

The Role of Clonal Reproduction as a Life History Strategy
and its Contribution on the Distribution Patterns of
Liana Species in a Temperate Forest

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Chapter 1 General introduction

Lianas (woody vines) are characterized by the slender stems with various forms due to the mechanically dependent growth habit. Lianas are defined as woody plant species that germinate in the soil but require mechanical support (i.e. host tree) to grow and survive in some part of their life history. Climbing habit of lianas has evolved independently in the angiosperms, gymnosperms, and ferns (Burnham 2015). Lianas are widely found in major lineages of Mesangiosperms; more than 60% of eudicots and magnoliids include at least one liana species (Isnard and Field 2015). At family level, over one-third of all seed plant families include at least one climbing species (Gianoli 2015). Lianas exhibit various strategies for climbing their hosts to capture sufficient light resources in the forest canopy. For example, various types of biomechanical properties of lianas (climbing mechanism) allow them to climb up to the forest canopy; these include stem twiners, branch twiners, tendril climbers, root climbers, and hook climbers (scrambler) (Putz and Holbrook 1992). Stem twiner is the most common climbing mechanism which comprises about half of the total number of liana species in both temperate and tropical forests (Barik et al. 2015). It is also important to note that strategy of lianas to climb trees has a trade-off between the light capture efficiency and the risk of fall due to the negative impact on host trees (Ichihashi and Tateno 2011). Ichihashi and Tateno (2011) found that *Actinidia arguta*, a temperate deciduous liana species, spread their leaves aggressively in host tree crowns while reducing the risk of falls enhanced by the top-heavy architecture by climbing many host trees. Their variety of life-forms, structure and behaviour of lianas had attracted scientists for a long time (e.g. Darwin 1865).

Lianas are most diverse in tropical forests, while species richness and abundance of lianas in the northern hemisphere decrease along latitudinal and geographical gradients due to high sensitivity to temperature and precipitation of lianas (Schnitzer 2005; Hu et al. 2010; Guo et al. 2012). However, lianas are present in high abundance and great diversity in temperate forests characterised by mild temperatures and plentiful soil water, such as found in the floodplain forest of the southern USA (Allen et al. 1997) and in the temperate rainforests of southern Chile (Jiménez-Castillo and Lusk 2009). The necessity of abundant soil water and mild temperatures is due to the large-diameter vessels and

disproportionately large leaf area of lianas, which lead to a higher susceptibility to freeze-thaw embolism (Jiménez-Castillo and Lusk 2013).

Recently, lianas are considered as an important component due to a significant contribution to forest dynamics and other forest ecological functions by influencing tree regeneration and composition in both temperate and tropical forests (reviewed in Schnitzer and Bongers 2002; 2012). For example, lianas rapidly colonize canopy gaps, which inhibits the establishment of shade-tolerant species (Schnitzer and Bongers 2002) and reduces the forest carbon gain (Schnitzer et al. 2014). Furthermore, lianas are able to dominate in canopy gaps even after canopy closure (Schnitzer et al. 2001) and result an arrested succession (Tyman et al. 2016). Lianas compete intensely with trees for light resources because lianas often overtop tree canopy for their growth and survival. Lianas also compete with trees for below-ground resources such as water and nutrients (Schnitzer et al. 2005). There has been increasing research interests in the ecology of lianas over past three decades due to the substantial contribution of lianas in forests. However, their fundamental ecological characteristics, such as life history strategies and distribution patterns, are still less explored especially in temperate forests.

Lianas are not only important as an ecological component in forests but also important in terms of forest management and conservation. For example, removing lianas from host trees (liana-cutting) is an essential procedure for timber production because lianas have negative impact on host trees (Suzuki 1989). Number of previous studies have shown effectiveness of liana-cutting for tree growth and survival (e.g. Schnitzer et al. 2004). Furthermore, many liana species that natively distributed in East Asia are non-native, aggressive invaders in North America (e.g. *Celastrus orbiculatus*, *Euonymus fortunei*, *Lonicera japonica*, *Peuraria montana* var. *lobata*, *Wisteria floribunda*; reviewed in Leicht-Young and Pavlovic 2015). On the other hand, lianas are considered to play a positive role in species diversity; Schnitzer et al. (2000) reported that both species richness and density of pioneer trees were enhanced by lianas in places where the canopy gap disturbance occurred, while shade-tolerant tree species richness and density were inhibited. Lianas are also important for the conservation of animals and birds. For example, lianas provide a pathway between tree crowns which

is critical for inter-crown movement of arboreal animals (e.g. ants; Yanoviak 2015), produce a tangled structure in the understory for birds to escape from the predator (Michel et al. 2015), and represents as an important food resource to animals (Arroyo-Rodríguez et al. 2015). Thus, fundamental ecological knowledge of lianas would help the understanding of the role of lianas on forest management and conservation.

Clonal reproduction is a common and key life history process for colonization and regeneration success of liana species. For example, tropical liana species respond to canopy gap disturbances via clonal reproduction, resulting in aggregated distribution patterns (Ledo and Schnitzer 2014). Despite the ecological significance of clonal reproduction to the life history and distribution patterns of liana species, previous findings were based on observations (i.e. liana inventory, Schnitzer et al. 2012; excavation, Sakai et al. 2002), which means that the evaluation of clonal reproduction of liana species are still limited in terms of identification of genetically distinct individuals (clone, genet), mainly due to methodological limitations. Clonal reproduction of lianas is difficult to evaluate via observational methods because clonally reproduced stems (stolons) are easily buried underground and connections between rooted stems (ramets) tend to decay over time. Precise identification of clonal reproduction for both above-ground and below-ground clonal reproduction, and past connectivity is essential for the comprehensive understanding the contribution of clonal reproduction as a potential driver of distribution patterns of liana species. Evaluation of clonal reproduction using genetic tools such as microsatellite markers is an effective approach for such conditions. Genetic analysis on clonal plant species has been widely used in number of previous studies, and methods for clonal analysis have been well standardized (reviewed in Arnold-Haond 2007); however, few studies have applied genetic tools to evaluate the clonal structure of liana species in their natural habitat.

To evaluate the contribution of clonal reproduction on the distribution patterns of liana species in a temperate forest, I conducted the set of studies as follows;

- 1) I described liana community structure and ramet-level distribution patterns in a 6-ha plot in an old-growth cool temperate forest of Japan (Chapter 2). Species name and size of all liana stems higher than 1.3m above ground on trees (5 cm > diameter at breast height;

DBH) were recorded and mapped in the study plot. Liana community structure in the present study site was compared with other temperate forests. Spatial distribution patterns and the preferences of host tree and microsite characteristics of lianas were assessed. This chapter was published in Mori et al. (2016a).

- 2) I studied the contribution of clonal reproduction to the distribution patterns of a deciduous liana species *Wisteria floribunda* in an old-growth cool temperate forest of Japan (Chapter 3). Following liana inventory in chapter 2, I collected either leaf or inner bark samples from all *W. floribunda* individuals in the study plot. Samples were genotyped using microsatellite markers designed for this species (Mori et al. 2016b). Clonal structure and distribution patterns of clones of *W. floribunda* were assessed. This chapter was published in Mori et al. (2017a).
- 3) I studied the role of clonal reproduction and canopy gap disturbances on the distribution patterns of *Wisteria floribunda* to examine the mechanism—lianas respond to canopy gap disturbances via clonal reproduction—reported in tropical forests (Chapter 4). Canopy gap disturbances were identified from the 25-year canopy height data in the study plot (Nakashizuka et al. 1995b). Effects of canopy gap disturbances on distribution of *W. floribunda* were evaluated using statistical modelling with accounting for differences in life history stages and the magnitude of clonal ability.
- 4) To evaluate the contribution of seed reproduction to the distribution patterns of the liana species, I studied the distribution pattern of current-year seedlings of *Wisteria floribunda* because post-dispersed seed to seedling stage respond most dramatically to surrounding environment throughout the life history (Chapter 5). Emergence and survival rate of current-year seedlings were investigated with three years of continuous observation on current-year seedlings in the study plot. Effects of environmental factors that might affect the distribution of seedlings (e.g. light and water) were assessed.
- 5) I studied the clonal structure of three liana species (*Schizophragma hydrangeoides*, *Euonymus fortunei*, *Rhus ambigua*) to evaluate the relative importance of clonal

reproduction to the distribution patterns of liana species in a temperate forest (Chapter 6). I also studied the clonal structure of ramets on the forest floor of three most abundant liana species (*W. floribunda*, *S. hydrangeoides*, *E. fortunei*) to examine the inter-specific variation of clonal reproduction on the forest floor via stolons (Chapter 6). Leaf samples on the forest floor were collected in the belt transect established in the centre of the study plot. Samples were genotyped using microsatellite markers described in Mori et al. (2017b) and Hsu et al. (2013).

In the final chapter, I made a general discussion regarding to life history strategies of liana species in a temperate forest (Chapter 7).

Chapter 2 Liana distribution and community structure in an old-growth temperate forest: The relative importance of past disturbances, host trees, and microsite characteristics

2.1 Introduction

Lianas contribute to forest dynamics and other forest ecological functions by influencing tree regeneration and composition in both temperate and tropical forests (Putz 1984; Schnitzer and Bongers 2002; Ladwig and Meiners 2009). They are most abundant and diverse in tropical forests, but there is increasing interest in the ecology of temperate lianas based on recent recognition of their importance in temperate tree communities (Ladwig and Meiners 2015).

Within forest stands in temperate forests, liana density and diversity vary at a local scale. Thus, liana distribution is determined in part by the degree of support provided by the diameter and height, species, bark texture, allelopathy, and other characteristics of the host trees (e.g. Talley et al. 1996; Buron et al. 1998; Carrasco-Urra and Gianoli 2009; Ladwig and Meiners 2010a; Castagneri et al. 2013). These preferences are closely related to the climbing type (stem twiners, root climbers, and tendril climbers) (Putz and Holbrook 1992) and the size (Putz 1984; Ichihashi and Tateno 2011) of the lianas. Small-stem twiners require smaller trees in the understory to climb; root climbers, with their adhesive roots, do not have upper size limits for host trees; and large lianas that ascend to the forest canopy require larger host trees for support (Ichihashi and Tateno 2011). Thus, an analysis of liana distribution must take into account both liana size and climbing type. Microsite characteristics, including microscale habitat, water and nutrient availability, also influence liana distribution (e.g. Collins and Wein 1993; McNab and Loftis 2002; Leicht-Young et al. 2010; West et al. 2010; Kusumoto et al. 2013). Lianas in temperate forests often follow a “sit and wait” strategy, persisting in the forest understory until conditions cause an opening in the canopy (Greenberg et al. 2001).

Disturbance is another important determinant of the liana community (Allen et al. 1997; Schnitzer and Carson 2001; Londré and Schnitzer 2006; Ledo and Schnitzer 2014). Large-scale

disturbances, whether natural (e.g. hurricanes) or anthropogenic, produce forest edges and thereby increase liana abundance (Laurance and Williamson 2001; Londré and Schnitzer 2006). Small-scale disturbances, such as treefall gaps in mature or old-growth forests, also contribute to the maintenance of the liana community (Schnitzer and Bongers 2002; Ledo and Schnitzer 2014). Recent studies in tropical forests have determined that treefall gaps are necessary for the maintenance of liana populations and their species richness (Schnitzer and Carson 2001; Ledo and Schnitzer 2014). By contrast, in a study of temperate forests in South America, Carrasco-Urra and Gianoli (2009) showed that liana abundance was independent of light availability related to treefall gaps. These findings imply that the impact of canopy disturbance on the liana community differs between temperate and tropical forests (see Ladwig and Meiners 2015).

