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Acclimation potential of three evergreen tree species to wind-induced water stress in an urban green-roof environment

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Abstract

We compared acclimation potential of three native, evergreen tree species to wind-exposure in an urban green-roof environment. One year after planting on the green roof, *Machilus thumbergii* retained all leaves and produced new leaves. In contrast, *Fraxinus griffithii*, and *Quercus myrsinifolia* shed all leaves but produced more new leaves than the previous year. After two years, current-year leaves of all three species had acclimated hydraulically (lower osmotic potentials at saturation and turgor loss) to wind-induced water stress and leaf number increased to four to eight times the initial amount. When trees were exposed to simulated winds in a greenhouse experiment, osmotic adjustment was observed for current-year leaves of *M. thumbergii*, whereas leaves of *F. griffithii* and *Q. myrsinifolia* had hydraulic traits more vulnerable to wind-induced water stress (higher osmotic potential and relative water content at turgor loss). We inferred that, *M. thumbergii* invests in hydraulic acclimation to retain current-year leaves in response to increased wind, whereas *F. griffithii* and *Q. myrsinifolia* allocate resources to new leaf production. Our results suggest both strategies achieve tree-level acclimation to wind exposure.

Keywords: leaf dynamics, leaf hydraulics, osmotic adjustment, turgor loss

INTRODUCTION

Green roofs are a popular aesthetic component of urban design (Brenneisen, 2004; Yuen and Hien, 2005). Green roofs can mitigate heat island effects (Lin and Lin, 2011; Srivanit and Hokao, 2013; Takebayashi and Moriyama, 2007), reduce surface water runoff (Carter and Jackson, 2007; Getter et al., 2007), sequester carbon (Getter et al., 2009), and help solve various urban environmental issues (Oberndorfer et al., 2007 Dunnett and Kingsbury, 2008; Vijayaraghavan, 2016). However, harsh growing conditions, such as shallow substrate, limited water availability, exposure to wind and radiation, limit the number of plant species that can be used on green roofs (Durhman et al., 2006; Nagase and Dunnett, 2010; Sendo et al., 2010). Drought-resistant herbaceous species such as succulent plants (e.g., *Sedum* spp.) and CAM (Crassulacean Acid Metabolism) plants are a popular choice for green roofs (Butler and Orians, 2011; Getter and Rowe, 2008; Snodgrass and Snodgrass, 2006). Long-term monitoring, however, has shown that planted species are eventually displaced by ruderal vegetation as succession proceeds (Kohler, 2006).

Planting native woody species can improve ecological integrity and long-term sustainability of urban forests and green space (Almas and Conway, 2016; Hotta et al., 2015; Ordonez and Duinker, 2012). To apply this to green roofs, we must select native species adapted to the harsh growing conditions of rooftop environments. Wind exposure is especially severe on rooftops of downtown areas because tall buildings amplify winds via downdraught, eddy, and channeling effects (Gromke, 2011; Offerle et al., 2007; Oke et al., 1989; Tominaga et al., 2008). Strong winds can have adverse effects on urban trees, causing physical damage and physiological stress (Duryea et al., 2007; Francis, 2000). Combined with limited access to soil water, high evaporative demand caused by wind exposure could lead to extreme water stress for urban trees, having deleterious effects on physiological function (Bijoor et al., 2012； Kagotani et al., 2013; Osone et al., 2014; Whitlow et al., 1992). Therefore, when selecting tree species for use on green roofs in built-up areas, we must evaluate their acclimation potential to wind-induced water stress.

Wind can have variable effects on canopy evapo-transpiration and leaf water-relations (Barnard and Bauerle, 2016; Huang et al., 2015). While some studies have found decreasing transpiration rates with increasing wind speed (e.g., Dixon and Grace, 1984), strong winds increase leaf boundary layer conductance and vapor pressure deficit (Daudet et al., 1999), which can exacerbate water loss by transpiration (Kim et al., 2014; Martin et al., 1999). Trees leaves acclimate to wind-induced water stress in various ways. Immediate and short-term responses include stomatal control, osmotic and elastic adjustments to maintain leaf water potential, and increased hydraulic conductivity (Iogna et al., 2013; Telewski, 1995; White et al., 2000). In desert shrub species exposed to wind, leaf water potentials were similar between windward and leeward sides of the canopy, indicating that homeostasis of leaf water status was achieved by acclimation of leaf hydraulic traits (Iogna et al., 2013). Morphological acclimation of tree leaves to wind exposure include smaller leaf area, shorter internode lengths, greater leaf mass per area, etc. (e.g., Garcia-Verdugo et al., 2009). Leaves and branches, which are physically damaged in high winds need to be replaced (Dewit and Reid, 1992; Van Gardingen et al., 1991; Vogel, 2009). Many tree species adapted to wind-prone environments recover after wind damage by resprouting (Bellingham, 2000; Duryea et al., 2007; Lawton and Putz, 1988; Putz and Brokaw, 1989). These observations suggest that while some species may invest in physiological acclimation of existing leaves to wind, adaptation to strong wind may select for leaf shedding and replacement.

