Biomass allocation and long-term growth patterns of temperate lianas in comparison with trees

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Summary

- The host-dependent support habit of lianas is generally interpreted as a strategy designed to reduce resource investment in mechanical tissues; this allows preferential allocation to leaf and stem extension, thereby enhancing productivity and competitive abilities. However, this hypothesis has not been rigorously tested.
- We examined the aboveground allometries regarding biomass allocation (leaf mass and current-year stem mass (approximated as biomass allocated to extension growth) vs total aboveground mass) and long-term apparent growth patterns (height and aboveground mass vs age, i.e. numbers of growth rings) for nine deciduous liana species in Japan.
- Lianas had, on average, three- and five-fold greater leaf and current-year stem mass, respectively, than trees for a given aboveground mass, whereas the time course to reach the forest canopy was comparable and biomass accumulation during that period was only one-tenth that of co-occurring canopy trees. The balance between the lengths of yearly stem extension and existing older stems indicated that lianas lost *c.* 75% of stem length during growth to the canopy, which is probably a consequence of the host-dependent growth.
- Our observations suggest that, although lianas rely on hosts mechanically, allowing for short-term vigorous growth, this habit requires a large cost and could limit plant growth over protracted periods.

Introduction

Lianas (woody climbers) rely on the external structures of other plants to support their own weight and climb these host structures to reach higher canopy positions. This growth habit has evolved in a variety of lineages, forming a significant group of functionally similar, yet phylogenetically diverse, land plants (Gentry, 1991; Gianoli, 2004). Over the past few decades, an increasing number of studies have examined the community structure of lianas and their impacts on forest ecosystems worldwide, especially in the tropics, and have shown that they play essential roles in forest dynamics and function (reviewed by Schnitzer & Bongers, 2002, 2011). Far fewer studies have addressed organism-level attributes of liana plants that are relevant to their growth and life histories. We have a less than comprehensive understanding of the benefits and costs associated with the host-dependent support strategy.

Lianas are often hypothesized to have reduced biomass allocation to the support function (stem thickening and development of dense wood) and, instead, show preferential biomass allocation to leaves and/or stem elongation (Darwin, 1865; Monsi & Murata, 1970; Putz, 1990; Schnitzer & Bongers, 2002; van der Heijden *et al.*, 2013). Such an allocation pattern would enable lianas to have increased productivity and a superior ability in exploring and using space. The hypothesized allocation pattern

of lianas, however, has long been expected, and is based on the patterns of distribution of their standing organ biomass, but has not been clearly demonstrated. For example, tropical liana communities are known to have a greater contribution to forest leaf area (up to 40%) than to aboveground plant biomass (< 10%) (Putz, 1983; Hegarty & Caballé, 1991), indicating that forest lianas generally have a greater leaf to aboveground mass ratio than co-occurring trees. Liana stems are generally longer and thinner for their mass than those of self-supporting trees or shrubs (Gartner, 1991; Niklas, 1994; Selaya & Anten, 2008). Although these observations are consistent with the idea that lianas show preferential allocation to leaf biomass and stem length, as opposed to stem thickness, the distribution patterns of standing biomass observed at a certain point in time may not directly reflect the dynamic biomass allocation pattern (i.e. partitioning of newly acquired biomass among organs) of plants. In this regard, the review of Wyka *et al.* (2013) pointed out that only a few studies have examined biomass allocation of lianas at the seedling or small juvenile stages, in which the allocation pattern was generally similar to that of tree seedlings; little information was available on biomass allocation for larger liana plants. By comparing published allometric equations for Amazonian trees and lianas, Wyka *et al.* (2013) were able to demonstrate that, except for small individuals, lianas had greater leaf mass than trees at a given amount of aboveground plant mass across a

wide range of plant sizes. This report provided stronger support than previous studies for the idea of preferential allocation to leaves in lianas. Nevertheless, interspecific variation of leaf life-span (Reich *et al.*, 1991) could still have obscured the intrinsic biomass allocation pattern of plants in this evaluation (i.e. leaf mass of plants increases with leaf longevity for given biomass allocation patterns). Here, we re-evaluate this hypothesis regarding biomass allocation of lianas by examining allometric relationships of leaf mass and current-year stem mass (i.e. stem mass of current-year shoots, which was approximated as biomass allocated to extension growth) vs total aboveground mass in deciduous lianas and trees in cool-temperate regions. We employed a similar approach to that used by Wyka *et al.* (2013), but analysed measured data and included the aspect of stem extension growth. Moreover, winter-deciduous species are useful for this analysis in that the biomass allocated to leaves and newly extended stems produced during the current year may be readily determined.

Although the hypothesized allocation pattern of lianas will enhance plant growth from the ecophysiological viewpoint, the growth of lianas in the field may be greatly affected by the availability and stability of supporting host structures. Many lianas repeatedly move from the current host to other trees to reach the forest canopy, and lianas probably fail to find new host trees on some occasions (Putz, 1984; Putz & Holbrook, 1991). Lianas are dragged down when host trees or their branches collapse; in extreme cases, the entire liana may fall to the ground (Putz, 1983). Mechanical failures in supporting host structures are frequent, as indicated by the simple observation of liana basal stems hanging in the high forest canopy caused by the collapse of former hosts (Ichihashi & Tateno, 2011). These mechanical events will retard the ascent of lianas towards the forest canopy and negatively impact whole-plant biomass accumulation. Lianas produce long, thick shoots that search for host structures (French, 1977; Putz & Holbrook, 1991; Ichihashi *et al.*, 2009), which show rapid senescence and are lost if they fail to attach to host structures (Putz & Holbrook, 1991). Lianas may lose parts of their canopies (even if they do not fall to the forest floor) as they are dragged down by collapsing hosts. Although the significant dependence of liana growth on host availability has been documented for plants in the early stages of development (Putz, 1984; Sakai & Suzuki, 1999), little is known about how these mechanical factors impact long-term growth of liana plants. Here, we examined the time course during the developmental stages of the cool-temperate lianas between juveniles and adult canopy plants based on the relationships of height and aboveground mass with age estimated from the number of annual rings. We also determined the magnitude of stem turnover during this period by examining the balance between the lengths of yearly stem extensions and those of existing older stems. By combining information on biomass allocation, long-term apparent growth patterns and stem turnover, we estimated the degree to which the growth of liana plants is affected by mechanical factors.