Investigations of the factors that determine liana species density and diversity must therefore consider disturbances, host tree conditions, and microsite characteristics comprehensively. However, this was not the case in previous ecological studies of lianas in temperate forests (e.g. Allen et al. 1997; Londré and Schnitzer 2006; Carrasco-Urra and Gianoli 2009; Leicht-Young et al. 2010; Pavlovic and Leicht-Young 2011; but see Leicht-Young et al. 2010). Other studies were limited geographically to either North or South America (McNab and Loftis 2002; Carrasco-Urra and Gianoli 2009; Ladwig and Meiners 2010a; West et al. 2010; Leicht-Young et al. 2010; but see; Hu 2011). Furthermore, all of those studies were done in small (≤ 1 ha) plots, and a spatial perspective on liana populations was accordingly absent. As shown in Barro Colorado Island, Panama, studies of large forest plots can provide important insights into the liana community, highlighting factors such as habitat preference, disturbance dependency, and density effects (Ledo and Schnitzer 2014; Schnitzer et al. 2015).

In this chapter, I examined the structure and distribution of the liana community, focusing on past disturbances, host tree preferences, and microscale characteristics, in a 6-ha plot established in a temperate forest in Japan and containing lianas of different sizes and climbing types. Specifically, the following questions were addressed: 1) How similar is the liana community structure in the study plot to that in other temperate forests with respect to flora, basal area and climbing mechanisms? 2) Considering host trees, microsites, and past disturbances, which of these factors is the most important

determinant of liana distribution? 3) Does the answer to the latter question change as a function of liana climbing type or size class?

This study was published in Mori et al. (2016a). Figures and tables used in this chapter is from Mori et al. (2016a).

2.2 Material and Methods

2.2.1 Study site

The study was conducted in a 6-ha plot (300 m × 200 m) in the Ogawa Forest Reserve (OFR), an old-growth temperate deciduous forest located in the southern Abukuma Mountains, Ibaraki Prefecture, central Japan (36°56' N, 140°35' E, elevation 610–660 m). The dominant species in the forest canopy are *Quercus serrata* Murray, *Fagus japonica* Maxim., and *Fagus crenata* Blume (Masaki et al. 1992). The mean monthly temperature is 10.7°C, with a maximum typically occurring in August (22.6°C) and a minimum in January (−0.9°C). Mean annual precipitation is approximately 1,910 mm, with a maximum in August (338.2 mm) and a minimum in December (42.1 mm). In winter, the maximum snow depth often reaches 50 cm (Mizoguchi et al. 2002).

The area where the OFR is located was altered by large-scale human disturbances, probably in the form of fire, in the 1930s (Masaki et al. 1992). Tanaka and Nakashizuka (1997) showed that these disturbances occurred both at the edge of the plot and outside it, resulting in large patches (>1500 m²) within the plot mainly composed of *Quercus serrata* (Masaki et al. 1992; Nakashizuka et al. 1995b). The presence of smaller patches (<400 m²) of other tree species around the plot's centre reflect tree regeneration after local disturbances (see Masaki et al. 1992). Thus, the OFR is the complex of patches differing in their age and size and indicative of past disturbances. Masaki et al. (1992) classified tree species in the study plot into shade-tolerant species (e.g. *Acer palmatum* var. *amoenum*, *Carpinus cordata*, *Carpinus laxiflora*, *F. crenata*, and *F. japonica*,) and shade-intolerant species (e.g. *Betula grossa*, *Castanea crenata*, *Cornus controversa*, *Q. serrata*, and *Styrax obassia*) based on the DBH distribution of each tree species.

2.2.2 Field methods

I conducted an inventory of the trees in the 6-ha plot in 2009 by dividing the study plot into 2,400 cells, each with an area of $5\text{ m} \times 5\text{ m}$ (see Masaki et al. 1992). The girth at breast height of the trees was measured using a steel measuring tape. Tree species and locations within each cell were recorded for all stems with a girth $>15\text{ cm}$. The diameter at breast height (DBH) was calculated by dividing the girth by π .

A census of the lianas in the study plot was conducted from July to November 2013 to determine the size (DBH, measured using a caliper) of all liana stems more than 1.3 m above the ground and present on the inventoried trees. Species names and locations within each cell were recorded. For liana stems with an elliptical cross section, the longest diameter was measured. If a liana stem dug into the trunk of the host tree, the breadth of the exposed part was measured using a calliper. I also recorded whether the lianas reached the canopy. Since it was impossible to distinguish the true individual liana (i.e. ramets and genets; Gerwing et al. 2006) without the use of excavations or genetic tools, liana individuals were identified based on their above-ground connectivity.

The microsite characteristics determined within every $5\text{ m} \times 5\text{ m}$ cell were slope inclination (degrees; Masaki et al. unpublished), soil moisture content (volumetric percentage; Masaki et al. 2015), and microscale landform (Yoshinaga et al. 2002). The last was classified according to the criteria proposed by Tamura (1981): crest slope, head hollow, upper side slope, lower side slope, flood terrace, and river bed (Yoshinaga et al. 2002).

2.2.3 Analysis

All liana stems recorded in the 6-ha OFR plot were separated to one of two classes, “small” or “large”, based on the vertical position of the liana in the host tree and the size of that tree. Liana individuals that reached the forest canopy and climbed large trees (tree DBH $\geq 25\text{ cm}$) were classified as “large”, whereas those that did not reach the canopy or that climbed small trees (DBH $< 25\text{ cm}$) were classified as “small”. A diameter of 25 cm was set as the host-tree size threshold because 85% of the forest canopy comprised trees with a DBH $> 25\text{ cm}$.

The spatial aggregation pattern of each liana species in each size class was characterised using a $L(r)$ function, derived from Ripley's K -function (Law et al. 2009):

$$L(r) = \sqrt{K(r)/\pi} - r \quad (\text{eq. 2.1})$$

A positive $L(r)$ value indicates aggregation, and a negative value indicates regularity at scale r . First, spatial distribution patterns were determined by calculating the $L(r)$ values for each liana species with respect to size class. The significance of the aggregation was tested with 95% local confidence limits of the null hypothesis of complete spatial randomness (CSR). Confidence limits were generated with 1000 Monte Carlo simulations. Second, conspecific spatial correlation among different size class and heterospecific spatial correlation within each size class were examined by expanding $L(r)$ to $L_{12}(r)$ (Lan et al. 2009). Significance was tested by generating 1000 random distributions using a torus translation. Both $L(r)$ and $L_{12}(r)$ were calculated for a total distance of up to 100 m at 5-m intervals.

For each size class, the probability of liana presence on non-liana trees was analysed using a trend surface generalised additive model based on five variables (trend surface GAM), with logit as a link function:

$$\text{logit}(q_i) = \beta_0 + \beta_1 z_{1i} + \beta_2 z_{2i} + \beta_3 z_{3i} + \beta_4 z_{4i} + \beta_5 z_{5i} + f(x, y) + \varepsilon_i \quad (\text{eq. 2.2})$$

where β_0 is a constant (intercept), $\{\beta_1, \beta_2, \beta_3, \beta_4, \beta_5\}$ are the parameters, $\{z_1, z_2, z_3, z_4, z_5\}$ the covariates, $f(x, y)$ is a trend surface (i.e. a spline for the geographic component), and ε_i is the error term. The parameters β_1 and β_2 represent the effects of the size (DBH) and shade intolerance of the host trees (defined in Masaki et al. 1992), respectively. The parameter β_3 , β_4 , and β_5 represent the effects of the microsite characteristics: slope inclination, soil water content, and microscale landform, respectively. The variables used in the model and their data sources are summarised in Table 2.1. Among the covariates, z_1 , z_3 and z_4 were numerical; the others were categorical. When the shade intolerance (established after a relatively recent disturbance) of a host tree had a positive effect on liana species distribution, then that liana species was considered disturbance dependent. When shade intolerance had a negative effect on liana species distribution, that species was considered less

disturbance dependent. Bias due to spatial autocorrelation was corrected by including the x-y coordinates of the host tree as $f(x, y)$ (Dormann et al. 2007). Each liana species within each size class was evaluated using this method. A model was then selected according to Akaike's information criterion. All statistical analysis were performed in R version 3.2.2 (R Development Core Team 2015). The "ads" package was used for the spatial analysis (Pélissier and Goreaud 2015), and the "mgcv" package for statistical modelling (Wood 2011).

2.3 Results

Nine liana species were found on tree stems in the OFR study plot (Table 2.2), with *Wisteria floribunda*, a stem twiner, as the most dominant. This species accounted for 85% and 57% of the total basal area and abundance of the liana community respectively. The abundances of other stem twiners, including *Actinidia arguta*, *Akebia trifoliata*, and *Schisandra repanda*, were relatively low. *Euonymus fortunei*, *Schizophragma hydrangeoides*, *Hydrangea petiolaris*, and *Rhus ambigua* were root climbers, and their abundances were higher than those of stem twiners, other than *W. floribunda*. The only tendril climber found in the OFR was *Vitis coignetiae* which consisted mostly of large-class stems. Spatial analyses and the trend surface generalised additive model were conducted for populations with an abundance of >10 individuals within a size class; these analyses were applied to the following populations: *W. floribunda* (large and small), *E. fortunei* (small), *S. hydrangeoides* (large and small), *H. petiolaris* (small), *R. ambigua* (large and small), and *V. coignetiae* (large).

I recorded 856 liana stems on 700 tree stems with DBH >5 cm (4,751 stems); thus, 18% of the trees in the study plot carried at least one liana. The total liana basal area was 0.47 m² ha⁻¹, which was 1.4% of the tree basal area (34.8 m² ha⁻¹). Larger trees were often more infested by lianas (Fig. 2.1a). Lianas of different climbing types climbed host trees of different size classes. For those host trees infected by lianas, the occurrence of stem twiners was negatively correlated with that of root climbers along tree size gradients (Fig. 2.1b).

Both small and large liana species were significantly aggregated, with an average scale of 25 m (Table 2.3). An analysis of conspecific distribution patterns between different size classes revealed

the significantly positive spatial correlations of *W. floribunda* and *R. ambigua* at 5–80 m and 30–35 m respectively, whereas for *S. hydrangeoides* the correlation was random (Table 2.4). With respect to heterospecific distribution patterns, significantly positive spatial correlations were determined between the small lianas of *W. floribunda* and *E. fortunei* at 20–30 m and between those of *S. hydrangeoides* and *R. ambigua* at 30–35 m. None of the other combinations of species showed significant spatial correlations.

Host tree size had a significantly positive effect ($p < 0.05$) on the occurrences of five liana species in the large class (*W. floribunda*, *E. fortunei*, *S. hydrangeoides*, *R. ambigua*, *V. coignetiae*) and four liana species in the small class (*E. fortunei*, *S. hydrangeoides*, *R. ambigua*, *H. petiolaris*) but their effects on small *W. floribunda* were significantly negative (Table 2.5). The shade intolerance of host tree species positively affected liana distribution, except in the case of small *S. hydrangeoides*, whose distribution was negatively correlated with the shade intolerance of its host tree species (Table 2.5, Fig. 2.2).