In this study, we compared acclimation potential to a wind-exposed, urban rooftop environment of three native evergreen tree species commonly used as street trees in Japan, *Machilus thunbergii* Sieb. Et Zucc. (Japanese bay, Lauraceae), *Fraxinus griffithii* C.B. Clarke (Himalayan ash, Oleaceae), and *Quercus myrsinifolia* Blume (Japanese white oak, Fagaceae). *M. thunbergii* is an evergreen tree (15-30 m height) originating in warm-temperate to sub-tropical regions of Asia (Wu et al., 2006). In Japan, this species often grows along shorelines and is resistant to salt and wind (Department of Parks and Recreation, 2001). *F. griffithii* is an evergreen, pioneer tree (10-20 m height), which grows on old lava flows and open rain forest in sub-tropical to warm-temperate Asia. In Japan it is grown as an ornamental tree that is drought-resistant and highly resilient to typhoon damage (Department of Parks and Recreation, 2001). *Q. myrsinifolia* is an evergreen tree (10-20 m height), which grows in lucidophyllous forests of warm-temperate Japan. As an ornamental tree, it is resistant to heat, salt, and wind (Department of Parks and Recreation, 2001). The leaf phenology of *M. thunbergii* and *Q. myrsinifolia* is flush-type leaf emergence with a short shoot elongation period (ca. 15 days, Nitta and Ohsawa, 1997) and leaves take up to 50 days to fully mature (Miyazawa et al., 1998)). *F. griffithii* has successive leaf emergence with a long shoot elongation period (up to 100 days, personal observation). Here, we focused on leaf turnover and hydraulic traits to infer each species' physiological acclimation potential to wind-induced water stress. We also conducted a greenhouse experiment where trees were exposed artificial wind and compared results with observations in the field.

MATERIALS AND METHODS

The study site is located in Shinjuku Ward, Tokyo, Japan (35.7°N, 139.7°E, elevation 29.2 m). According to the Japan Meteorological Agency database (www.data.jma.go.jp), annual mean temperature and total precipitation in Tokyo during 1996−2015 were 15.8-17.3 ˚C and 1302-1857 mm, respectively. Soil collected from a near-by riverbank was spread over a 30×50 m area on the rooftop of a two-story building in 2011 (hereafter "green roof"). Now the green roof is dominated by ruderal herbaceous species. A 40-story (193-m) building stands to the west of the green roof and two buildings (11- and 14-stories) stand to the east (Fig. 1a). The north and south sides are open to the street. Thus, prevailing winds are northerly and southerly.

Four-year-old, potted trees (170−250 cm height) of *M. thunbergii*, *F. griffithii*, and *Q. myrsinifolia* were placed on the green roof at 3-m spacing in Nov 2016 (Fig. 1b c). All trees were watered regularly. Wind direction and speed were recorded using a propeller-type wind logger (WDL-01 WindLog, RainWise Inc., Trenton, ME, USA). We also set up wind loggers at ground level on the north side of the building as a reference.

In 2018, two-year-old potted trees (50-100 cm height) of the same three species as above were placed in a greenhouse at the Tsukuba Research Institute of Sumitomo Forestry Co. Ltd., in Tsukuba, Japan (36.1°N, 140.0°E, elevation 28 m) and exposed to experimental wind generated by electric fans (SFJ-300D1-1M Portable Exhaust Fan for strong wind and SF-45VS-1VP2 Stand-type Factory Fan for mild wind, Suiden Inc., Osaka, Japan). Wind speeds and duration for the experiment were based on data obtained from the green roof in 2017 (Table 1).

Leaf retention and shedding

We marked three current-year shoots on each tree on the green roof for measurement. Number of current-year leaves and leaf scars were counted on Nov 2016 to estimate the total number of leaves in spring 2016. Leaves on all shoots originating from each marked shoot were counted in Nov 2017 and Nov 2018.

Leaf hydraulic traits

To measure leaf hydraulic traits, we obtained the pressure-volume curve using the bench-drying approach to the pressure-volume technique (Boyer, 1967; Schulte and Hinckley, 1985; Tyree and Hammel, 1972). Using a pressure chamber (Model 1505D, PMS Instruments, Corvallis, USA), we repeatedly measured leaf water potential (Ψ_L, MPa) and fresh weight (g) of leaves (repeat pressurization method, Hinckley et al., 1980; Parker and Colombo, 1995; Ritchie and Roden, 1985). Care was taken to increase and decrease the pressure in the chamber very slowly (less than 0.01 MPa s^{-1}) so as not to damage the leaves. Measurements were made in Nov of 2016, 2017, and 2018 for trees on the green roof and in Sep 2018 for trees in the greenhouse.