In the present study, we sampled specimens of nine deciduous liana species. Individuals spanned a broad size range (0.5–18 m in maximum height above the ground) and occurred in a cool-temperate forest in Japan. Related data for trees in the same climatic regions were collected from published literature. Our objectives were to test whether biomass allocation to leaves and stem extension is greater in lianas than in trees, and to estimate the time course and magnitude of stem turnover of individual lianas during the developmental stages as lianas enter the forest canopy. It should be noted that, in these analyses, we presumed that natural selection has favoured growth patterns that allow a liana to reach the forest canopy efficiently vs spreading widely in subcanopy or lower positions; thus, we treated the height attained in the vegetation as an important measure of performance, independent of total stem length. The presumption was based mainly on the observations that lianas were obviously able to enhance their accumulation of biomass and basal diameter growth and/or decreased searching activities after they entered the forest canopy (details in Supporting Information Notes S1). Based on these evaluations, the benefits and costs associated with the host-dependent support habit are discussed.

Materials and Methods

Study site and species

Most of the study was conducted in the Yakushidake National Forest (36°43′N, 139°31′E), *c.* 800–1100 m above sea level (m asl), in Nikko, Japan; additional samples were collected in a neighbouring secondary stand at a lower elevation (*c.* 500 m asl; 10 km east of the Yakushidake site). The mean annual temperature and precipitation over the 20-yr period from 1993 to 2012 were 7.1°C and 2229 mm, respectively, at the Okunikko Weather Station (1292 m asl; 3 km north of the site), and 11.6°C and 1930 mm, respectively, at the Imaichi Weather Station (414 m asl; 14 km east of the site). The cool-temperate zone forest is dominated by deciduous trees, including *Fagus japonica*, *Quercus crispula*, *Betula grossa*, *Carpinus japonica* and *Acer* spp. Much of the forest was *c.* 15 m in height with 50–80-yr-old canopy trees (Ichihashi & Tateno, 2011). According to local people, forest trees at the study site had often been selectively logged, and trees had been used mainly as fuel wood until *c.* 1950s, but the site has been basically untouched since then. The canopy was almost leafless in winter from November to late April.

We examined a total of nine large liana species belonging to eight angiosperm families (Table S1). This selection of higher taxa included the majority of plant families containing common liana species in cool-temperate regions of Japan (*c.* 30 deciduous liana species belonging to 16 genera in 11 families, including semi-woody and relatively small woody vines, listed in cool-temperate Japanese flora compiled by Satake *et al.*, 1989). We chose four species (hereafter, 'main species') with diverse ecological habits (Ichihashi *et al.*, 2010; Ichihashi & Tateno, 2011) for intensive sampling and full analysis as follows: *Actinidia arguta* (Siebold *et* Zucc.) Planch. *ex* Miq. (Actinidiaceae) and *Celastrus orbiculatus* Thunb. var. orbiculatus (Celastraceae) are aggressive competitors that regenerate mostly in disturbed sites and spread into many tree crowns by intercepting a large amount of light in the forest canopy; *Schisandra repanda* (Siebold *et* Zucc.) Radlk.

(Schisandraceae) and *Schizophragma hydrangeoides* Siebold *et* Zucc. (Hydrangeaceae) regenerate mainly in the forest understorey and mature in shady positions within the forest canopy. The following five species were also sampled and included in the analyses of biomass allocation and apparent growth pattern: *Akebia trifoliata* (Thunb.) Koidz. (Lardizabalaceae), *Wisteria floribunda* (Wild.) DC. (Fabaceae), *Vitis coignetiae* Pulliat *ex* Planch. (Vitaceae), *Actinidia polygama* (Siebold *et* Zucc.) Planch. *ex* Maxim. (Actinidiaceae) and *Berchemia racemosa* Siebold *et* Zicc. (Rhamnaceae). *Actinidia polygama* and *B. racemosa* were studied at our lower altitude site. All other species were studied at the Yakushidake site. Species other than *S. hydrangeoides* (root climber) and *V. coignetiae* (tendril climber) are stem-twining lianas.

Sampling and measurement procedure

Sampling and measurements were conducted between 2006 and 2009, and in 2013, from late August to early October of each year, when stem elongation and leaf expansion had terminated. Leaf fall began after the sampling period. Approximately 20 plants, ranging from small juveniles to large canopy plants, were sampled for each of the four main species. We collected 15 plants of *A. trifoliata* (which had been collected for another purpose, Ichihashi *et al.*, 2010; 13 of these 15 samples lacked age data), and five to eight middle-sized plants of the remaining species. In most cases, juvenile samples were taken from forest edges or gaps, but juveniles of *S. repanda* and *S. hydrangeoides* were collected from the forest understorey (their main regeneration habitat). We excluded seedlings that had not started to climb and plants in which extension growth had apparently been retarded for many years because of a lack of nearby suitable host structures (e.g. lianas colonizing isolated short trees). Furthermore, we intentionally avoided plants that had originated by vegetative propagation (sprouts from roots and stolons of adult plants) or regrowth from fallen adult stems. This was performed because we aimed to acquire data on the developmental stages that were comparable with trees (i.e. from seedlings to their first entry to the forest canopy). Thus, we excluded plants whose physical connections with other stems were revealed, or plants on which apparent signs of regrowth were recognized after removing the litter, and we avoided sampling from places in which lianas were densely aggregated. However, the origins of liana individuals were difficult to determine properly, and our samples may have included some clonal ramets. Among the liana species selected, we often observed vegetative propagation from adult lianas in *C. orbiculatus* (from extensively spreading belowground organs) and in *W. floribunda* (from stolons), but not in *A. arguta*, *S. repanda* or *S. hydrangeoides*, through 10 yr of field observations. We were unable to make definitive observations on vegetative propagation in the other species (R. Ichihashi, pers. obs.)