Among the microsite characteristics, soil moisture and slope angle had significant negative effects on small *W. floribunda* and *S. hydrangeoides*, respectively ($p < 0.05$) (Table 2.5). None of the other species in the study plot were significantly affected by the respective microsite characteristics.

2.4 Discussion

2.4.1 The liana community of a cool temperate forest

The basal area of the lianas was lower ($0.47 \text{ m}^2 \text{ ha}^{-1}$; 1.4% to the total basal area) than that of the trees ($34.8 \text{ m}^2 \text{ ha}^{-1}$), as reported for liana communities in tropical (2.5%, DeWalt and Chave 2004; 2.2%, Schnitzer et al. 2012) and other temperate (0.2%, Allen et al. 1997) forests. Several liana genera detected in the study forest have also been reported in other temperate forests of the northern hemisphere. *Vitis*, *Rhus* (*Toxichodendron*) and *Eunonymus* are also found in temperate deciduous forests in North America (Talley et al. 1996; Ladwig and Meiners 2010a; Leicht-Young et al. 2010; Ladwig and Meiners 2015), and both *W. floribunda* and *E. fortunei* are invasive species in North American forests (e.g. Trusty et al. 2007; Kuhman et al. 2010; Smith and Reynolds 2012). Conversely,

only a few liana genera in the study plot, such as *Hydrangea* (Carrasco-Urra and Gianoli 2009; Gianoli et al. 2012), also occur in South American forests. The substantial difference in the liana flora of temperate South American and that of North American forests might reflect differences in origin, as the flora of temperate forests originated from Gondwanaland in the southern hemisphere (Hofstede et al. 2002).

Carrasco-Urra and Gianoli (2009) and Leicht-Young et al. (2010) found that stem twiners and root climbers in forests were negatively associated along the tree size gradient. The two studies were conducted in a temperate rain forest of southern South America and in an old-growth beech-maple forest of northern North America respectively. In this study, I found a similar relationship (Figs. 2.1a, b), in that root climbers climbed most host trees regardless of their DBH, whereas stem twiners seemed to initially require the support of trees of smaller DBH. Higher proportions of root climbers than of other climbing types have also been reported on the larger trees of other temperate forests (Schnitzler and Heuzé 2006; Carrasco-Urra and Gianoli 2009; Leicht-Young et al. 2010; but see Nabe-Nielsen 2001), suggesting the universality of this pattern in temperate forests from East Asia to America.

An analysis of the spatial distribution of each species within each size class showed that the distribution patterns of all liana species were fairly aggregated over a scale of 5–40 m (25 m on average). This likely reflects the seed dispersal process and/or the spreading of genet by stolon, as both facilitate the colonisation of sites that have suffered disturbances. In contrast to the large class, which showed no significant spatial correlations among species, in the small class, some of the heterospecific spatial correlations were significantly positive. These species were therefore probably recruited from the same sites and following the same disturbance events, as discussed below.

2.4.2 Effects of past disturbances

Three species, including the most dominant, *W. floribunda*, were positively correlated with the shade intolerance of their host trees; a negative correlation was determined for only one species. This implies that liana distribution in temperate forests depends on past disturbances where shade

intolerant species colonize effectively and grow rapidly. Generally, lianas are able to rapidly colonise gaps in both tropical (Paul and Yavitt 2011) and temperate (Londré and Schnitzer 2006; Ladwig and Meiners 2010a) forests owing to their faster elongation growth (Paul and Yavitt 2011), ability to survive treefalls (Putz 1984), and reproduction of clonal stems that can root independently (Ledo and Schnitzer 2014). The aggregated distribution patterns of the lianas in this study might therefore be related to the colonisation by lianas of disturbed sites, as is often found in the tropics (Schnitzer et al. 2000). The negative correlation of small *S. hydrangeoides* with the shade intolerance of its host trees suggested that this species is less dependent on disturbance. Gianoli et al. (2010) examined the distribution of liana species along the light gradient of South American temperate forests and showed that two of the seven dominant species were more abundant in the shaded understory. This suggests that adaptation to light exploitation explains the abundance of lianas across a disturbance-mediated environmental light gradient (Gianoli et al. 2012). However, the detection of overlapping or non-exclusive distribution patterns between liana species in the study plot would indicate that niche differentiation is a less relevant determinant of the liana community in the OFR.

The liana community in this forest might change in the future based on the presence or absence of disturbance. Masaki et al. (1992) examined projected compositions of this forest and suggested that it was likely to be shifting from a composition dominated by shade intolerant tree species to one dominated by shade tolerant tree species under the current disturbance regime, which lacks large and intensive disturbances. A similar shift might be possible in the liana community; without any new large disturbance, an evergreen liana (*E. fortunei*) could become more abundant than other deciduous liana species because evergreen plants can be more shade tolerant than deciduous plants (Miyashita and Tateno 2014).

2.4.3 Host tree and microsite characteristics

Overall, in the studied liana community, host tree conditions were a greater influence than were microsite characteristics, and host tree size significantly affected all species within the large class. The greater importance of host tree conditions than microsite characteristics on liana species

distribution has also been reported for temperate forests in North America (Leicht-Young et al. 2010) and for tropical forests (Nabe-Nielsen 2001; Nesheim and Økland 2007). The correlation between host tree size and the presence of all large-class liana species in the study plot was significantly positive, consistent with the generally larger surface area, older age, and consequent longer susceptibility to liana infestation of larger trees (Ladwig and Meiners 2015). Recent study in a cool temperate forest of Japan indicated that the growth of lianas synchronizes with that of their hosts (Ichihashi and Tateno 2015). Moreover, since larger trees are more likely to constitute the forest canopy, their crowns are more light exposed. By contrast, the effect on *W. floribunda* of small class was negative, which could be explained by its climbing type. Stem twiners have adapted to climb smaller-diameter supports, either switching with growth to large trees (a process known as “laddering”; Leicht-Young 2014) or continuing their growth along the same tree. After reaching the forest canopy, twiners can expand by spreading their shoots to host crowns. However, stem twiners often cover host tree crowns before the host grows large enough, and the host barely survives. This explains the lower frequency of *W. floribunda* on large host trees (as opposed to that of root climbers such as *E. fortunei*, which do not reduce the growth of host trees) (Fig. 2.1). These observations emphasise the importance of distinguishing among size classes within liana species.

Our observation that small *W. floribunda* was negatively affected by soil moisture was somewhat surprising, given that lianas require more ground moisture to achieve rapid elongation growth and thus are more likely to be distributed in moister habitats (McNab and Loftis 2002; Kusumoto et al. 2008). A recent study in the OFR found that during their transition from small to large classes, several tree species exchanged their drier habitats for wetter ones (Masaki et al. 2015). This might also be the case for the liana *W. floribunda*. An alternative explanation is related to the fact that the soil moisture content of our 6-ha plot varied spatially over short distances (10–20 m) (Masaki et al. 2015). *W. floribunda* has a highly developed and connected root system that spreads horizontally over a >20-m radius (Sakai et al. 2002); thus, stems of this species in drier habitats may well be connected with those in wetter habitats via horizontally reproduced stolons. This possibility can be evaluated using genetic tools to determine the horizontal spreading of each clone of this species. The

same approach should also be applied to other liana species, as high clonality and highly developed root systems are features of lianas in both tropical and temperate forests (Nabe-Nielsen and Hall 2002; Yorke et al. 2013), where they serve to enhance below-ground competition between lianas and trees (Schnitzer et al. 2005; Toledo-Aceves and Swaine 2008). Moreover, the apparent preference of small *W. floribunda* for drier soils would be consistent with the slower growth and thus smaller size of host trees in these soils.

The negative correlation of both small and large *S. hydrangeoides* with slope inclination indicated the greater sensitivity of this species to the soil surface disturbance caused by a steeper slope. This might be due to the fact that *S. hydrangeoides*, like many other root climbers, spreads stolons (vegetative growth) along the ground surface (Kato et al. 2014). However, the effects of slope inclination were not detected in the other three root climbers that extend stolons on the forest floor. In addition, the lack of significant effects of microscale landforms (Table 2.5) suggested that, compared with host tree size, microsite characteristics are not substantial determinants of liana distribution, at least in the OFR.

2.5 Figures

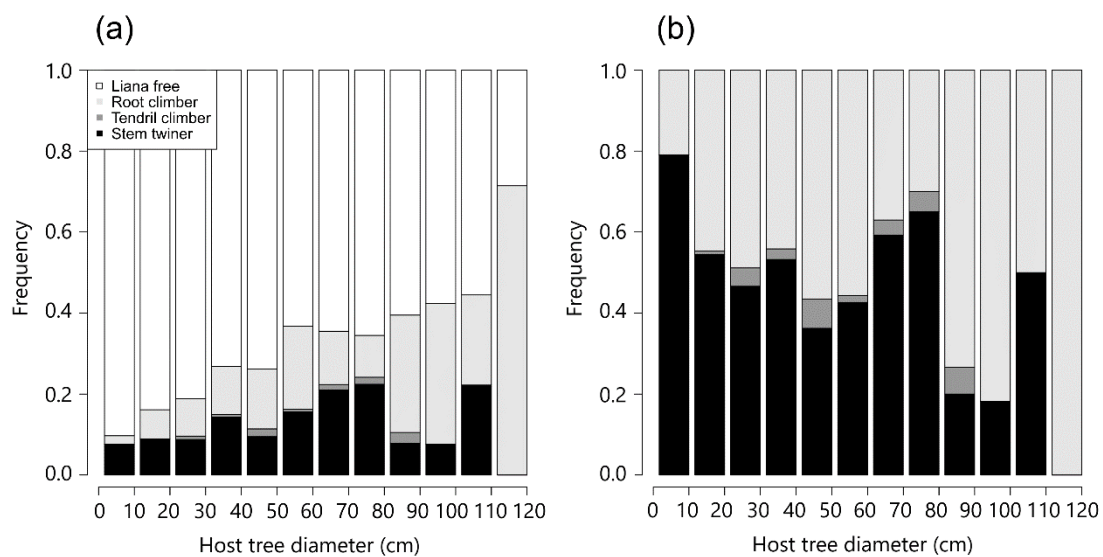


Fig. 2.1 Proportion of lianas of different climbing types with respect to host tree size class: (a) all trees and (b) trees infested by lianas. The climbing type of each liana species is described in Table 2.1.