The pressure-volume curves were analyzed to calculate osmotic potential at saturation and turgor loss (Ψ_{sat} and Ψ_{tlp}, respectively) and relative water content at turgor loss (RWC_{tlp}) following methods described in Schulte and Hinckley (1985). The linear part of the curve was used to calculate leaf capacitance (C) and modulus of elasticity (ε) according to Woodruff et al. (2009). Lower Ψ_{sat} reflects osmotic adjustment to water stress, while lower Ψ_{tlp} and RWC_{tlp} reflect greater drought tolerance of leaves (Bartlett et al., 2014). Among leaf hydraulic traits, ε and C are often negatively correlated because more rigid cell walls (high ε) enable leaves to retain water, while reducing water storing capacity (low C). Therefore, high ε represents tolerance to water stress, while high C represents stress avoidance strategy (Sack and Holbrook, 2006).

Statistical analysis

For trees on the green roof, we compared leaf number and hydraulic traits among observation years for each species using repeated measures analysis of variance with year as a fixed factor. Because we sampled multiple leaves from each tree, trees were used as the blocking variable and the interaction term “year × block” was used as the error term in the model. In the wind exposure experiment we compared leaf hydraulic traits between wind-exposed and control trees of each species in a *t*-test. All statistical tests were conducted using JMP software (ver. 10, SAS Inc.).

RESULTS

Wind gusts up to 19.7 m s^{-1} were observed on the green roof (Table 2). Both mean and maximum velocities were greater than at ground level, indicating that the green roof is exposed to strong winds induced by the surrounding tall buildings.

M. thunbergii retained most of its leaves over the first winter (Nov 2016 – Mar 2017), while *F. griffithii* and *Q. myrsinifolia* shed all leaves (Fig. 2). In 2017, *M. thunbergii* produced about the same number of new leaves as the previous year, whereas *F. griffithii* and *Q. myrsinifolia* produced significantly more new leaves (Fig. 3). In 2018, *Q. myrsinifolia* shed most of its leaves, but produced significantly more leaves than in the previous year. At end of the study, all three species had 400-800% of the number of leaves in spring 2016.

For trees on the green roof, we observed changes in hydraulic traits of current-year leaves reflecting acclimation during the two-year study period (Table 3). For *M. thunbergii*, both Ψ_{sat} and Ψ_{tlp} decreased after the second year (Nov 2018), indicating osmotic adjustment and greater drought tolerance of leaves. For *F. griffithii*, Ψ_{sat} increased after the first year (2017), but decreased in the second year (2018). Similarly, for *Q. myrsinifolia*, Ψ_{tlp} increased after the first year, but C increased. After the second year, $\mathrm{RWC}_{\mathrm{tlp}}$ and Ψ_{tlp} decreased, while ε decreased.

In the wind-exposure experiment, we observed differences in hydraulic traits of current-year leaves between wind-exposed and control trees reflecting short-term leaf acclimation during the growing season (Table 4). For *M. thunbergii*, Ψ_{sat} was lower for wind-exposed trees indicating osmotic adjustment in response to wind-induced water stress. For *F. griffithii*, $\mathrm{RWC}_{\mathrm{tlp}}$ and Ψ_{tlp} were higher for wind-exposed trees, indicating lower drought tolerance, i.e., lack of acclimation. Similarly, for *Q. myrsinifolia*, Ψ_{tlp} was higher for wind-exposed trees. For all three species, there was no significant difference in C nor ε between wind-exposed and control trees.

DISCUSSION

Our results indicated that exposure to wind makes growing conditions on the green roof more stressful than at ground level. The three study species showed different responses to wind-induced stress. *M. thunbergii* was stress tolerant. It retained most leaves after the first year, continued to produce new leaves, and current-year leaves acclimated hydraulically after the second year. In contrast, *F. griffithii* and *Q. myrsinifolia* were resilient, shedding all leaves over the first winter. New-leaf production increased for both species in the following years, although to a lesser extent in *Q. myrsinifolia* than *F. griffithii*. Although leaf capacitance increased for *Q. myrsinifolia*, current-year leaves of both species were not hydraulically acclimated until after the second year. Results of the wind-exposure experiment agreed with observations on the green roof. Current-year leaves of wind-exposed *M. thunbergii* trees acclimated to wind-induced water stress by osmotic adjustment (lower Ψ_{sat}). In contrast, wind-exposed leaves of *F. griffithii* and *Q. myrsinifolia* were less tolerant of water stress (higher $\mathrm{RWC}_{\mathrm{tlp}}$ and Ψ_{tlp}).