For each sample, plant vertical height from the ground was determined by lowering a measuring tape from the uppermost position of the individual (it should be noted that this position was not necessarily close to the main body of the

liana canopy). Host trees were climbed when necessary using ropes to access the canopy. The basal stems of lianas that trailed on the ground were often buried in the litter layer and generated adventitious roots. We defined the position at which the stem completely penetrated into the soil after the litter was removed as the initial rooting point. We collected the entire aboveground portion above the initial rooting point for each plant sample.

The ages of samples were determined in the laboratory; we cut the main stems of samples 50 cm from each initial rooting point and counted the number of annual rings. We made thin sections of the cut surfaces (cut with a microtome and stained with 1% safranin) and examined them under an optical microscope. We assumed that the number of annual rings at the 50-cm point represented the number of years since the plants started to climb by extending climbing shoots (seedlings of liana species did not show extensive trailing before climbing and free-standing seedlings rarely exceeded 50 cm in height; R. Ichihashi, pers. obs.).

All current-year shoots were detached from sample plants. Masses of leaves, current-year stems and stems that were not current-year shoots were determined separately after drying to constant weights at 80°C. Petioles (including rachises and petiolules) were considered to be a supporting organ and thus included in the stem category. This organ comprised c. 15% of the total current-year shoot mass in species with compound leaves (*A. trifoliata* and *W. floribunda*) and ≤5% in species with simple leaves (remaining species). The results of the allometric analyses were largely unaffected by the inclusion or exclusion of petioles in leaf or stem categories (data not shown). For the four main species, we measured the lengths of all current-year 'climbing shoots' and the total length of older stems (i.e. stems that were not current-year shoots) that formed the framework of a liana's aboveground body for each sample before drying. Climbing shoots are long and have the ability to twine (in stem-twiners) or generate adventitious roots (in root-climbers), thereby acquiring external support (it should be noted that a large proportion of current shoots on these lianas were free-standing, and these were shorter and leafier than climbing shoots; Ichihashi *et al.*, 2009). Successive production of climbing shoots on former climbing shoots constructs the framework of a liana's aboveground body. The total lengths of current-year climbing shoots and existing framework stems (originating from former climbing shoots) were used to analyse the magnitude of stem turnover in these lianas (described in the subsection on Data analyses). Further descriptions of shoot structures of lianas and the criteria used to distinguish climbing shoots and framework stems are noted in Notes S2. Basic information on the samples is listed in Table S1.

Collection of tree data

Data for trees were collected from published studies that examined the allometry of deciduous trees in cool-temperate forests in Japan (Ikushima, 1964; Segawa & Kato, 1970; Ogino, 1977; Katagiri *et al.*, 1984; Takahashi *et al.*, 1999; Komiyama *et al.*,

2002). Data of evergreen species (seven plants in total) were excluded. We obtained data related to aboveground mass (M_A) and leaf mass (M_L) for a total of 245 trees (44 species) from six sites; among them, height (H) data were available for 206 trees (35 species) from four sites. We also used the mean value (3.56) of the 'leaf–stem ratio of a population of current-year shoots, LSRpop' of 10 deciduous tree species in Yagi (2000) to estimate current-year stem mass (M_{CS}) of trees from their leaf mass (i.e. M_{CS} was calculated as M_L divided by 3.56). For information about tree growth, we present ages, heights and estimated aboveground masses of canopy trees ($n = 74$) at the present study sites. The data at the study site were collected for a previous study (Ichihashi & Tateno, 2011). The age of the trees was determined from the number of growth rings in core samples at a height of 1.3 m, tree height was measured using triangulation and total aboveground mass (M_A) was estimated by assigning height (H) and diameter at breast height (DBH) to an allometric equation: $M_A = 0.0394(DBH^2 \times H)^{0.941}$ (Komiyama et al., 2002). Tree data collected from the literature and data related to canopy trees at the present site are listed in Tables S2 and S3, respectively.

Data analyses

The leaf mass (M_L), current-year stem mass (M_{CS}) and height (H) were regressed against the total aboveground mass (including leaf and current-year stem mass, M_A) for lianas and trees after data had been log-transformed: $\log Y = \beta + \alpha \log M_A$, where Y represents M_L, M_{CS} or H. The coefficients α and β were determined by applying a linear mixed model in which 'species' was included as a random factor. To compare allometric relationships between lianas and trees, we performed linear mixed model analyses in which species was incorporated as a random factor, and tested whether M_A, functional group (lianas or trees) and the interaction between the factors ($M_A \times$ functional group) had significant effects on the dependent variables (M_L, M_{CS} or H). H and M_A were regressed against age to estimate the time course of height gain and biomass increment for lianas using a procedure similar to that employed for allometric analysis. The relationships represent apparent growth patterns in the field, which are the cumulative results of gains and losses of height and biomass over the developmental stages. We also analysed these relationships separately for each of the four main liana species (Table S4), although variation among liana species was not a focus of the present study.

The magnitude of stem loss over the developmental stages of lianas was evaluated for each of the four main species. We regressed the total length of current-year climbing shoots on age to estimate the average stem length by which a plant extends every year. The estimated extension length was then accumulated year by year to calculate the total length of stem by which a plant has extended by a given age. The actual stem length of an average plant at a given age was estimated by regressing the total length of framework stems against age. The regressions were conducted for each liana species using the ordinary least-squares method for log-transformed data (Table S4).

