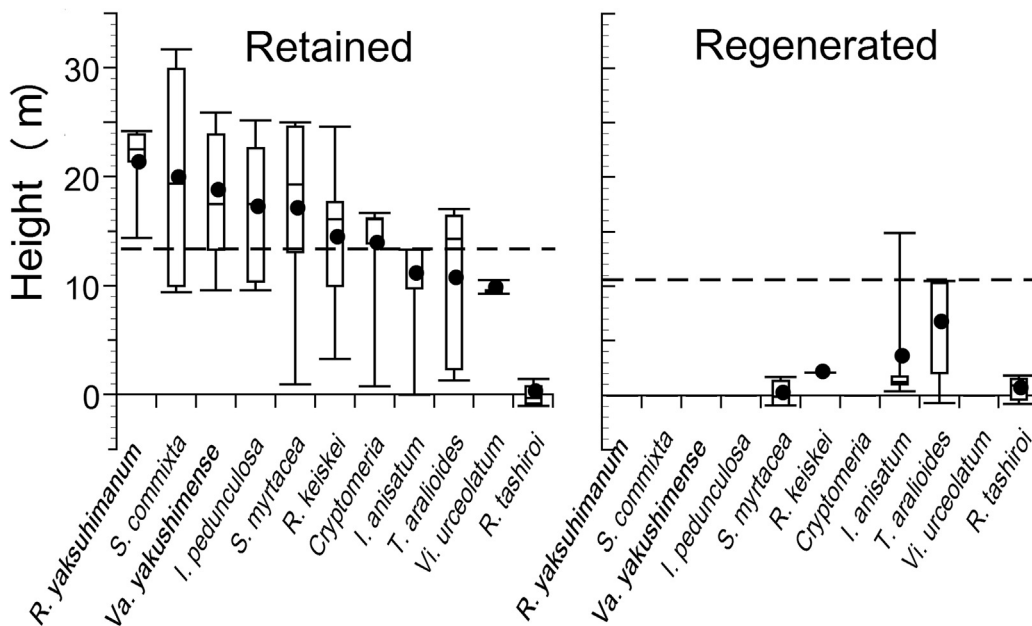
Fig. 7. Vertical distribution of woody plant stems on retained and regenerated trees of *Cryptomeria japonica* in Yakushima Island, Japan. Box length is the interquartile range. Circles and lines inside boxes represent mean and median height of individuals, respectively. Bars represent 10 and 90 percentiles. Negative height reflects woody plants on the trunk below average ground level for trees standing on steep slopes. Dashed horizontal line indicates mean crown base height. Species are in order of decreasing mean height. Species names in bold indicate those not found on the ground.

individuals ( > six individuals per ha, see Table 2) are shown in Fig.7. Light-demanding species, which did not occur or were scarce on the ground, occurred mainly in the crown of the retained trees. Species that were abundant on the ground occurred mainly on the lower trunk below crown-base height. Except for one stem of *R. keiskei* on tree Koh, all woody plants on regenerated trees were also common on the ground and occurred mostly on the lower trunk near ground level.

We grouped species with more than two individuals into four regeneration-types based on each species' stem-diameter distribution and mean number of stems per individual, plus our visual observations in the canopy (Fig. 8). For the three species endemic to Yakushima, (*V. yakushimense*, *Viburnum urceolatum* Sieb. et Zucc., and *Rhododendron yakushimanum* Nakai), number of stems in the smallest size class was less than the next larger size class and mean number of stems was > 2.0. This reflected regeneration mainly by sprouting because establishment size is large and many individuals are multi-stemmed. In contrast, for species such as *S. commixta*, *Rhododendron tashiroi* Maxim., and *Cryptomeria* stem-diameter distributions were positive-skewed and mean number of stems was < 2.0. This reflected regeneration mainly by seeding because establishment size is small and most individuals are single-stemmed. For *R. keiskei* and *Ilex pedunculosa* Miq., stem-diameter distributions were positive-skewed and mean number of stems was > 2.0. This reflected regeneration by both seeding and sprouting because establishment size is small and many individuals are multi-stemmed. For *I. anisatum*, *Eurya japonica* Thunb., and *Stewardia monadelpha* Sieb. et Zucc., stem-diameter distributions were bimodal and all large stems belonged to single individuals. We observed that this reflected two generations as a result of regeneration from a single founder individual.

During our seven-year study period, we visually confirmed flowers and fruits of all species shown in Fig. 8. Seeds of 12 woody species (*V yakushimense*, *S. commixta*, *R. keiskei*, *R tashiroi*, *Cryptomeria*, *T. aralioides*, *Symplocos myrtacea* Sieb. et. Zucc.*, *I. anisatum*, *Skimmia japonica* Thunb. *var. japonica*, *Cleyera japonica*, *Styrax japonica* Sieb. et. Zucc., and *Kalopanax septemlobus* (Thunb.) Koidz.) were collected from traps in the crown of retained trees. Of these, all but two species (*S. japonicas* and *K. septemlobus*, both bird-dispersed) occurred on retained trees. In contrast, only *Cryptomeria* seeds were collected from regenerated trees.