Reductions in $\mathrm{RWC}_{\mathrm{tlp}}$ and Ψ_{tlp} are common responses of plants to drought allowing leaves to maintain physiological function over a greater range of hydraulic conditions (Bartlett et al., 2014). Reduction of Ψ_{tlp} is often observed in urban trees exposed to drought or water-stressed conditions (e.g., Sjoman et al., 2015) and thus, leaf turgor loss point is proposed as a measure for evaluating drought tolerance of urban trees (Banks and Hirons, 2019; Sjoman, 2018). Osmotic adjustment is an effective short-term acclimation response to water stress, which has been observed under drought conditions in both forest and urban trees (e.g., Inoue et al., 2017; Sjoman et al., 2015). Osmotic adjustment, however, involves costs such as production of soluble carbohydrates for increasing osmotic potential (Bartlett et al., 2012; Kuang et al., 2017; McCree, 1986; Wang and Stutte, 1992). Our results suggest that *M. thunbergii* invests in short-term wind acclimation to retain current-year leaves, while *F. griffithii* and *Q. myrsinifolia* invest in new-leaf production. Although their strategies differed, current-year leaves of the three species had acclimated to conditions on the green roof after the second year and had four to eight times more leaves than at the beginning of the study.

The amount of time required for leaves to acclimate to changes in environmental conditions varies among evergreen species depending on the pattern of leaf emergence and elongation (Miyazawa et al., 1998). For example, when understory saplings of evergreen species were transplanted from high- to low-light environment, leaf-level acclimation potential was high for *Cinnamomum japonicum* Sieb. ex Nakai (Lauraceae), whereas it was low for *Quercus glauca* Thunb. ex Murray (Fagaceae) (Ishii and Ohsugi, 2011). Leaves of *Q. glauca* retained physiological traits from the previous light environment (carry-over effects), but were not shed. Such differences in acclimation potential of leaves may be attributed to patterns of leaf emergence and maturation. Species whose leaves mature slowly are able to acclimate to changing environmental conditions within a growing season, while such changes may be stressful for species whose leaves mature early rendering low acclimation potential (Ishii and Ohsugi, 2011; Miyazawa et al., 1998).

Conclusions

Future climate change scenarios predict more skewed spatial-temporal distribution of rainfall and more extreme droughts, which pose risks to the health of urban trees (May et al., 2013; Moore, 2011; Savi et al., 2015). Urban trees are already faced with harsh growing conditions, such as limited soil volume (Grabosky and Gilman, 2004) soil compaction (Day and Bassuk, 1994), exposure to air pollution (Takagi and Gyokusen, 2004), and limited access to ground water (Bijoor et al., 2012; Savi et al., 2015; Vico et al., 2014). When selecting tree species for urban greening, we must take into account not only their native distribution range, but also short- and long-term acclimation potential to stressful growing conditions induced by urban environments, as well as future climate change. Our study showed that, although the three study species responded differently to short-term wind exposure, all of them were able to eventually acclimate at the individual level to wind-induced water stress. Our results suggest that *M. thunbergii* is a tolerant tree for planting in urban, wind-exposed environments. *F. griffithii* and *Q. myrsinifolia* may also be suitable if watered sufficiently to avoid initial leaf loss due to water stress. Similar studies comparing various native trees are needed to select species suitable for future use in urban greening.

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Table 1. Timeline of wind speed and duration used for the wind exposure experiment.

Month	Mar	Apr	May-Aug
Strong wind	4 m s^{-1}, 4 h d^{-1}	4 m s^{-1}, 2 h d^{-1}	4 m s^{-1}, 8 h d^{-1}
Mild wind	10 m s^{-1}, 4 h d^{-1}	10 m s^{-1}, 6 h d^{-1}	10 m s^{-1}, 8 h d^{-1}
Control	No wind	No wind	No wind

Table 2. Wind velocities of the green roof and at ground level during 2017.

Month	Site	Mean daily (m s^{-1})	Max daily (m s^{-1})	Monthly max (m s^{-1})	Gust frequency* (%)
Mar	Roof	2.52	8.10	18.0	7.92
	Ground	0.99	5.37	8.1	0.00
Apr	Roof	1.78	9.60	19.7	3.70
	Ground	0.69	4.96	11.1	0.11
May	Roof	1.55	7.20	16.4	0.39
	Ground	0.43	3.89	6.6	0.00
Jun	Roof	2.02	9.80	18.6	2.19
	Ground	0.63	4.28	7.0	0.00

* Gust frequency: Percent occurrence of winds greater than 10 (m s^{-1}).

Table 3. Hydraulic traits of current-year leaves of trees on the green roof.