Results

Biomass allocation and the height–mass relationship of lianas and trees

The slopes for the allometric (log–log) relationship (α) between leaf mass (M_L) and aboveground mass (M_A) were similar and < 1 for both lianas and trees (Table 1), indicating that the proportion of leaf mass relative to aboveground mass decreases as plants grow in both groups. The relationship for lianas was located along the upper end of the range of that for trees (Fig. 1a). In linear mixed model analysis, both M_A and functional group (trees or lianas) had significant effects on M_L, but the interaction term ($M_A \times$ functional group) did not (Table 2); lianas had a greater amount of leaves than trees at a given aboveground mass. M_A and functional group also had significant effects on current-year stem mass (M_{CS}), although the effect of functional group was qualified by the significant interaction term. This was reflected in the M_{CS}–M_A relationship for lianas, which was generally located at a higher level, but the slope of which was slightly smaller, than that for trees (Table 1; Fig. 1b). Nevertheless, lianas had a greater amount of current-year stems than trees at given aboveground masses throughout the range of plant sizes. The magnitudes of the differences in leaf mass and current-year stem mass between lianas and trees were about three- and five-fold, respectively (e.g. based on the regressions, average plants of lianas and trees with an aboveground mass of 5 kg had 493 g and 175 g of leaves, respectively, and 262 g and 51 g of current-year stems, respectively). M_A, functional group and their interaction term also had significant effects on height (H, Table 2). In this case, the slope of the H–M_A relationship for lianas was greater than that for trees (Table 1; Fig. 1c). As the intercept (β) was also larger in lianas, the regression for lianas was always above that for trees. Thus, lianas generally attained a higher vertical position than trees of the same aboveground mass (based on the regressions, lianas and trees with an aboveground mass of 5 kg attained heights of 9.5 and 7.0 m, respectively).

Among the four main liana species, significant differences were not found in the slopes, but were found in the intercepts, in all the relationships (Fig. 1; Table S4). Although up to a three-fold difference was found for M_{CS} (between *A. arguta* and *S. hydrangeoides*), the differences among liana species were relatively small compared with those between lianas and trees.

Long-term apparent growth patterns of lianas

Maximum height above the ground of lianas increased linearly with age (Table 1; Fig. 2a). Twenty to 40 yr were required for the lianas to reach 10 m in height (34 yr based on the regression). Similarly, young canopy trees at our site exceeded 10 m in height by 30 yr of age (Fig. 2a), suggesting that lianas and trees took comparable times to reach the canopy layer. The aboveground mass of the lianas increased exponentially with age (Table 1; Fig. 2b). Canopy lianas (≥ 40 yr old) had aboveground masses of 4–60 kg (17.0 kg at 50 yr of age, based on the regressions). The aboveground masses of similarly aged canopy trees at the present

Table 1 Coefficients of log-linear regression model, $\log Y = \beta + \alpha \log X$, for allometric relationships for lianas and trees, and for growth relationships for lianas

Relationship	Group	n (no. of species)	α (95% confidence interval)	β (95% confidence interval)
M_L vs M_A	Lianas	121 (9)	0.82 (0.79–0.84)	−0.88 (−0.93 to −0.82)
	Trees	245 (44)	0.85 (0.81–0.89)	−1.35 (−1.43 to −1.28)
M_{CS} vs M_A	Lianas	121 (9)	0.77 (0.73–0.81)	−1.12 (−1.25 to −1.00)
	Trees	245 (44)	0.85 (0.81–0.89)	−1.89 (−1.96 to −1.82)
H vs M_A	Lianas	121 (9)	0.34 (0.32–0.37)	0.74 (0.69 to 0.80)
	Trees	206 (35)	0.25 (0.24–0.27)	0.67 (0.64 to 0.69)
H vs age	Lianas	107 (9)	0.99 (0.89–1.09)	−0.51 (−0.56 to −0.38)
M_A vs age	Lianas	107 (9)	2.79 (2.53–3.04)	−3.51 (−3.96 to −3.08)

M_L, M_{CS}, H and M_A represent leaf mass, current-year stem mass, height and aboveground mass, respectively. The linear mixed model was used to determine the coefficients, where species was incorporated as a random factor.

site were estimated at 45–580 kg; thus, canopy lianas had an order of magnitude smaller aboveground mass than similarly aged canopy trees (Fig. 2b).

Estimation of stem lengths that were lost over the developmental stages of lianas

The framework stem lengths of lianas were smaller than the accumulated lengths of yearly stem extensions (Fig. 3). At 30 yr of age, *A. arguta* was estimated to retain 103 m (23%) of 450 m of stems that had been extended in the past, whereas *C. orbiculatus* retained 52 m (25%) of 208 m, *S. repanda* retained 48 m (55%) of 86 m and the root-climber *S. hydrangeoides* retained 24 m (71%) of 34 m. Thus, species that showed greater stem extension also lost a greater proportion of the extended stems.

Discussion

The nine cool-temperate liana species commonly showed several times greater amounts of leaves and current-year stems, and attained higher vertical positions per unit aboveground mass, than trees inhabiting the same climatic regions. Although we were unable to determine the actual biomass allocated to stem thickening, the relationship between existing stem mass (total stem mass − current-year stem mass) and current-year shoot mass (leaf mass + current-year stem mass) (Fig. S1, a modification of the relationships presented in Fig. 1a,b) indicated that biomass accumulation in existing stems relative to the increase in current-year shoot mass was smaller in lianas than in trees. This suggests that lianas allocated a proportionally smaller amount of biomass to secondary stem growth relative to biomass production for new shoots when compared with trees. The present results support the traditional hypothesis related to the growth strategy of lianas – that lianas reduce biomass allocation to stem thickening and instead show greater allocation to leaves and stem elongation, and attain efficient biomass use to achieve higher positions (nevertheless, lianas do not ascend as efficiently when lost stems are included, as discussed later). However, the distinct biomass allocation pattern did not appear to accelerate the vertical height gain and biomass increment of these lianas over a protracted period. Liana plants took c. 20 yr or more to reach the canopy layer,

which did not greatly exceed the time taken for trees at the present site (Fig. 2a). Moreover, biomass accumulation during growth to the canopy was much smaller in lianas than in trees (Fig. 2b). Among the liana species, *A. arguta* and *C. orbiculatus* were shown to thrive in well-lit, productive environments (Ichihashi *et al.*, 2010). We also noted that the ability of leaf-level photosynthesis of the lianas was similar to that of dominant tree species in our measurements (Fig. S2). Thus, the smaller aboveground biomass of these lianas in comparison with the tree species cannot be explained by differences in the leaf photosynthetic capacities of the two groups of plants.