## 4. Discussion

It is estimated to take many decades to centuries for diverse canopy

plant communities to develop in tree crowns (Sillett and Goslin, 1999). Thus, host-tree age/size is an important factor determining the abundance and diversity of canopy plants (Zotz and Vollrath, 2003; Díaz et al., 2010; Werner et al., 2011; Woods et al., 2015; Nakanishi et al., 2016). In addition to sufficient time for establishment, substrate, such as upper surfaces of large-diameter branches, crotches, and trunk irregularities are needed for establishment of species-rich and abundant canopy plant communities (Sillett & Bailey 2003; Sillett and Van Pelt, 2007; Chen et al., 2010; Nakanishi et al., 2016). Our results suggest that, in addition to size, age, and substrate, structural complexity is an important factor contributing to abundance of canopy woody plants. Large, old trees are characterized by complex crown structure, which is a consequence of past crown disturbances (Ishii et al., 2000; VanPelt and Nadkarni, 2004; Sillett and Van Pelt, 2007). For these reasons, a few large trees host majority of the canopy plant biomass in many forests (Sillett and Van Pelt, 2007; Díaz et al., 2010; Nakanishi et al., 2016). The maximum height of *Cryptomeria* on Yakushima is constrained by trunk breaks due to typhoons (Ishii et al., 2010). *Cryptomeria* has high re-sprouting ability and broken trunks are usually replaced by reiterated trunks. In addition, due to temporary loss of apical control (Wilson, 2000), numerous epicormics branches sprout directly beneath the trunk break (Ishii et al., 2010). In the retained trees, such epicormic branches created platform-like structures increasing the surface area upon which large amounts of arboreal soil accumulated and woody plants established. Similar dynamics of crown reiteration and complex crown structure has been documented for *Sequoia sempervirens* D. Don, a close relative of *Cryptomeria* (Sillett and VanPelt 2007). Given structural complexity of the retained trees in this study, their effective surface area for plant establishment is likely to be much larger than our conservative estimates.

Large amounts of leaf litter were collected in the crown of retained trees, reflecting their large leaf area. As conifers increase in age, their crown form changes from conical to more cylindrical form (VanPelt and Sillett, 2008). This difference in crown form likely contributed to increasing amount of leaf litter in the upper crown of retained trees. Litter accumulates in crotches or on branch surfaces and eventually decomposes to form arboreal soil (Enloe et al., 2006, 2010). The relationship between volume of arboreal soil and stem size suggested that increasing amounts of arboreal soil allow woody plants to grow large, likely to reproductive size.

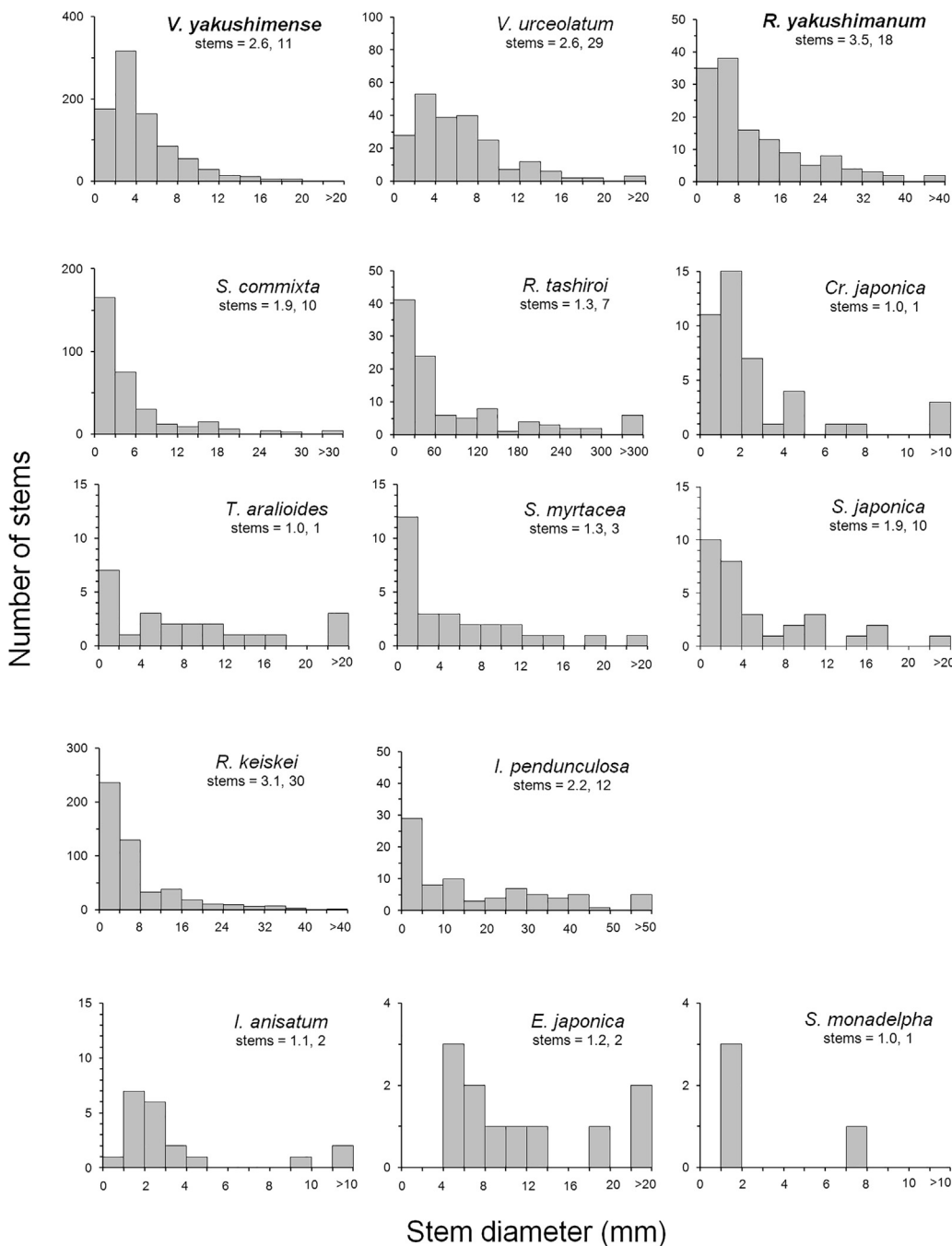Growth of canopy plants is constrained by many factors, including