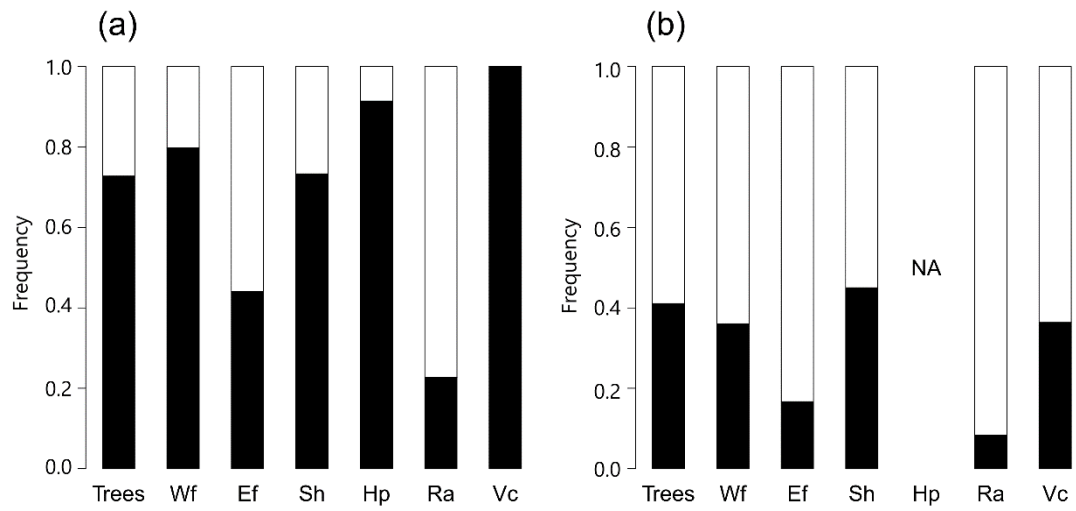


Fig. 2.2 Proportion of (a) small and (b) large liana species according to host-tree shade tolerance. Solid bars: shade-tolerant tree species; open bars: shade-intolerant tree species. “Trees” includes all trees within the plot. Wf: *Wisteria floribunda*, Ef: *Euonymus fortunei*, Sh: *Schizophragma hydrangeoides*, Hp: *Hydrangea petiolaris*, Ra: *Rhus ambigua*, Vc: *Vitis coignetiae*.

2.6 Tables

Table 2.1 Summary of environmental variables and data sources

	Environmental variable	Resource indicator	Data source
Host tree conditions	Size (DBH)	Light availability Mechanical support	Tree inventory in 2009
	Shade intolerance	Past disturbance	Masaki et al. 1992
	Slope	Soil surface disturbance	Masaki et al. <i>unpublished</i>
Microsite characteristics	Soil water	Water availability	Masaki et al. 2015
	Microscale landform	Soil resource and soil surface disturbance	Yoshinaga et al. 2002

DBH, diameter at breast height

Table 2.2 Summary of all liana species (1.3 m above the ground) found on trees (>5 cm DBH) in the Ogawa Forest Reserve within a 6-ha plot. Liana diameter is expressed as mean DBH \pm standard deviation.

Family	Species	N			Mean DBH (mm)	Basal area (m ² ha ⁻¹)	Climbing type ^a	Dispersal mode
		Small	Large	Total				
Fabaceae	<i>Wisteria floribunda</i>	375	111	486	48.7 \pm 61.5	0.402	ST	Explosive
Celastraceae	<i>Euonymus fortunei</i>	159	7	166	10.2 \pm 23.4	0.014	RC	Birds
Hydrangeaceae	<i>Schizophragma hydrangeoides</i>	91	21	112	26.5 \pm 38.7	0.032	RC	Wind
	<i>Hydrangea petiolaris</i>	35	0	35	11.0 \pm 10.7	0.001	RC	Wind
Anacardiaceae	<i>Rhus ambigua</i>	23	12	35	25.5 \pm 34.0	0.008	RC	Birds
Vitaceae	<i>Vitis coignetiae</i>	2	12	14	64.0 \pm 38.1	0.012	TC	Mammals/birds
Actinidiaceae	<i>Actinidia arguta</i>	3	2	5	44.1 \pm 31.0	0.002	ST	Mammals/birds
Lardizabalaceae	<i>Akebia trifoliata</i>	2	0	2	16.7 \pm 3.8	< 0.001	ST	Mammals/birds
Schisandraceae	<i>Schisandra repanda</i>	1	0	1	1.5	< 0.001	ST	Mammals/birds

^a Climbing types are abbreviated as ST (stem twiners), RC (root climbers), and TC (tendrill climbers).

Table 2.3 The spatial aggregation patterns of six liana species.

Species	Small ^a	Large ^a
<i>Wisteria floribunda</i>	+ (15: 5–75)	+ (25: 5–50)
<i>Euonymus fortunei</i>	+ (40: 5–100)	ND
<i>Schizophragma hydrangeoides</i>	+ (10: 5–55)	+ (5: 5)
<i>Hydrangea petiolaris</i>	+ (40: 5–100)	ND
<i>Rhus ambigua</i>	+ (40: 10–100)	+ (5: 5–10)
<i>Vitis coignetiae</i>	ND ^b	+ (20: 5–100)

^a “+”, aggregated pattern ($p < 0.05$). Values in parentheses show the spatial scale of significant values of the L functions [r for the largest value of $L(r)$] and the significant spatial range.

^b ND indicates a species in which there were <10 individuals within a size class; these were excluded from the analysis.

Table 2.4 Conspecific spatial correlations among the different size classes and the heterospecific spatial correlations within the size classes of six liana species.

	Wf	Ef	Sh	Hp	Ra	Vc
Wf	++ (35: 5-80)	+ (25: 20-30)	ns	ns	ns	ND
Ef	ND	ND	ns	ns	ns	ND
Sh	ns	ND	ns	ns	++ (35: 25-60)	ND
Hp	ND	ND	ND	ND	ns	ND
Ra	ns	ND	ns	ND	+(35: 30-35)	ND
Vc	ns	ND	ns	ND	ns	ND

Conspecific spatial correlations among different size class is shown in the diagonal of the table.

Heterospecific spatial correlations within the small class are shown in the upper right portion of the table, and those within the large class, in the lower left. Plus and minus symbols indicate significant positive and negative L_{12} (r) values, respectively, and are followed by the spatial scales determined to be significant (see Table 2.3): +++; ---; $p < 0.01$; ++; --; $p < 0.05$; +; -; $p < 0.1$. ns indicates no significant spatial correlation; ND indicates that number of individuals was < 10 for the size class.

Wf: *Wisteria floribunda*, Ef: *Euonymus fortunei*, Sh: *Schizophragma hydrangeoides*, Hp: *Hydrangea petiolaris*, Ra: *Rhus ambigua*, Vc: *Vitis coignetiae*.

Table 2.5 Summary of the best models to explain liana distribution.

Species	Climbing types	Class	Host tree conditions		Microsite characteristics						SAC ^a	
			Host size	Shade tolerance	Slope	Soil water	Micro-scale habitat	Head hollow	Upper slope	Lower slope		Flood terrace
<i>Wisteria floribunda</i>	ST	small	---									***
		large	+++	--								**
<i>Euonymus fortunei</i>	RC	small	+++	--								***
<i>Schizophragama hydrangeoides</i>	RC	small	+++	+		--						*
		large	+++			-						
<i>Hydrangea petiolaris</i>	RC	small	+									*
<i>Rhus ambigua</i>	RC	small	++	-								
		large	++	-								
<i>Vitis coignetiae</i>	TC	large	+									

The abbreviations for the climbing types are provided in Table 2.1.

^a SAC, spatial autocorrelation; significance is indicated by asterisks. Plus and minus symbols indicate positive and negative coefficients, respectively, for the corresponding variables. (+++; p < 0.001; ++; p < 0.01; +; p < 0.05; ---; ***, **; p < 0.01; +, -, *; p < 0.05.)

Chapter 3 Large contribution of clonal reproduction to the distribution of deciduous liana species (*Wisteria floribunda*) in an old-growth cool temperate forest: Evidence from genetic analysis

3.1 Introduction

Lianas are woody vine species that require mechanical support (i.e. host tree) to grow up to the forest canopy. Lianas are not only able to establish from seeds and suppressed saplings but also via clonal (vegetative) reproduction, whereas most tree species reproduce in only the two former ways (Schnitzer and Bongers 2011). Extensive clonal reproduction in lianas is thought to be a major driver of their regeneration and colonization success (Schnitzer et al. 2012; Yorke et al. 2013; Ledo and Schnitzer 2014), with a recent increase in their abundance and basal area reported in temperate and tropical forests around the world (Phillips et al. 2002; Allen et al. 2007; Yorke et al. 2013). Also importantly, clonal reproduction is known to be one of the major potential drivers of spatial distribution patterns of liana species in tropical forests (Ledo and Schnitzer 2014). However, studies of liana distribution patterns are often conducted in tropical forests where studies in temperate forests are lacking. Therefore, studies of liana clonal reproduction are essential to understanding their distribution and growth patterns in temperate forests.

Previous studies of clonal reproduction in lianas have provided important insight into their regeneration processes at the stand level in both temperate and tropical forests; however, most of these studies are still limited in their ability to accurately identify genetically distinct individuals (i.e. genets, clones). These studies utilized above-ground (i.e. liana inventory; Schnitzer et al. 2012; Yorke et al. 2013; Ledo and Schnitzer 2014; Chapter 2) and below-ground censuses (i.e. excavation; Peñalosa 1984; Putz 1984; Sakai et al. 2002). An above-ground census detects rooted stems that have above ground physical connections with other rooted stems (i.e. rooted ramets), which is different from branches in terms of connectivity to the ground (Gerwing et al. 2006; Schnitzer et al. 2008, 2012); however, these methods are unable to detect clonally reproduced ramets below the forest floor or

ramets that were previously connected to each other (i.e. clonal ramets) (Parks and Werth 1993; Suyama et al. 2000; Schnitzer et al. 2012). While a below-ground census detects the presence of below ground connections, it is often difficult to conduct below-ground census in large area as it requires the destruction of the surrounding vegetation, thus making it difficult to apply this methodology widely to study plots. Furthermore, a below ground census can only detect the current connectivity between ramets.

Clonal analysis using genetic tools such as microsatellite markers is an effective approach for the precise evaluation of clonal reproduction in lianas. Although some previous studies have applied genetic analysis to some liana species (Foster and Sork 1997; Grashof-Bokdam et al. 1998; Arnold and Schnitzler 2010; Kartzinel et al. 2015), these studies were either conducted in rural ecosystems and disturbed forests, and/or were based on non-continuous sampling within small plots. To the best of our knowledge, no studies have conducted genetic analyses on lianas with a focus on the contribution of clonal reproduction to regeneration processes and distribution patterns under natural conditions. In addition, genetic analysis for the evaluation of the liana clonal structure and distribution patterns of clones should be conducted in large plots (i.e. > 1 ha). Sakai *et al.* (2002) showed that individual ramets of the deciduous liana species *Wisteria floribunda* (Willd.) DC. could be up to 310.6 m in total length. It is also important to test the clonal ability of liana species in various topographies to assess any potential impact of the spatial heterogeneity of the forest floor environment on clonal reproduction, as clonal growth below the ground and on the forest floor via rhizomes and stolons—horizontal connections between plant organisms—is often sensitive to microsite characteristics (Parks and Werth 1993; Suyama et al. 2000; Waters and Watson 2015). In contrast, micro-topography often has a relatively small impact on liana distribution patterns in both tropical and temperate forests (Dalling et al. 2012; Chapter 2). Thus, it is necessary to assess the contribution of clonal reproduction on the distribution patterns of liana species over various micro-topographies.

To evaluate the contribution of clonal reproduction on the distribution of a liana species in its natural habitat, I conducted a genetic analysis using 10 microsatellite markers in the deciduous liana species *W. floribunda*, with continuous sampling of a 6-ha plot in an old-growth cool temperate forest

of Japan. Specifically, the following questions were addressed: 1) Does clonal reproduction significantly contribute to the distribution of *W. floribunda*? 2) How large and long is the clone (i.e. genet) patch and what is the distance between ramets within one genet? 3) Are distribution patterns of *W. floribunda* clones affected by micro-topography? Answering these questions is important not only to further elucidate the clonal structure of this species, but also to evaluate the contribution clonal ability makes to liana distribution and survival strategies.

This study was published in Mori et al. (2017a). Figures and tables used in this chapter are from Mori et al. (2017a).