One factor that may well limit biomass accumulation in lianas is the large-scale turnover of stems. By comparing the lengths of yearly stem extension and that of the existing stems, we estimated that liana plants of the aggressive species (*A. arguta* and *C. orbiculatus*) lost c. 75% of stem length that had extended before reaching the forest canopy (Fig. 3). Simple calculations using the mass per unit length data for the stems (details in Notes S3) demonstrate that the loss of stems during the first 30 yr accounted for c. 25% of the total stem biomass (equivalent to an average loss of c. 8% of aboveground biomass each year), assuming that all of these stems were lost within 1 yr of production. The losses accounted for c. 45% of total stem biomass (equivalent to a loss of c. 17% of aboveground biomass every year) when we assumed that the lost stems included not only current-year stems, but also the relatively thin portions of older axes (≤ 1 cm in diameter). Although we do not have comparable data for trees, annual production of woody litter was recorded to be 0.4–1.6% of total aboveground biomass in 10 temperate forest stands in Japan (Sassa, 1982; Inagaki & Kitazawa, 1989; Tadaki, 1995; Ohtsuka *et al.*, 2005), suggesting that the impact of stem turnover on the biomass budget of plants could be much greater in lianas than in trees. Another possible factor limiting the accumulation of aboveground biomass of lianas is that they invest a greater amount of resources in belowground organs (including carbohydrate reserves in the organs) than trees. At present, little information is available regarding biomass allocation between above- and belowground organs in lianas (Wyka *et al.*, 2013), and this should be examined in future studies.

The stem loss in lianas could result from various factors, including rapid senescence of searcher shoots that failed to
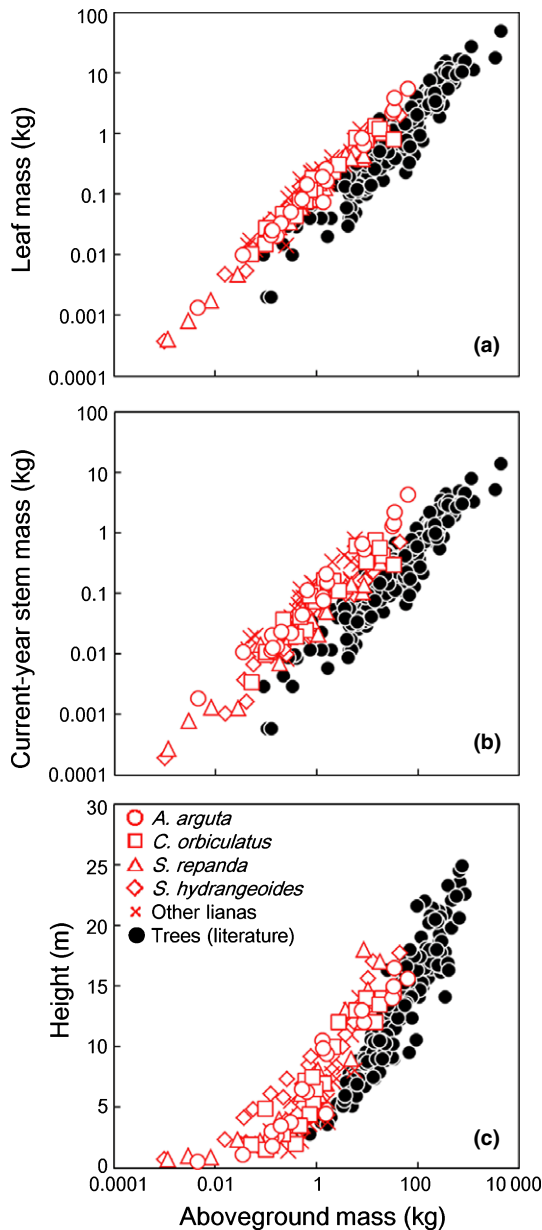
Fig. 1 Relationships of (a) leaf mass, (b) current-year stem mass and (c) height with the aboveground mass of lianas and trees: *Actinidia arguta* (*n* = 20), *Celastrus orbiculatus* (*n* = 20), *Schisandra repanda* (*n* = 22), *Schizophragma hydrangeoides* (*n* = 21), other liana species (five species, *n* = 38) and trees in cool-temperate forests (44 species, *n* = 245, for leaf mass and current-year stem mass, and 35 species, *n* = 206, for height). Tree data were taken from the literature (Ikushima, 1964; Segawa & Kato, 1970; Ogino, 1977; Katagiri *et al.*, 1984; Takahashi *et al.*, 1999; Komiyama *et al.*, 2002).

acquire host structures (Putz & Holbrook, 1991), partial loss of the liana canopy caused by fallen host trees and, similar to trees, senescence of old branches on which the light environment may not be good enough to contribute to carbon acquisition of the plants (Takenaka, 2000; Henriksson, 2001; Umeki *et al.*, 2006). Although the relative importance of each of these factors is unknown, the large loss of stems may represent a cost of the host-dependent support habit. Thus, lianas grow upwards by

discarding a large amount of branches, whereas trees grow higher by accumulating supporting wood in the stems to stand upright. Apart from this difference, the host-dependent growth also requires a considerable cost of stem production to achieve higher positions. However, the rapid discarding of unnecessary branches would enable lianas to maintain a high photosynthetic to non-photosynthetic organ ratio, and the large branch loss following large extension in lianas may facilitate the location of well-lit sites for leaf display within heterogeneous light environments (cf. Selaya & Anten, 2008). Even if the host-dependent habit does not reduce the cost of stem production required for upward growth, lianas could gain an advantage from the productive aboveground structure and the ability to explore large spaces to locate well-lit sites. The magnitude of stem turnover varied among liana species; both stem extension and the relative losses of stems were greatest in the aggressive stem twiners (*A. arguta* and *C. orbiculatus*) and smallest in the root climber with a commensal habit (*S. hydrangeoides*) (Fig. 3). This variation may reflect different demands on the location of well-lit sites and new hosts, and the frequency of trans-host movements in these species, an issue discussed by Ichihashi & Tateno (2011).