**Fig. 8.** Frequency distributions of stem basal area of woody plant species on retained trees of *Cryptomeria japonica* in Yakushima Island, Japan. Numbers below species names indicate mean and maximum number of stems per individual. Species were grouped into four regeneration types (sprouting, seeding, sprout + seed, and founder) based on their size distribution and mean number of stems per individual. Species names in bold indicate those not found on the ground. Note varied Y-axis ranges.

limited growing space, light, water, and nutrients (Holbrook and Putz, 1996; Laube and Zotz, 2003), as well as increasing mortality from falling as plants increase in size. We found that maximum stem length of the tree species *S. commixta* was constrained to one-half to one-fourth of its potential size on the ground (5–10 m). Although potential stem length of the five shrub species, all of which grow to 1–3 m height, was not constrained in the canopy, many individuals were smaller than their estimated potential size, suggesting growth limitation. Five of the six most abundant species belonged to Ericaceae, which is the most species-rich family among canopy woody plants worldwide (Zotz, 2013). *Vaccinium ovatum* Pursh. is the most abundant woody plant in the crown *S. sempervirens* (Sillett and Van Pelt, 2007) and has similar ecological characteristics as *V. yakushimense* in this study. In a tropical montane forest in northern Thailand, Nakanishi et al. (2014) found that Ericaceae are distributed mainly in middle-to-upper canopy positions and inferred that this distribution pattern reflected their low shade

tolerance and high water-stress tolerance.

Woody plants on retained trees contributed to increasing woody plant diversity of the forest. Woody species absent or scarce on the ground, maintained stable populations in the canopy by both vegetative reproduction and seed dispersal. In addition, flowers, fruits, and seeds of the most abundant species were observed and collected, indicating reproduction in the canopy. Establishment size tends to be larger for sprouts than seedlings of many woody plants (Bond and Midgley, 2001; Del Tredici, 2001), suggesting that vegetative reproduction may be the main mode of regeneration for the three endemic species (*V. yakushimense*, *V. urceolatum*, and *R. yakushimanum*), for which the greatest number of stems were observed in the second smallest size class. The three endemic species are all bird dispersed, suggesting canopy populations are maintained by vegetative reproduction following initial establishment from bird-dispersed seeds. Seed-type species and seed-sprout type species included both bird- (*S. commixta, S. japonica, S.*

*myrtacea, I. pedunculosa*) and wind- (*Cryptomeria, R. tashiroi, T. aralioides, R. keiskei*) dispersed species, suggesting continuous regeneration from constant seed rain.

## 5. Conclusions

Biological legacies increase resilience of ecological communities after disturbance (Seidl et al., 2014). Thus, green-tree retention practices are expected to contribute to enhancing ecosystem function of subsequent secondary forest after logging (Rosenvald and Lohmus, 2008; Gustafsson et al., 2012). Even at 350 years after logging, woody plant communities were almost non-existent on regenerated trees. This indicates that canopy plant communities on retained trees existed before logging and that retained trees functioned as refugia for these species to persist. In addition, retained trees hosted species (including two endemic species) that occurred only in the canopy of this forest, as well as light-demanding species, which were scarce on the ground. This gives support to the importance of conserving large *Cryptomeria* trees for enhancing plant species diversity in secondary forests. Further research on ecological function of retained trees and demography of canopy plant species would provide valuable information for designing effective green-tree retention practices in warm-temperate Asia and other forests where canopy plants contribute to species diversity.

## Authors' contributions

HI conceived the study, established canopy access, and wrote the paper. TM and WA proposed the core-sampling and litter/seed-trap studies. HI and TM lead field work. WA and AN assisted with canopy work, while KH lead the ground survey.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.11.034.

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