3.2 Materials and Methods

3.2.1 Study site

This study was conducted in the Ogawa Forest Reserve (OFR) (Nakashizuka and Matsumoto 2002). See Chapter 2 for descriptions of the study site. Data from a tree inventory conducted in 2013 was used for this analysis. DBH, species name, host tree, and location of all lianas on trees (DBH \geq 5 cm) higher than 1.3 m above the ground were measured in 2013 (Chapter 2).

This study plot includes a variety of landforms including a crest slope (CS), head hollow (HH), upper side slope (US), lower side slope (LS), flood terrace (FT), and river bed (RB) (Fig. S3.1; Yoshinaga et al. 2002; see illustration in Nagamatsu and Miura 1997), which are landform classifications proposed by Tamura (1981). These landform types were classified based on discontinuities in slope angles and the forms of adjacent units (i.e. convexity and concavity; for details, see Tamura 1981). CS and US are stable landforms that are characterized by decreased soil disturbance, whereas the other landforms often experience more frequent soil disturbances (Nagamatsu and Miura 1997). A small stream runs through the centre of the plot, and thus the variety of its topographic conditions is suitable for the evaluation of clonal reproduction in lianas on the forest floor.

3.2.2 Study species

Wisteria floribunda (Fabaceae) is a deciduous, stem twining liana species that is widely distributed throughout Japan (Ohashi et al. 1989). This species produces stolons on the ground surface via clonal reproduction (Fig. S3.2; Sakai et al. 2002). *Wisteria floribunda* often predominates temperate forests; representing 57% of the abundance and 85% of the basal area of the liana community in this study plot (Chapter 2). Other liana species in this study plot are mostly root climbers (e.g. *Euonymus fortunei*, *Schizophragma hydrangeoides*, *Hydrangea petiolaris*, *Rhus ambigua*). *Wisteria floribunda* and other root-climbing species accounted for 98% and 97% of the total abundance and basal area in this liana community, respectively. *Wisteria floribunda* often reaches the forest canopy and covers the host tree canopy, while root climbers are suppressed under the host tree canopy (Ichihashi and Tateno, 2011; Chapter 2). There are no significantly exclusive distribution patterns between the liana species in this study plot (Chapter 2).

3.2.3 Sampling, DNA extraction, and genotyping

Following the liana census conducted in 2013 (Chapter 2), I collected either fresh leaf or inner bark samples from all *W. floribunda* individuals that were higher than 1.3 m above-ground in 2015. I defined individuals as being independently rooted ramets that had no apparent above-ground connection to other rooted ramets ('apparent genet'; Gerwing et al. 2006). Within the study plot, I did not observe any rooted ramets with obvious connections to other rooted ramets. Therefore, the term "ramets" used in this study refers to rooted above-ground stems that sprouted from stolons or emerged from seeds. Inner bark samples were collected in cases where leaf samples could not be collected owing to the difficulty in distinguishing individuals, which often occurred when no leaves were available under the forest canopy and/or multiple individuals were tangled on the same host tree. The collection of leaf and inner bark samples ($N = 391$; 326 leaves and 65 bark samples) were stored at -30°C prior to DNA extraction. DNA extraction was conducted using the DNeasy kit (Qiagen, Valencia, CA, USA). Polymerase chain reaction (PCR) was performed using the 10 microsatellite markers designed for *W. floribunda* as described by Mori et al. (2016b). Genotyping data was checked and binned with Geneious R9.0 (Kearse et al. 2012).

3.2.4 Data analysis

Clones were identified with standardized methods (Arnaud-Haond et al. 2007). In brief, the ability of 10 microsatellite markers to distinguish multilocus genotypes (MLGs) was examined by calculating the distinct number of MLGs for all combinations of a given locus. The results were confirmed from the plateau of the genotype accumulation curve (Fig. S3.3). To ascertain whether ramets of the same MLG belonged to the same clone, the probability of a given MLG occurring in a population under Hardy-Weinberg equilibrium was calculated (P_{gen}) (Parks and Werth 1993):

$$P_{gen} = \sum_{i=1}^l (f_i) 2^h \quad (\text{eq. 3.1})$$

where f_i is the frequency of each allele at the i -th locus estimated with a round-robin method, and h is the number of heterozygous loci. Then, the probability of obtaining n repeated MLGs from a population more than once by chance in N samples (P_{sex}) was calculated (Parks and Werth 1993):

$$P_{sex} = \sum_{i=n}^N \frac{N!}{i!(N-i)!} [P_{gen}]^i [1 - P_{gen}]^{N-i} \quad (\text{eq. 3.2})$$

To ascertain each distinct MLG that belonged to a distinct clone, multilocus lineages (MLLs) were defined based on pairwise genetic distances. This procedure was necessary to prevent the false detection of clones owing to slightly different MLGs resulting from somatic mutation and genotyping errors. The threshold of pairwise genetic distance was determined as one by changing the threshold from zero to five following the recommendations of Meirmans and Van Tienderen (2004) (Table S3.1). The MLLs are equivalent to the term ‘genet’ in ecological studies and thus, I will use this term hereafter for MLLs to avoid further confusion.

Genets were mapped to show the clonal structure across the study plot. The patch size for all genets with three or more ramets was measured by the area of a convex hull polygon for each genet calculated in QGIS version 2.16.2 (QGIS Development Team, 2009). The robustness of habitat composition based on the landforms of both clonal and non-clonal ramets was tested using the jack-knife procedure: mean and 95% confidence intervals for habitat composition of landforms were

obtained from datasets that were generated excluding one genet. This was done for all combinations of genets. If the contribution of single genet on the habitat composition of landforms was large, then a 95% confidence interval would be a high value compared to that of the mean value. To evaluate the degree of aggregation and intermingling between genets, the aggregation index (A_c) was defined as $A_c = (P_{sg} - P_{sp})/P_{sg}$, where P_{sg} is the average probability of clonal identity for all pairs and P_{sp} is the average probability for clonal identity among the nearest neighbours. A_c is zero when all genets are intermingled and one when all genets are distinctly distributed. Finally, to evaluate the clonal diversity the following indices were obtained: clonal richness (R), Simpson's evenness index (V), and the Pareto index (β). The equation for clonal richness (genotypic richness) was $R = (G - 1)/(N - 1)$ where G is the number of genets in N samples. Simpson's evenness index was then estimated as $V = (D - D_{\min})/(D_{\max} - D_{\min})$ where D is the Simpson index $D = 1 - \sum_{i=1}^G [n_i(n_i - 1)/N(N - 1)]$, $D_{\min} = \{[(2N - G)(G - 1)]/N^2\} \times [N/(N - 1)]$, $D_{\max} = [(G - 1)/G] \times [N/(N - 1)]$, G is the number of unique MLGs, and N is the number of samples. The Pareto index is the negative value of the slope of the power law (Pareto) distribution of clonal membership. The equation for Pareto index is $N_{\geq X} = \alpha X^{-\beta}$, where $N_{\geq X}$ is the number of genets containing X or more ramets. The Pareto index (β) is higher when genets have a higher density and the distribution of ramets per genet has higher evenness. P_{gen} and P_{sex} were calculated in R version 3.3.2 (R Development Core Team 2016) with the 'poppr' package version 2.2.0 (Kamvar et al. 2014, 2015). Determination of genets (i.e. MLLs) was conducted in GenoDive version 2.0 (Meirmans and Van Tienderen 2004). The calculation of clonal indices was done in R version 3.3.2 (R Development Core Team 2016) with the 'RClone' package version 1.0 (Arnaud-Haond and Bailleul 2015).

3.3 Results

All ramets ($N = 391$; 326 leaf and 65 bark samples) sampled from the study plot were genotyped, and a total of 168 genets were detected. There was a low probability of obtaining a given

genotype ($P_{\text{gen}} < 0.001$) and obtaining repeated genotypes that originated from distinct sexual reproductive events by chance ($P_{\text{sex}} < 0.001$); thus, it was assumed that errors were unlikely to occur in the identification of clones. The number of ramets in one genet ranged from one to 29 (Figs. S3.4a and b). Clones contributed 71% and 62% to abundance and total basal area, respectively, or 57% and 31% when the largest ramet within a genet (presumed parent ramet) was excluded. The number of unique genets (i.e. a single-ramet genet) was 29% of all ramets sampled in the study plot, while multiple ramet genets with 2–4, 5–9, or 10 or more ramets were found to consist of 21%, 24%, and 26% of all individuals, respectively. Similarly, the basal area of unique genets was 38%, while multiple ramet genets with 2–4, 5–9, or 10 or more ramets were found to make up 20%, 26%, and 16% of the sampled individuals, respectively. The clonal richness (R), Shannon evenness Index (I), Pareto index (β), and Aggregation index (Ac) were 0.43, 0.96, 0.76 ($P < 0.001$), and 0.38 ($P < 0.001$), respectively. The number of clonally reproduced ramets and the maximum stem diameter within one genet were positively correlated (Fig. 3.1).

Spatial distribution maps of *W. floribunda* clones are shown in Figure 3.2. Clones ranged over a 180 m distance in the study plot. With the exception of the two largest genets, most of the clones did not spread over both sides of the slope, which was divided by a stream or valley landform (Fig. 3.2). The largest genet had a patch size of 0.47 ha (Figs. S3.4 and 3.2). The total area of a clone patch size for all *W. floribunda* clones detected in the study plot was approximately 1.1 ha or 18% of the plot.

The composition of microscale landforms was significantly different between clonal and non-clonal ramets in terms of abundance (χ^2 test; $df = 5$; $P < 0.05$) and basal area (χ^2 test; $df = 5$; $P < 0.001$; Fig. 3.3). The non-clonal ramets were distributed to a greater extent on LS in both abundance and basal area than were trees and clonal-ramets in comparison to other landforms. These results indicate that the clonal reproduction of *W. floribunda* led to different distribution patterns over the micro-topography.

3.4 Discussion

Genetic analysis of the *W. floribunda* population revealed that clonal reproduction makes a large contribution to abundance (71%) and basal area (62%) in this study plot. This contribution was 57% and 31%, respectively, when the largest ramet within a genet was excluded, still indicating a significant contribution. To our knowledge, this is the first study to provide direct evidence for the clonal reproduction of a liana species in natural forest conditions using genetic tools with fine-scale sampling. Yorke et al. (2013) found that in old-growth tropical forests, long-distance clonal reproduction contributed 19% and 60% to abundance and basal area, respectively. Schnitzer et al. (2012) reported that clonal rooted stems contributed 43% to the total density and 23% to total basal area in a 50-ha plot on the Barro Colorado Island (BCI) in Panama. They also found a strong relationship between stem diameter and the number of rooted ramets that had apparent connections to other rooted ramets. A similar correlation was found in the present study, a positive correlation was observed between maximum DBH and the number of ramets within one genet (Fig. 3.1). This indicates that larger lianas could produce a large amount of clonal ramets above (i.e. apparent rooted clones) or below (i.e. stolons) ground. Overall, the high contribution of clonal reproduction to *W. floribunda* abundance and basal area is consistent with previous observational studies of lianas in tropical forests.