In the present study, we have demonstrated that cool-temperate lianas in Japan allocate several times more biomass to leaves and stem extension than do trees. By using host trees for mechanical support, lianas are able to allocate resources in a manner that enhances productivity and vigorous extension growth over the short term. This confers powerful competitive abilities; lianas can quickly overtop the current host trees and possibly locate better lit sites by exploring large spaces. Nevertheless, the time course to reach the forest canopy for lianas was comparable with that of trees, and biomass accumulation during this period was smaller than that for trees, creating large-scale stem turnovers in liana plants. These observations suggest that the host-dependent growth requires a considerable cost, and could be restricted by the availability and stability of host structures. However, it should be noted that liana growth and impacts of mechanical restrictions thereon may vary greatly in other ecosystems with different vegetative structures and climatic conditions, and in liana species with different growth habits.

Lianas are most abundant and diverse in the tropics, where their dynamics have a marked impact on the dynamics of entire forests (Schnitzer & Bongers, 2002, 2011). At present, only limited information is available on the long-term growth of individual tropical lianas or the impacts of mechanical restrictions on their growth (Wyka *et al.*, 2013). Thus, the relevance of our results to the ecology of tropical lianas should be examined in future studies. Based on currently available data, tropical lianas may grow upwards more rapidly than lianas growing in cool-temperate climates. For example, after liana-cutting treatments in tropical and subtropical managed forests, sprouts that generated from the stumps reached the forest canopy within 10 yr (Gerwing, 2006; Campanello *et al.*, 2012). In Panamanian forests, a large proportion of lianas with basal diameters of 2 cm had grown up into the canopy c. 40 m above the forest floor (Kurzel *et al.*, 2006), which implies that they may climb rapidly into the canopy. The lianas examined in this study were leafless and therefore

Table 2 Summary statistics for linear mixed model analyses that tested effects of aboveground mass (M_A), functional group (trees or lianas) and their interactions on the dependent variables leaf mass (M_L), current-year stem mass (M_{CS}) and height (H)

Dependent	M_A			Functional group			$M_A \times$ functional group		
	df	t	P	df	t	P	df	t	P
M_L	311	38.98	<0.001	51	8.78	<0.001	311	1.37	0.17
M_{CS}	311	33.95	<0.001	51	11.73	<0.001	311	2.98	0.003
H	281	38.72	<0.001	42	3.15	0.003	281	6.26	<0.001

Species was incorporated as a random factor. Data were log-transformed before the analyses.
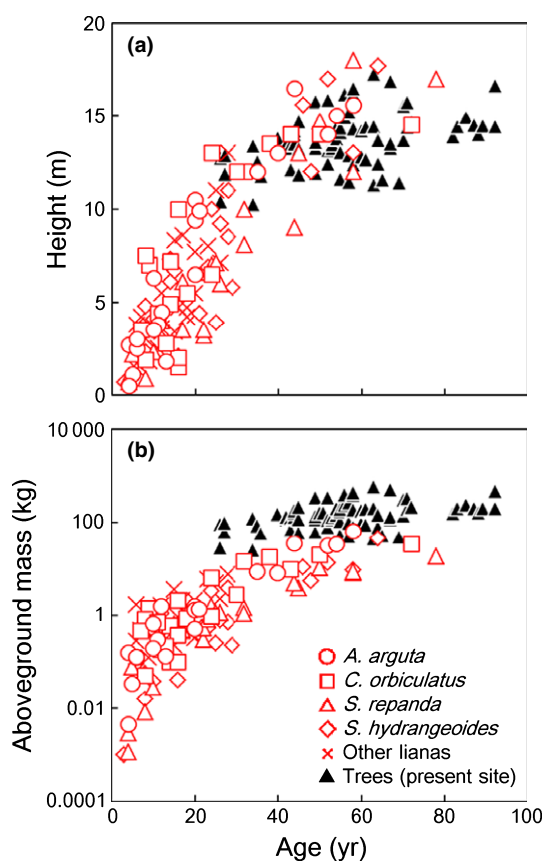

Fig. 2 Relationships between (a) height and (b) aboveground mass with age of lianas and trees: *Actinidia arguta* (*n* = 20), *Celastrus orbiculatus* (*n* = 20), *Schisandra repanda* (*n* = 22), *Schizophragma hydrangeoides* (*n* = 21), other liana species (five species, *n* = 24) and canopy trees at the present site (12 species, *n* = 74). Aboveground mass of trees was estimated from the height and diameter at breast height.

Fig. 3 Estimations of total stem length by which a liana extends by given ages (total extension length, open symbols) and live stem length retained by a liana at these ages (framework stem length, closed symbols). Total extension length was estimated by accumulating average yearly extension lengths that were obtained from the relationship between current-year extension length and age. Supporting Information Table S4 presents the relationships of current-year extension length and framework stem length with age for each species.