Species	Year	Ψ_{sat} (MPa)	RWC_{tlp}	Ψ_{tlp} (MPa)	C (mol m^{-2} MPa^{-1})	ε (MPa)
Machilus	2016	-1.56 ± 0.097	0.936 ± 0.006	-2.18 ± 0.029	0.214 ± 0.043	29.7 ± 1.71
	2017	-1.33 ± 0.039	0.947 ± 0.004	-2.06 ± 0.059	0.258 ± 0.031	30.7 ± 3.85
	2018	-1.95 ± 0.136 **	0.934 ± 0.006	-2.34 ± 0.047 **	0.298 ± 0.027	31.0 ± 2.29
Fraxinus	2016	-1.76 ± 0.122	0.861 ± 0.043	-2.21 ± 0.179	0.408 ± 0.093	18.6 ± 3.59
	2017	-1.30 ± 0.085 *	0.901 ± 0.009	-1.96 ± 0.119	0.779 ± 0.250	14.9 ± 1.02
	2018	-1.84 ± 0.076 **	0.888 ± 0.012	-2.29 ± 0.061	0.401 ± 0.035	19.8 ± 2.16
Quercus	2016	-1.67 ± 0.083	0.897 ± 0.009	-2.39 ± 0.059	0.240 ± 0.048	21.4 ± 2.15
	2017	-1.53 ± 0.103	0.906 ± 0.014	-2.09 ± 0.044 **	0.287 ± 0.025 *	19.7 ± 1.02
	2018	-1.83 ± 0.071	0.870 ± 0.004 *	-2.34 ± 0.055 **	0.352 ± 0.041	15.0 ± 1.11 *

Ψ_{sat}: osmotic potential at saturation, RWC_{tlp}: relative water content at turgor loss, Ψ_{tlp}: osmotic potential at turgor loss, C: leaf capacitance, ε: modulus of elasticity. Values are mean ± one standard error. Asterisk indicates significant difference from previous year (* $P < 0.05$, ** $P < 0.01$).

Table 4. Hydraulic traits of current-year leaves of trees in the wind exposure experiment.

Species	Treatment	Ψ_{sat} (MPa)	RWC_{tlp}	Ψ_{tlp} (MPa)	Capacitance (mol m^{-2} MPa^{-1})	ε (MPa)
Machilus	Control	-1.46 ± 0.074	0.950 ± 0.006	-2.03 ± 0.091	0.246 ± 0.020	28.2 ± 1.90
	Wind	-1.85 ± 0.126 *	0.944 ± 0.006	-2.23 ± 0.005	0.287 ± 0.030	37.0 ± 4.02
Fraxinus	Control	-1.85 ± 0.074	0.890 ± 0.074	-2.29 ± 0.006	0.380 ± 0.029	18.9 ± 0.297
	Wind	-1.55 ± 0.147	0.910 ± 0.004 *	-2.09 ± 0.057 *	0.386 ± 0.028	18.1 ± 1.91
Quercus	Control	-2.02 ± 0.141	0.903 ± 0.011	-2.39 ± 0.037	0.239 ± 0.013	24.64 ± 1.30
	Wind	-1.67 ± 0.080	0.920 ± 0.013	-2.18 ± 0.052 *	0.186 ± 0.019	25.12 ± 3.28

Variables are as in Table 3. Values are mean ± one standard error. Asterisk indicates significant difference from control (* $P < 0.05$, ** $P < 0.01$).

Figure captions

Fig. 1. Bird's eye view from the northeast of the study site (a). The green area on the rooftop of the two-story building (arrow) is the green roof. Two-year-old potted saplings of three species were placed on the green roof at 3-m spacing for the study (b). (c) Layout of the pots and arrangement of species.

Fig. 2. Changes in appearance of saplings of three species on the green roof during the study period.

Fig. 3. Changes in leaf number of trees on the green roof. Leaf retention rate is the number of leaves on the measured shoot relative to spring 2016. Error bars indicate one standard deviation. Asterisk (*) indicates significantly more current-year leaves produced compared to previous year ($P < 0.05$).