I did not observe rooted clones of *W. floribunda* with apparent connections to each other in this study plot (Mori, *personal observation*); however, I did observe a substantial contribution of clonal reproduction to the abundance and basal area of *W. floribunda* in the present study. Our results indicate that genetic tools are useful in evaluating the clonal structure of liana populations in cases where physical connections between ramets are not entirely apparent (e.g. when they are connected below-ground), and where the connections have been lost in the past. In fact, underground clonal reproduction could be fairly common among liana species. For example, Putz (1984) excavated small individuals (< 50 cm tall) of five common liana species on BCI and found that 15-90% of these plants were not true seedlings but clonal ramets connected by stolons or rhizomes. Thus, while previous studies have observed the considerable contributions of clonal reproduction to the dynamics of tropical liana communities (Schnitzer et al. 2012; Ledo and Schnitzer 2014), the magnitude of the contribution may

be even greater if unapparent (below-ground) connections between individuals are included. This possibility may be addressed in the future by means of genetic analyses.

There was a slight intermingling of genets as indicated by the aggregation index of 0.38. The aggregation index of *W. floribunda* was comparable with those of other non-liana clonal woody plant species. For example, the Gondwanan conifer species *Athrotaxis cupressoides*, had aggregation index of 0.43 in average (Worth et al. 2016), while the aggregation index is reported to vary widely, both within species (0.1-0.79: *A. cupressoides*, Worth et al. 2016) and between species (0.03: *Nothofagus pumilio*, Mathiasen and Premoli 2013; 0.62: *Populus nigra*, Chenault et al. 2011). A slightly intermingled distribution pattern of genets was observed in the present study, while clonal patches of *W. floribunda* seemed to exhibit a lower degree of overlapping distribution (Fig. 3.2). This could be because many non-clonal ramets (i.e. single-ramet genet) were distributed within patches of large genets. These non-clonal ramets could have originated from sexual reproduction (i.e. germinated from seed) that was observed as one unique genet in the study plot by genetic analysis. Further observation on seed production and seedling distribution using both ecological and genetic approaches would provide important insight into the contribution of seed reproduction on liana distribution.

It is also important to note that the wide variation in patch size and range of *W. floribunda* clones (Figs. 3.1 and 3.2) was consistent with other non-liana clonal plants. For example, clones of the deciduous tree species *Padus siori* formed a large 0.4 ha genet, but it also had many small and unique genets distributed within the same population (Mori et al. 2009). Wide variation in clone patch size was also reported in *Fagus grandifolia* (Kitamura et al. 2001) and in dwarf bamboo (Suyama et al. 2000). The heterogeneous clonal structure was also indicated by clonal diversity indices. The clonal richness ($R = 0.43$) and Pareto index ($\beta = 0.76$) were comparable to the average value of other clonal plants ($R = 0.44$; terrestrial and marine plant species: $\beta = 0.60-1.49$ as reviewed in Honey and Jacquemyn 2008; Ohsako 2010, Kudzu (*Pueraria lobata*): $\beta = 0.03-1.47$; Kartzinel et al. 2015), whereas the evenness ($V = 0.96$) was relatively higher in the liana I measured in comparison to that of other clonal plants (clonal plant average: $V = 0.74$; Honnay and Jacquemyn, 2008). Kartzinel et al. (2015) showed that the clonal structure of Kudzu (*Pueraria lobata*), which is a deciduous vine species

that grows along roadsides and in abandoned farmlands, forms both small and large patches of clones. Although clonal indices are an effective way to compare clonal abilities between species, information of clonal indices of lianas is currently lacking. Further studies are needed to accumulate clonal indices for a general understanding of the relative importance of the clonal reproduction of liana species and how they relate to non-liana clonal plant species.

Clonal ramets were distributed more on the upper side of slopes (US) than the lower side of slopes (LS), whereas non-clonal ramets were distributed more on LS than US (Fig. 3.3). LS is the steepest slope of the landforms in our study plot and has the most intense amount of soil surface disturbance (Nagamatsu and Miura 1997). Consequently, non-liana trees in the study plot are more abundant on US than LS (Fig. 3.3) areas, in agreement with a previous study that vegetation is often more developed on US and more scarce on LS (Nagamatsu and Miura 1997). The contrasting distribution pattern of these ramets was more evident in basal area than in density (Fig. 3.3). This indicates that non-clonal ramets on LS are relatively mature, as indicated by their large stem diameter size, number of ramets larger than 5 cm DBH for clonal ramets (US: 39, LS: 21) and non-clonal ramets (US: 16, LS: 20). Although larger ramets are able to produce more clonal ramets, clonal ramets were found more on the US than the LS. Thus, the differences in preferred landforms between clonal and non-clonal ramets may reflect limitations of clonal growth on the forest floor by stolons. In summary, lianas derived from seeds do not particularly prefer growing in LS; however, those established in LS rarely succeed in clonal reproduction, leading to an accumulation of large single-ramet plants in this area.

The two largest genets (0.47 and 0.19 ha) were found to range over both sides of the slopes, which were divided by a stream and valley landform (Fig. 3.2). These results indicate that these clones were somehow able to override these topographic barriers. One possible explanation could be “laddering”. By laddering host tree crowns to one another, lianas can expand their distribution despite the topographical limitations. When a tree carrying stem twiners fall, lianas will also be pulled down to the forest floor and re-root from the stem and/or produce stolons (Schnitzer et al. 2000, 2004; Gerwing 2004). In the present study site, I found stolons that had produced from the fallen stems of

W. floribunda (Mori, *personal observation*), while I did not observe any rooted ramet higher than 1.3m above-ground that had apparent connections to another rooted ramet, as previously mentioned. This could be because stolons can be easily buried in the ground, rendering the observation of ramets produced from fallen stems more difficult. An alternative explanation could be the expansion of stolons over the streams and valleys; however, no stolons were observed to have crossed over or started to cross over the stream, despite the presence of stolons derived from mother ramets along the streams at the study site (Mori *personal observation*). Even if the stolons succeeded at crossing over the streams, ramets need to re-root to become independent from the mother ramet, making the probability that stolons can overcome topographic barriers minimal. The fact that the same clones were detected across streams and valleys implies that *W. floribunda* expanded its distribution clonally in two different layers of this forest, which were most likely the canopy and understory.

3.5 Figures

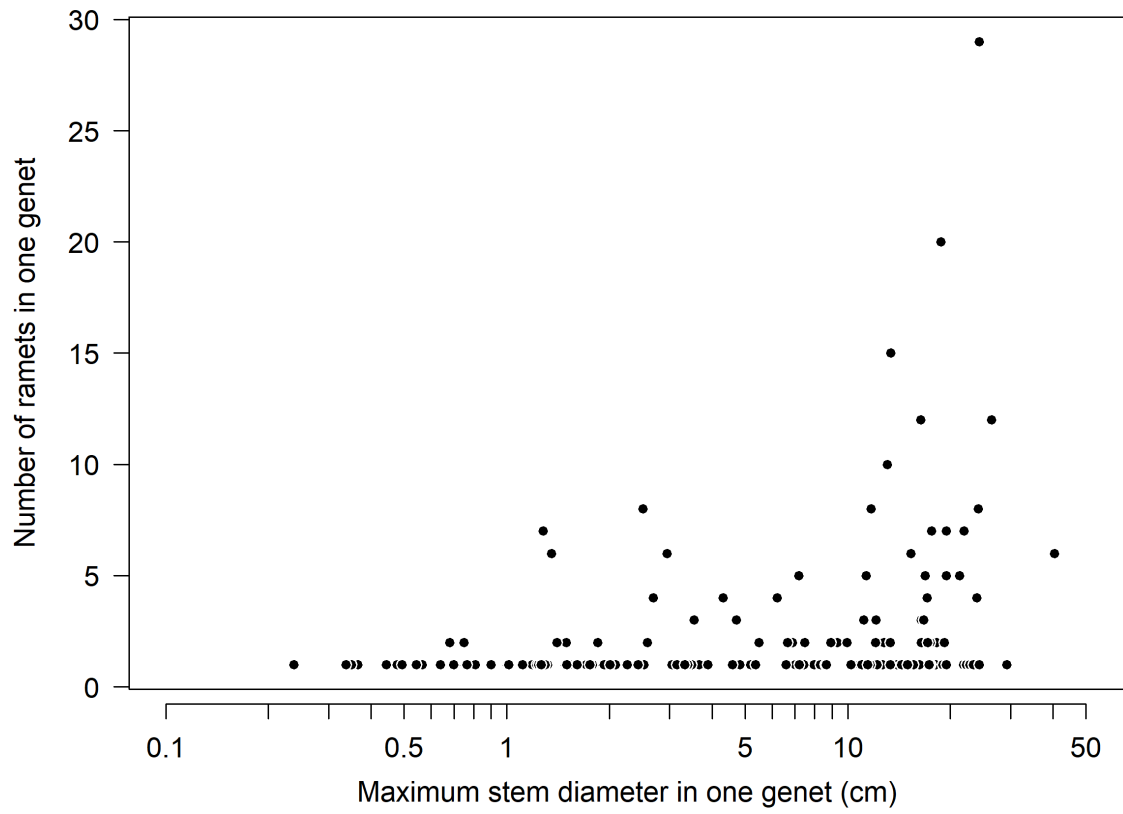


Fig. 3.1 Relationship between the maximum stem diameter and number of ramets in one genet.

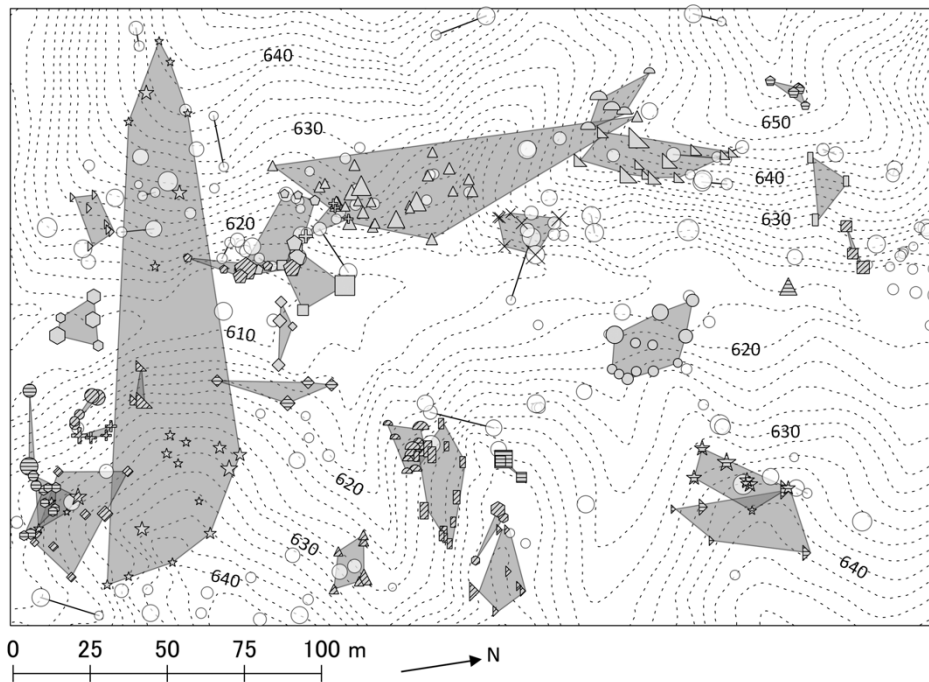


Fig. 3.2 Clonal patch size of *Wisteria floribunda* genets. Symbol size represents the DBH of each ramet. Polygons indicate the clone patches that have three or more ramets in one genet. Solid lines indicate clones that have two ramets in one genet. The different genets with three or more ramets are represented by closed symbols using combinations of different patterns and shapes, while those with one or two ramets are represented as open circles with a grey outline. Contour is presented in two meters. Numerals on contour lines indicate the altitude (m).