not growing for half of each year, whereas tropical lianas have a more protracted growing season (Schnitzer, 2005). The presence of abundant liana stems (Putz, 1984; Nabe-Nielsen, 2001) and perhaps the relatively rich and stratified understorey vegetation (Whitmore, 1998) in the interiors of tropical forests may also facilitate the growth of lianas by increasing host availability. In addition, we excluded liana plants that appeared to have sprouted vegetatively; this exclusion may reduce the relevance of our results for research in tropical forests, where lianas rely greatly on clonal proliferation for recruitment and expansion (Schnitzer *et al.*, 2012; Yorke *et al.*, 2013). Although the relative importance of
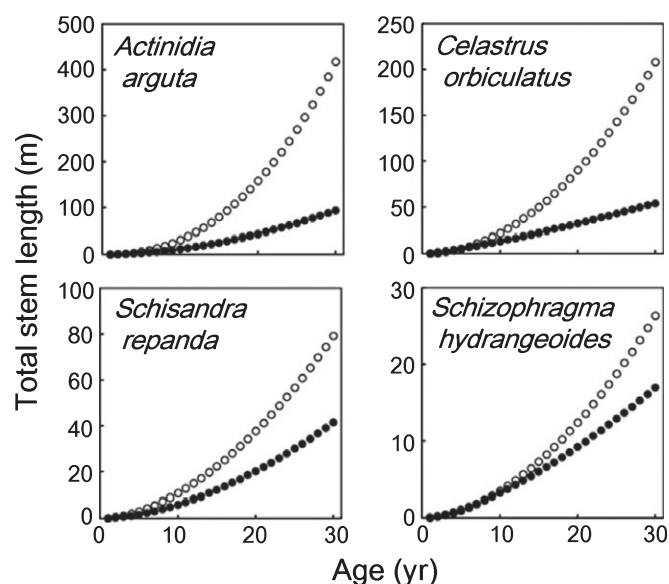
such clonal proliferation in the dynamics of temperate lianas is unclear, adult plants of *C. orbiculatus* and *W. floribunda* often produced clonal offshoots; these were much longer and thicker, elongating 1–2 m in the first year, than searcher shoots of seedlings that were usually < 1 m in length. Clonal sprouts grow more rapidly than seedlings in the early stages of development (R. Ichihashi, pers. obs.).

We suggest that studies on organism-level attributes of tropical lianas will promote a better understanding of the mechanisms underlying the vegetation dynamics and functional roles played by lianas in tropical forests. For example, stem turnover may be a significant factor causing the relatively small contribution of tropical lianas to forest carbon stocks (Phillips *et al.*, 2005; Durán & Gianoli, 2013; van der Heijden *et al.*, 2013) and the large contribution of lianas to the nutrient cycling of forests (Hegarty, 1991; Kusumoto & Enoki, 2008; Tang *et al.*, 2012). In addition, although lianas are much less abundant in temperate regions, they may also have considerable impacts on

temperate forest dynamics (Allen *et al.*, 2005; Ladwig & Meiners, 2009); thus, further explorations of temperate liana ecology will contribute to an improved knowledge of a broad range of vegetation processes.

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References

Allen BP, Sharitz RR, Goebel PC. 2005. Twelve years post-hurricane liana dynamics in an old-growth southeastern floodplain forest. *Forest Ecology and Management* **218**: 259–269.

Campanello PI, Villagra M, Garibaldi JF, Ritter LJ, Araujo JJ, Goldstein G. 2012. Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest. *Forest Ecology and Management* **284**: 213–221.

Darwin C. 1865. On the movements and habits of climbing plants. *Journal of the Linnean Society of London, Botany* **9**: 1–118.

Durán SM, Gianoli E. 2013. Carbon stocks in tropical forests decrease with liana density. *Biology Letters* **9**: 20130301.

French JC. 1977. Growth relationships of leaves and internodes in viny angiosperms with different modes of attachment. *American Journal of Botany* **64**: 292–304.

Gartner BL. 1991. Relative growth rates of vines and shrubs of western poison oak, *Toxicodendron diversilobum* (Anacardiaceae). *American Journal of Botany* **78**: 1345–1353.

Gentry AH. 1991. The distribution and evolution of climbing plants. In: Putz FE, Mooney HA, eds. *The biology of vines.* Cambridge, UK: Cambridge University Press, 3–49.

Gerwing JJ. 2006. The influence of reproductive traits on liana abundance 10 years after conventional and reduced-impacts logging in the eastern Brazilian Amazon. *Forest Ecology and Management* **221**: 83–90.

Gianoli E. 2004. Leaf litter production by lianas and trees in a sub-tropical Australian rain forest. *Proceedings of the Royal Society B: Biological Science* **271**: 2011–2015.

Hegarty EE. 1991. Evolution of a climbing habit promotes diversification in flowering plants. *Journal of Tropical Ecology* **7**: 201–214.

Hegarty EE, Caballé G. 1991. Distribution and abundance of vines in forest communities. In: Putz FE, Mooney HA, eds. *The biology of vines.* Cambridge, UK: Cambridge University Press, 313–335.

van der Heijden GM, Schnitzer SA, Powers JS, Phillips OL. 2013. Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica* **45**: 682–692.

Henriksson J. 2001. Differential shading of branches or whole trees: survival, growth, and reproduction. *Oecologia* **126**: 482–486.

Ichihashi R, Nagashima H, Tateno M. 2009. Morphological differentiation of current-year shoots of deciduous and evergreen lianas in temperate forests in Japan. *Ecological Research* **24**: 393–403.

Ichihashi R, Nagashima H, Tateno M. 2010. Biomass allocation between extension- and leaf display-oriented shoots in relation to habitat differentiation among five deciduous liana species in a Japanese cool-temperate forest. *Plant Ecology* **211**: 181–190.

Ichihashi R, Tateno M. 2011. Strategies to balance between light acquisition and the risk of falls of four temperate liana species: to overtop host canopies or not? *Journal of Ecology* **99**: 1071–1080.

Ikushima I. 1964. Productive structure of woody vegetation (in Japanese). In: National Parks Association of Japan, ed. *Reports of academic researches on Tanzawa Oyama.* Kanagawa, Japan: Kanagawa Prefecture, 106–125.

Inagaki A, Kitazawa Y. 1989. Difference between litterfall in a climax and in a secondary forest in the warm temperate forest zone of northern Kyushu. *Journal of University of Occupational and Environment Health* **11**: 247–259.

Katagiri S, Ishii H, Miyake N, Ando Y. 1984. Studies on mineral cycling in a deciduous broad-leaved forest at Sanbe forest of Shimane University (XII): difference of above ground biomass in a deciduous broad-leaved forest along a slope (in Japanese). *Bulletin of the Faculty of Agriculture, Shimane University* **18**: 53–60.

Komiyama A, Kato S, Ninomiya I. 2002. Allometric relationships for deciduous broad-leaved forests in Hida district, Gifu prefecture, Japan (in Japanese with English summary). *Journal of the Japanese Forestry Society* **84**: 130–134.

Kurzel BP, Schnitzer SA, Carson WP. 2006. Predicting liana crown location from stem diameter in three Panamanian lowland forests. *Biotropica* **38**: 262–266.