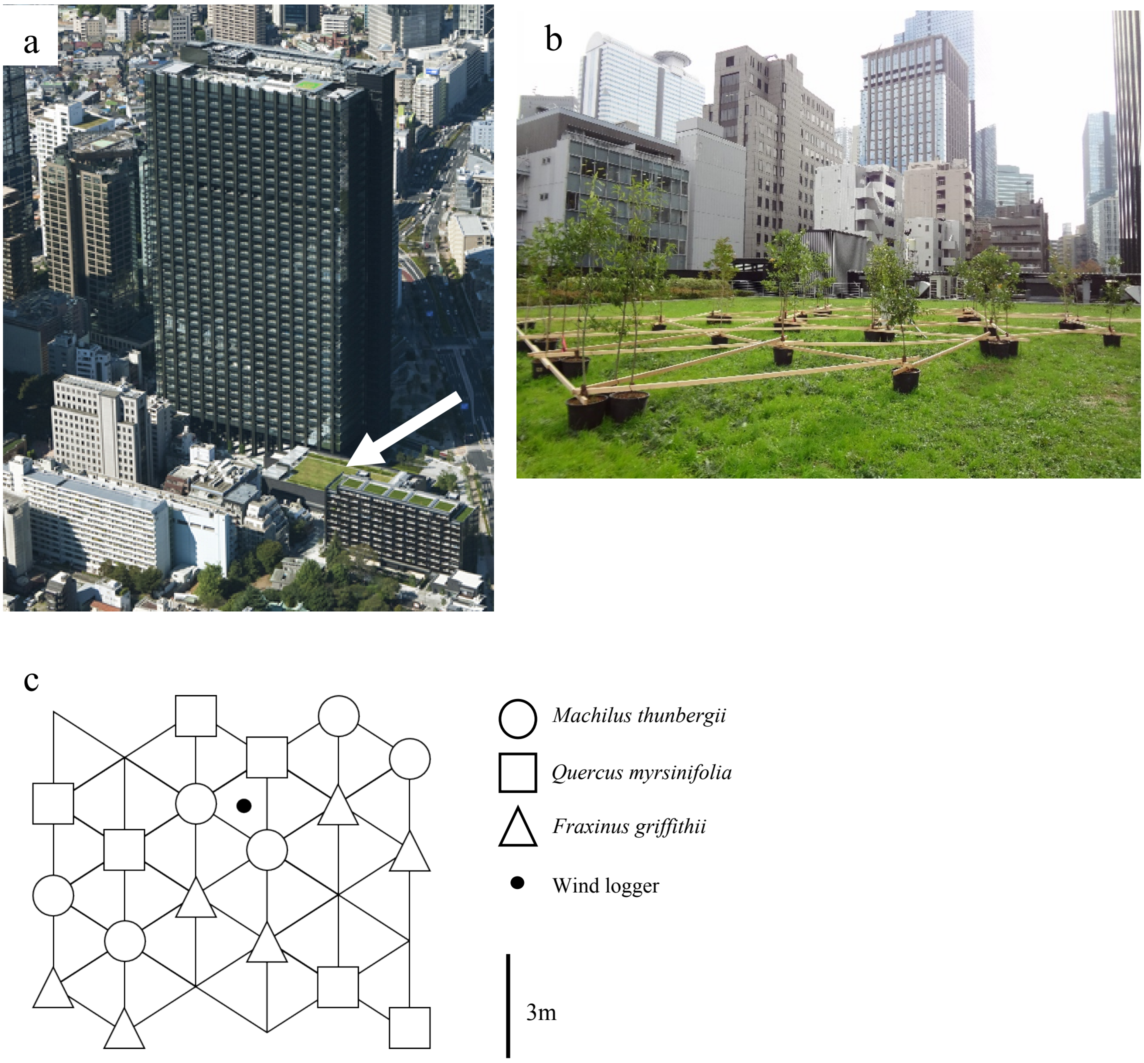

a
b
c
Machilus thunbergii
Quercus myrsinifolia
Fraxinus griffithii
Wind logger
3m

Fig. 1.


Nov 2016
Mar 2017
May 2017
Nov 2018
Machilus
Fraxinus
Quercus

Fig. 2.