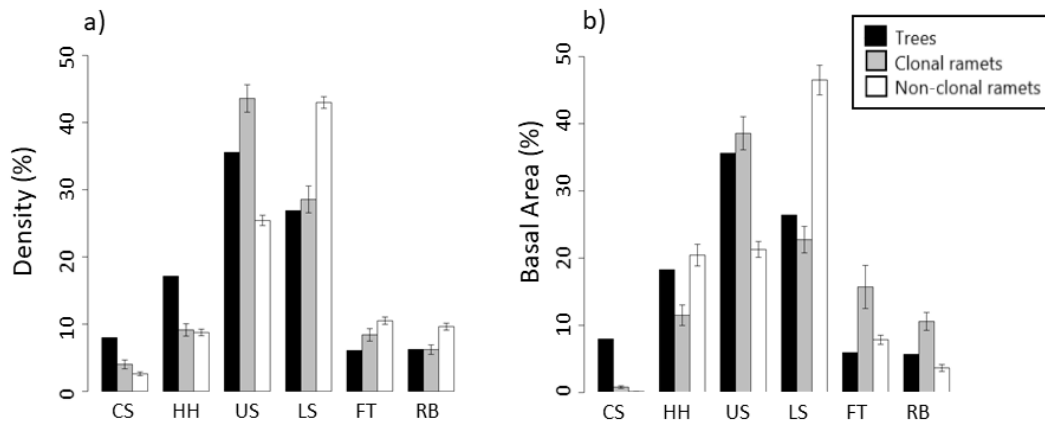


Fig. 3.3 Habitat composition of microscale landforms of the (a) abundance and (b) basal area of trees, clonal and non-clonal ramets. Clonal and non-clonal ramets represent genets with two or more ramets and genets with one ramet, respectively. The robustness of habitat composition for clonal and non-clonal ramets was tested by generating datasets that excluded one genet from all combinations. Error bars represent a 95% confidence interval for the generated datasets. Abbreviations of landforms are as follows: CS, crest slope; HH, head hollow; US, upper side slope; LS, lower side slope; FT, flood terrace; RB, river bed.

3.6 Appendix

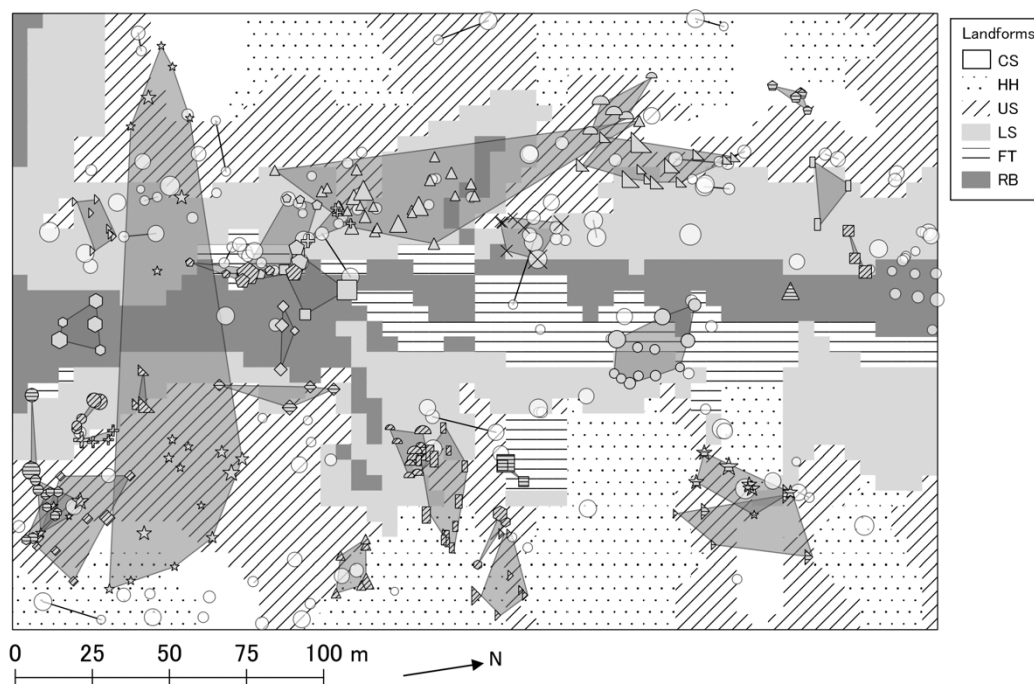


Figure S3.1: Spatial distribution map of *Wisteria floribunda* genets and landforms. Genets are represented the same as in Fig. 3.3. For abbreviations of landforms, see Fig. 3.3.



Figure S3.2: Photograph of *Wisteria floribunda* ramets and stolons in the study plot.

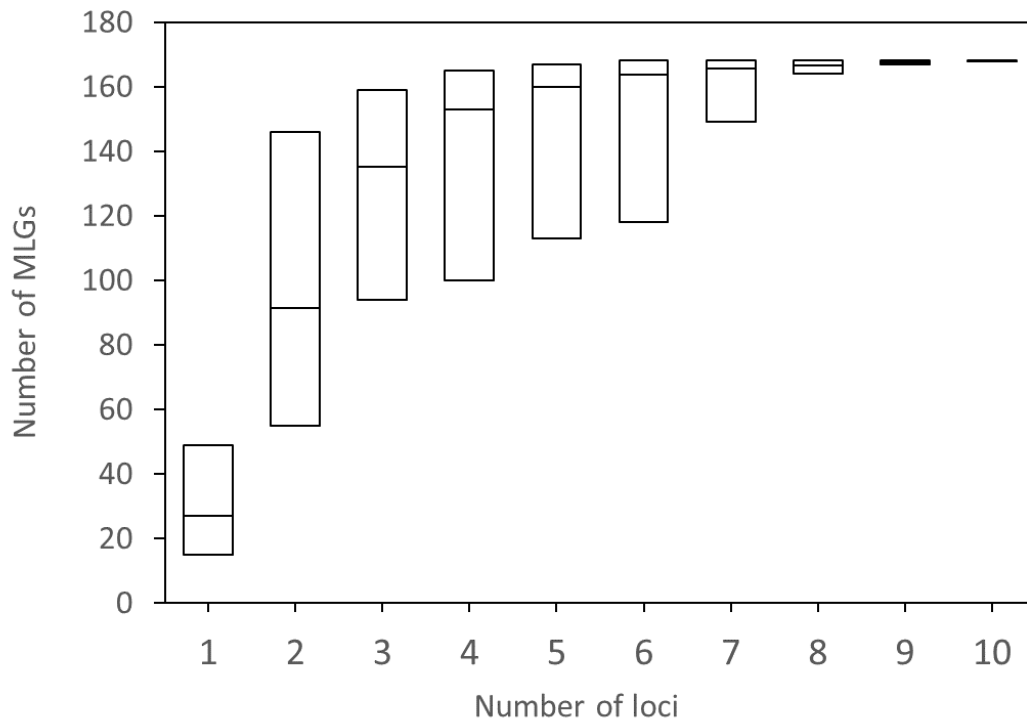


Figure S3.3: Genotype accumulation curve. The top and bottom of each closed box represents the maximum and minimum number of multilocus genotypes (MLGs) observed with the number of given loci (from 1-10), respectively. The horizontal line in the box indicates the mean number of observed MLGs.

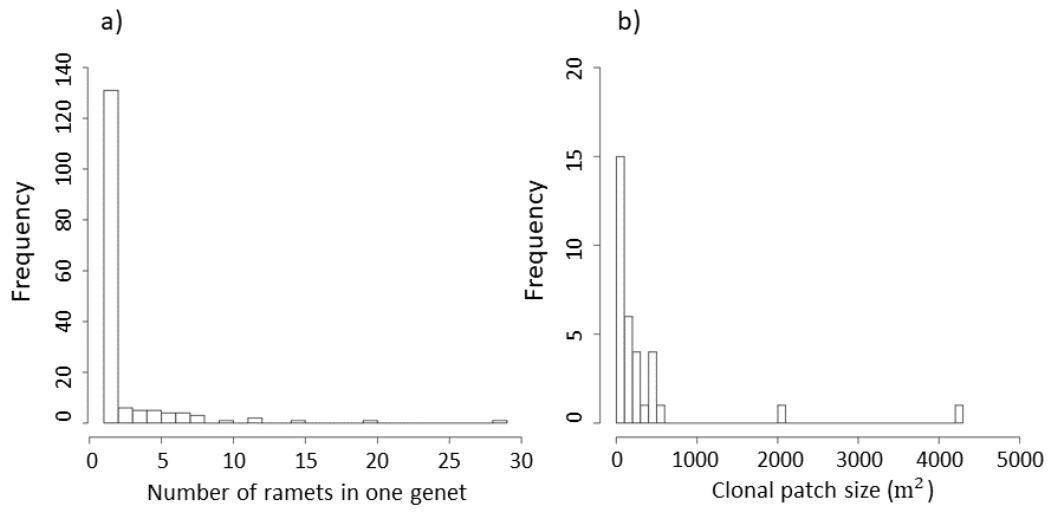


Figure S3.4: Histogram of (a) the number of ramets per genet and (b) clonal patch size.

Table S3.1: Number of multilocus lineages (MLLs) and clonal diversity indices with changing thresholds of genetic distance.

Threshold	No. MLLs	Clonal richness	Simpson's evenness index	Pareto index
0	168	0.43	0.96	0.76
1	168	0.43	0.96	0.76
2	165	0.42	0.96	0.76
3	165	0.42	0.96	0.76
4	163	0.42	0.96	0.74
5	163	0.42	0.96	0.74

Chapter 7 General discussion

7.1 Overview of the role of clonal reproduction on the distribution of liana species in a temperate forest

Ecology of lianas has become an area of increasing research interests in the past three decades due to the substantial role of lianas on forest ecological functions (i.e. forest dynamics) (Schnitzer and Bongers 2002, Schnitzer et al. 2015). However, fundamental ecological knowledge (e.g. life history, distribution patterns, community structure) of lianas is relatively lacking compared to trees. This tendency is far greater in temperate regions since most of the ecological studies of lianas had been carried out in tropics due to the high diversity of lianas in tropical forests (Schnitzer and Bongers 2002).

Liana community of Ogawa Forest Reserve was characterized by a deciduous stem twiner *W. floribunda* (Chapter 2); this species accounted for 85% and 57% of the total basal area and abundance, respectively. Root climbers (*E. fortunei*, *S. hydrangeoides*, *R. ambigua*, *H. petiolaris*) were also high in abundance. Distribution of liana species in ramet-level were mainly affected by host tree characteristics and past disturbances, while microsite characteristic was less influential.

Liana species often produce clonal stems (stolons) on the forest floor for clonal growth, however, the role of clonal reproduction as a life history strategy and its contribution to the distribution patterns remained unexplored (Chapter 1). The results of the genetic analyses on *W. floribunda* revealed that clonal reproduction contributed greatly on forming a population, which was indicated by large proportion of clonal ramets (71%) to the total abundance of ramets (Chapter 3). Furthermore, clonal reproduction played an important role in characterizing distribution patterns over different micro-topography; clonally reproduced ramets were less frequently distributed in lower part of the slope (characterized by steep slopes) while non-clonal ramets (presumed to be derived from seed reproduction) were often found in steeper slopes. This probably reflects the sensitivity of clonal growth via stolons to the ground surface conditions. It is also important to note that the significant effect of micro-scale topography was not found for the ramet-level distribution of *W. floribunda* (Chapter 2), which indicates the necessity and effectiveness of applying genetic tools on liana ecological studies.