Kusumoto B, Enoki T. 2008. Contribution of a liana species, *Mucuna macrocrpa* Wall., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest. *Journal of Forest Research* **13**: 35–42.

Ladwig LM, Meiners SJ. 2009. Impacts of temperate lianas on tree growth in young deciduous forests. *Forest Ecology and Management* **259**: 195–200.

Monsi M, Murata Y. 1970. Development of photosynthetic systems as influenced by distribution of matter. In: Šetlik I, ed. *Prediction and measurements of photosynthetic productivity.* Wageningen, the Netherlands: Pudoc, 115–129.

Nabe-Nielsen J. 2001. Diversity and distribution of lianas in a neotropical rainforest, Yasuni National Park, Ecuador. *Journal of Tropical Ecology* **17**: 1–19.

Niklas KJ. 1994. Comparisons among biomass allocation and spatial distribution patterns of some vine, pteridophyte, and gymnosperm shoots. *American Journal of Botany* **81**: 1416–1421.

Ogino K. 1977. A beech forest in Ashiu – biomass, its increment and net production. In: Shidei T, Kira T, eds. *Primary productivity in Japanese forest, JIBP synthesis 16.* Tokyo, Japan: University of Tokyo Press, 172–186.

Ohtsuka T, Akiyama T, Hashimoto Y, Inatomi M, Sakai T, Jia S, Mo W, Tsuda S, Koizumi H. 2005. Biometric based estimates of net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower. *Agricultural and Forest Meteorology* **134**: 27–38.

Phillips OL, Martinez RV, Mendoza AM, Baker TR, Vargas PN. 2005. Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology* **86**: 1250–1258.

Putz FE. 1983. Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro basin, Venezuela. *Biotropica* **15**: 185–189.

Putz FE. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **65**: 1713–1724.

Putz FE. 1990. Liana stem diameter growth and mortality rates on Barro Colorado Island, Panama. *Biotropica* **22**: 103–105.

Putz FE, Holbrook NM. 1991. Biomechanical studies of vines. In: Putz FE, Mooney HA, eds. *The biology of vines.* Cambridge, UK: Cambridge University Press, 73–97.

Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* **86**: 16–24.

Sakai A, Suzuki W. 1999. Effect of support on the growth of a woody vine, *Wisteria floribunda* DC (Leguminosae). *Journal of Forest Research* **4**: 183–186.

Sassa T. 1982. Stand biomass, increment and litter production in natural forests mainly consisted of Japanese fir and hemlock (*Abies firma* et *Tsuga sieboldii*) in Tokyo University Forest of Chiba and Chichibu (in Japanese). *Japanese Journal of Forest Environment* **24**: 29–36.

Satake Y, Hara H, Watari S, Tominari T. 1989. *Wild flowers of Japan: woody plants (in Japanese).* Tokyo, Japan: Heibonsha.

Schnitzer SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* **166**: 262–276.

Schnitzer SA, Bongers F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* **17**: 223–230.

Schnitzer SA, Bongers F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* **14**: 397–406.

Schnitzer SA, Mangan SA, Dalling JW, Baldeck CA, Hubbel SP, Ledo A, Muller-Landau H, Tobin MF, Aguilar S, Brassfield D et al. 2012. Liana

abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* 7: e52114.

Segawa K, Kato R. 1970. Growth of *Quercus serrata* stands in Kouma experimental forest (in Japanese). *Annual Report of the Tohoku Branch, Forest Experiment Station* 11: 188–198.

Selaya NG, Anten NPR. 2008. Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest. *Functional Ecology* 22: 30–39.

Tadaki Y. 1995. Structure and productivity of young *Castanopsis cuspidata* forests growing in different stand densities (in Japanese with English summary). *Bulletin of the Nagoya University Forests* 14: 1–24.

Takahashi K, Yoshida K, Suzuki M, Seino T, Tani T, Tashiro N, Ishii T, Sugata S, Fujito E, Naniwa A *et al.* 1999. Stand biomass, net production and canopy structure in a secondary deciduous broad-leaved forest, northern Japan. *Research Bulletin of the Hokkaido University Forests* 56: 70–85.

Takenaka A. 2000. Shoot growth responses to light microenvironment and correlative inhibition in tree seedlings under a forest canopy. *Tree Physiology* 20: 987–991.

Tang Y, Kitching RL, Cao M. 2012. Lianas as structural parasites: a re-evaluation. *Chinese Science Bulletin* 57: 307–312.

Umeki K, Seino T, Lim EM, Honjo T. 2006. Patterns of shoot mortality in *Betula platyphylla* in northern Japan. *Tree Physiology* 26: 623–632.

Whitmore TC. 1998. *An introduction to tropical rain forests, 2nd edn.* New York, NY, USA: Oxford University Press.

Wyka TP, Oleksyn J, Karolewski P, Schnitzer SA. 2013. Phenotypic correlates of the lianescent growth form: a review. *Annals of Botany* 112: 1667–1681.

Yagi T. 2000. Morphology and biomass allocation of current-year shoots of ten tall tree species in cool temperate Japan. *Journal of Plant Research* 113: 171–183.

Yorke SR, Schnitzer SA, Mascaro J, Letcher SG, Carson WP. 2013. Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization. *Biotropica* 45: 317–324.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Relationship between existing stem mass and current-year shoot mass for lianas and trees.

Fig. S2 Mean light-saturated photosynthetic rates for lianas and trees.

Table S1 Data of sample lianas examined in the present study

Table S2 Data of deciduous trees collected from the literature

Table S3 Data of canopy trees at the present site

Table S4 Coefficients of log-linear regression model, log $Y = \beta + \alpha \log X$, for allometric and growth relationships for liana species

Notes S1 About the relevance of measuring vertical height in the evaluation of the apparent growth patterns of lianas.

Notes S2 Shoot structures of lianas and the criteria used in this study to distinguish climbing shoots and framework stems.

Notes S3 Estimating impacts of stem loss on the aboveground biomass of lianas.

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