In conclusion, clonal reproduction of *W. floribunda* played a significant role in formation of a population and distribution patterns in a temperate forest.

Clonal reproduction of lianas is considered as an important life history strategy for the rapid response to canopy gap disturbances (Chapter 1). However, there were no significant positive effect of canopy gap disturbances to the magnitude of clonal reproduction of *Wisteria floribunda* indicated by the maximum width of the clonal patches (Chapter 4). Moreover, individuals with small clonal patch width, which is mostly composed with non-clonal ramets, were positively correlated with canopy gap disturbances occurred in approximately 25 years ago. This indicates that canopy gap disturbances could be important for individuals that derived from seed reproduction to establish. Interestingly, these results did not support the mechanism—lianas respond to canopy gap disturbances with clonal reproduction—which has been reported in tropical forests. This could be due to the difference in types and strategies of clonal reproduction of lianas reported in temperate and tropical forests; like other clonal plants in the understory, clonal reproduction of *W. floribunda* could be enhanced under unfavourable environments (i.e. dark light conditions in closed canopy) where regeneration via seed reproduction is not likely to be accomplished. On the other hand, clonal reproduction of lianas reported in tropical forests might be similar to re-sprouting in tree species, which is a strategy for the rapid response (recovery) after disturbance. Therefore, it may be important to distinguish and pay careful attention to what type of life history of liana species is in consideration because lianas exhibit various shapes and complex growth forms.

Precise evaluation of the contribution of seed reproduction to the distribution patterns of lianas is still limited in ability even using genetic approach. This is because information of ramets in the past is not available in most cases. Because post-dispersed seed to seedling stage shows the most dramatic response to the surrounding environment, investigation of current-seedlings can provide important information regarding to the role of seed reproduction to the distribution patterns. Continuous investigation of current-year seedlings of *W. floribunda* revealed that seedlings had higher survival rate in places where canopy openness is higher (Chapter 5). This was consistent with the findings based on genetic analysis (Chapter 4). These results indicate the necessity of light

environment for establishment via seed reproduction. Interestingly, current-year seedlings showed higher survival rate compared to other co-occurring tree species, which indicates that seedlings of *W. floribunda* are more shade-tolerant than tree species (Chapter 5). The high shade-tolerance allow seedlings to perform “sit and wait” strategy—the strategy to persist in the understory until canopy opens—which is reported for an invasive liana species (*Celastrus orbicellatus*) in North America (Greenberg et al. 2001). Further investigation on current-year seedlings of multiple liana species would provide comprehensive understandings on high shade-tolerance of seedlings of liana species in the understory (“sit and wait” strategy).

The contribution of clonal reproduction to three root climbing liana species (*Schizophragma hydrangeoides*, *Euonymus fortunei*, *Rhus ambigua*) was smaller compared to that of *W. floribunda* (Chapter 6). Similar tendency was also observed with clonal ramets on the forest floor for three liana species (*W. floribunda*, *S. hydrangeoides*, *E. fortunei*) (Chapter 7). These findings suggest that *W. floribunda* (a stem twiner) have greater clonal ability than root climbers. It is important to note that proportion of clonally reproduced ramets were larger on the forest floor compared to ramets that climbed trees. This indicates that a limited part of clonal ramets in the understory successfully climbed trees. Overall, the contribution of clonal reproduction was largest in *W. floribunda*, intermediate in *S. hydrangeoides*, and smallest in *E. fortunei*. The magnitude of clonal reproduction could be related to the shade-tolerance of three liana species. Species with high shade-tolerance such as *E. fortunei* (root climber, ever-green species) may allow this species to climb up to the tree canopy via high ability to cope with dark light conditions in the understory (Chapter 2), which might result the clonal growth being less important compared to *W. floribunda* (stem twiner, deciduous species). Interestingly, this mechanism could be consistent to the findings of Kudzu (*Pueraria lobata*), a deciduous vine species that grows along roadsides and in abandoned farmlands (Kartzinel et al. 2015). Kudzu is an invasive species in North America and often controlled via mowing, which is large and intense disturbance. Kartzinel et al. (2015) reported that intense and frequent mowing enhanced genotypic diversity of Kudzu, which means that disturbance allowed Kudzu to establish via seed reproduction. Similar findings are also reported in non-liana tree species, such as *Salix exigua* (Douhovnikoff et al. 2005)

and *Populus tremuloides* (Shepperd et al. 2001) (see Chapter 4). Furthermore, understory herbaceous plants reproduce clonally when seed reproduction cannot be accomplished (reviewed in Lezberg et al. 2001). Thus, liana species might also reproduce clonally when seed reproduction cannot be accomplished such as in shaded understory, which depends on the magnitude of the shade-intolerance of liana species. The role of clonal reproduction of lianas as a life history strategy could be similar to that of other clonal plants that reproduce clonally in the understory via stolons or rhizomes.

7.2 Comparison of the role of disturbance and clonal reproduction on the distribution of lianas between temperate forests and tropical forests

As mentioned earlier, the magnitude of the clonal reproduction of temperate liana species was comparable to that of lianas in tropical forests reported in the previous studies (Schnitzer et al. 2012). However, it is also important to highlight that there were some remarkable differences between temperate and tropical forests in terms of the role of clonal reproduction on life history of lianas. In the present series of studies, clonally reproduced individuals were not found based on the above-ground observation (chapters 3 and 6), while tropical lianas were found to reproduce clonally with apparent above-ground connections to each other (Schnitzer et al. 2012). This contrasting result indicates that unapparent clonal reproduction (in below-ground via stolons or rhizomes) is relatively more important for liana species in temperate forests than tropical forests. The response to the canopy gaps via clonal reproduction was also different between temperate and tropical lianas. Canopy gaps had no significant impact on the distribution nor the magnitude of clonal reproduction of temperate liana species, but rather, seed reproduction seemed to require canopy gaps to establish (chapters 3, 4 and 5), while tropical lianas are reported to respond to canopy gaps with clonal reproduction (Ledo and Schnitzer 2014). These differences could be explained by the different strategies of clonal reproduction for temperate and tropical lianas as mentioned earlier. Future study of clonality on species that belongs to the same family (i.e. Fabaceae) are needed to examine above hypothesis since phylogenetic bias could be also important. In summary, clonal reproduction seemed to play contrasting role on distribution patterns for liana species in temperate and tropical forests.

Disturbance dependency is often considered as an important mechanism for survival and growth of liana species in forests, which had been shown in number of previous studies (reviewed in Paul and Yavitt 2011; Letcher 2015). Lianas in tropical forests are highly adaptive to small-scale disturbances such as canopy gaps, which maintains species diversity of lianas (Schnitzer et al. 2012). Small-scale disturbance also contributes to the formation of the distribution of lianas with rapid response via clonal growth (Ledo and Schnitzer 2014), inhibits the establishment of shade-tolerant tree species (Schnitzer and Bongers 2002; Schnitzer and Carson 2010), and reduces the forest carbon gain in tropical forests (Schnitzer and Bongers 2011; Schnitzer et al. 2014). Conversely, light environment gradient caused by naturally occurred gaps in temperate forests often have little impact on liana abundance and distribution (Gianoli et al. 2010; 2012; Chapter 4), although the relations between canopy gaps and liana distribution in temperate forests are much less explored than tropics. On the other hand, large-scale disturbances such as clear cutting tend to have smaller or similar effect on stem density, biomass, and species richness of lianas when compared to that of trees, which had been shown in previous studies of post-agricultural secondary forests in temperate and tropical regions (Dewalt et al. 2000; Ladwig and Meiners 2010b; Letcher and Chazdon 2012). These results are not surprising because lianas are structural parasites, which potentially allow trees to be higher in density and larger in biomass than lianas in forests. However, because lianas have high host tree preferences (Chapters 2 and 4) with negative impact on trees (Ladwig and Meiners 2015), forest structure altered via large-scale disturbances could substantially contribute to the liana community structure and distribution patterns of lianas in both temperate and tropical forests (Chapter 2). Furthermore, lianas may alter tree community dynamics after large-scale disturbance with rapid growth and colonization, resulting an arrested succession (Tymen et al. 2016). In summary, most liana species are indeed adaptive to disturbances because 1) disturbance enhances establishment of liana seedlings that emerged from seeds and 2) disturbance allows rapid growth of lianas that climb trees. Thus, clonal growth of liana species in terms of re-sprouting may facilitate colonization to gaps due to the rapid growth of lateral shoots under plentiful of light environment. On the other hand, clonal growth with stolons or rhizomes is a common strategy to survive and persist in the dark light conditions under the

forest canopy. Thus, clonal reproduction of lianas with stolons or rhizomes are unlikely to be adaptive to canopy gap disturbances.

7.3 Applications and future directions

Because lianas are highly influential to host trees by negatively affecting tree growth and survival, fundamental ecological understanding of lianas could be used for the implications for forest management and conservation. Lianas are often problematic in forest management (e.g. timber production) because lianas often reduce tree growth and survival. Forest managers are required to conduct liana cutting to protect trees from lianas. As shown in the present study, lianas have an ability to grow horizontally via clonal growth in both understory and forest canopy (Chapter 3); thus, considering the magnitude of clonal reproduction of liana species could be significantly important for the effective management of forests. For example, it may be effective to cut not only lianas that are distributed inside the forest under management but also lianas that are distributed in surrounding area. Cutting stolons on the forest floor or in the below-ground could also be another effective way to suppress small clonal ramets that require physical connection to survive. Further study of effectiveness of the liana cutting and suppressing clonal growth is necessary for the examination of the above hypothesis. On the other hand, lianas might act as an important component in forest conservation; lianas could induce canopy gaps through negative impact on host trees with enlarged tree mortality, and promote heterogeneity from darker to brighter light condition across the closed forest canopy. Consequently, lianas might act as a potential driver for the higher species diversity in mature forests. One concern of this hypothesis is that lianas might colonize and predominate in the canopy gaps by covering the hole vegetation which is often reported in tropical forests (Schnitzer and Bongers 2011). However, because temperate liana species are less likely to colonize to canopy gaps via clonal reproduction (Chapter 4), induced canopy gaps in temperate forests may allow shade-intolerant species to establish. Both negative and positive roles of lianas in forests should be explored because fundamental ecological understanding is currently lacking, which necessitates the further ecological studies on lianas in order to facilitate the basic knowledge of lianas and their role in forest dynamics

which is essential for the application in forest management and conservation. For example, long-term ecological studies based on repeated observations on liana community would provide important insights into the evaluation of the role of lianas in forest dynamics because long-term dataset of liana and tree community are needed for the evaluation of the effect of lianas on gap dynamics and impact on tree community. Evaluation of the contribution of seed reproduction of lianas is also important for understanding life history strategy of liana species. Further studies using genetic tools will provide valuable insights into seed dispersal and pollen dispersal. Genetic tools are getting effective and powerful more than ever due to the rapid evolution of next-generation sequencing (NGS); thus, ecological studies with genetic approach could be a breakthrough for answering various research questions that remained unsolved in this study.

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