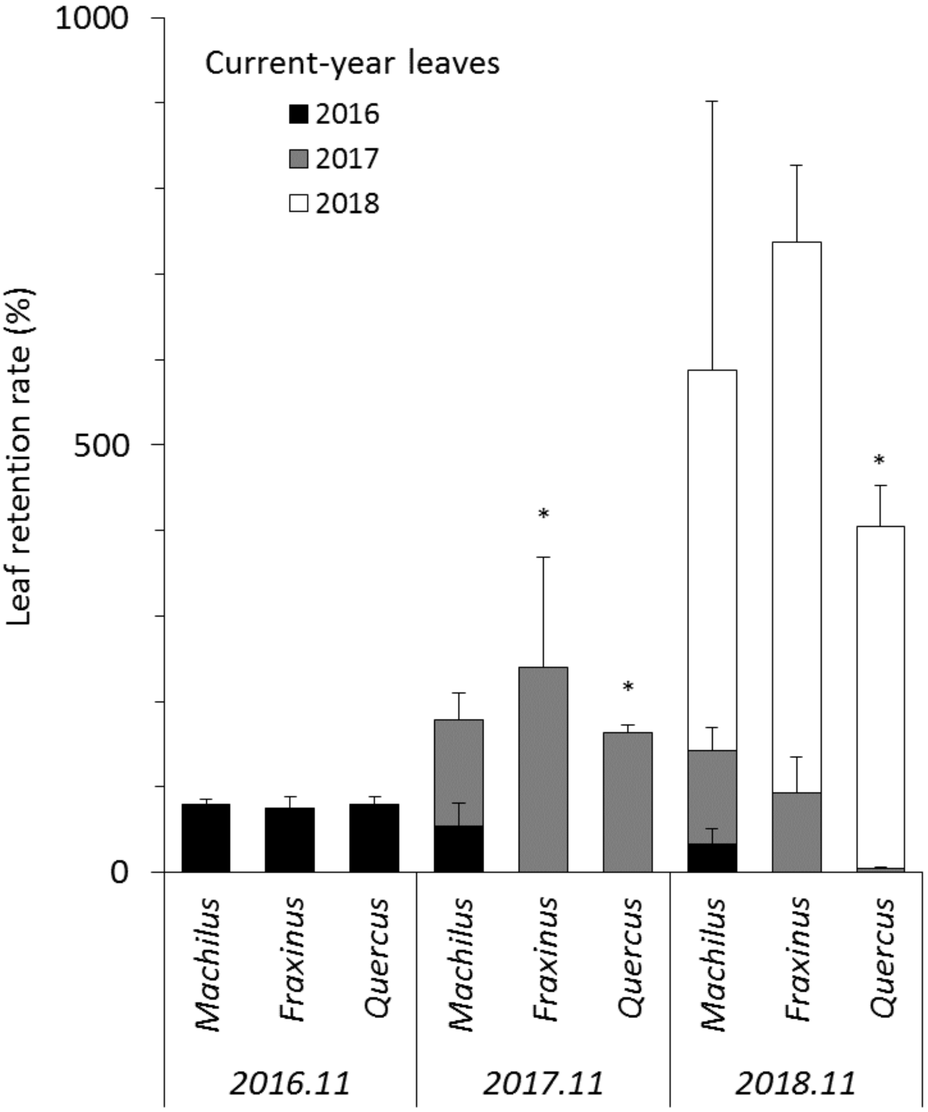
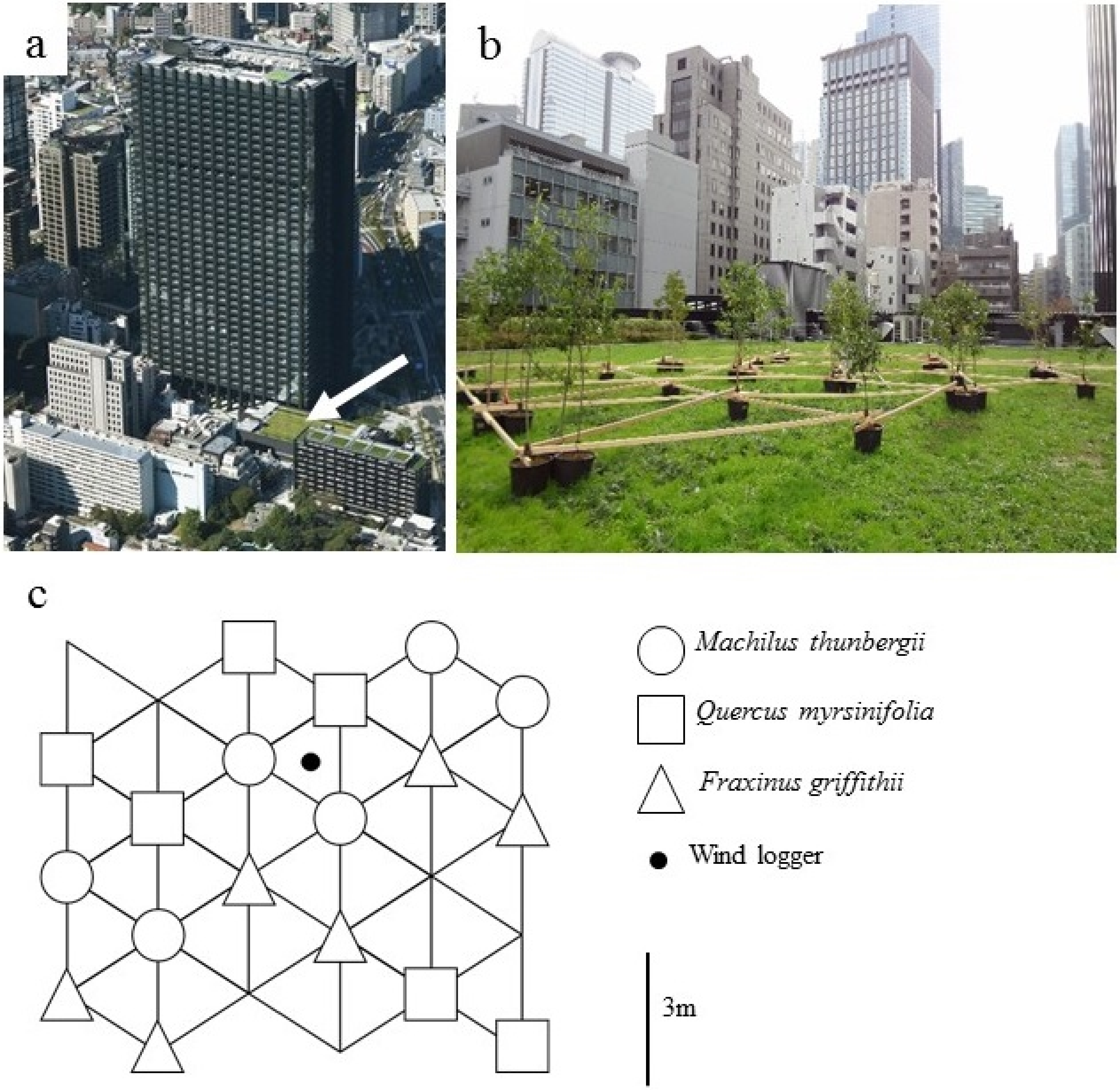
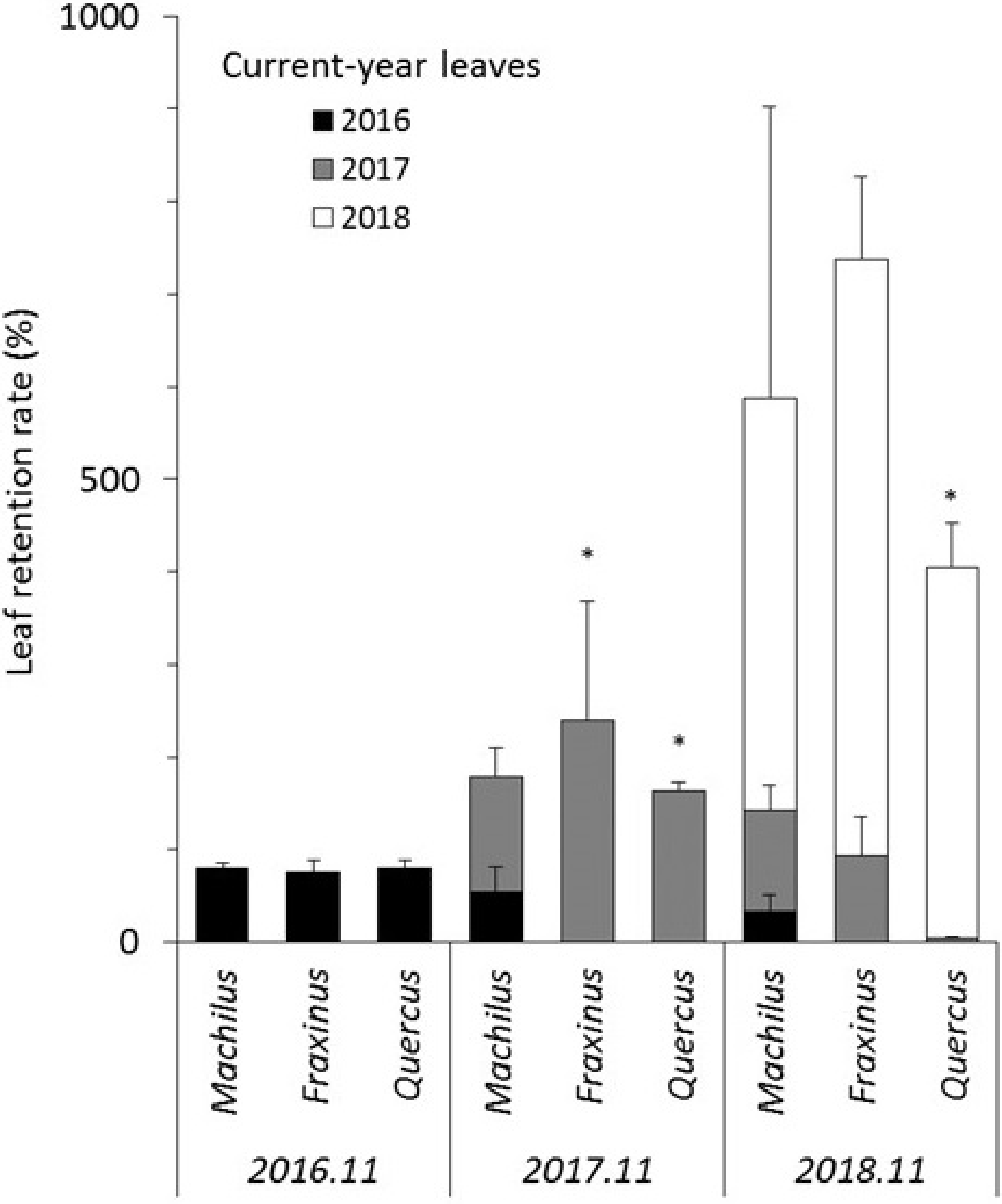

Leaf retention rate (%)
1000
500
0
Current-year leaves
■ 2016
▨ 2017
□ 2018
*
*
*
Machilus
Fraxinus
Quercus
Machilus
Fraxinus
Quercus
Machilus
Fraxinus
Quercus
2016.11
2017.11
2018.11

Fig 3.


a
b
c
Machilus thunbergii
Quercus myrsinifolia
Fraxinus griffithii
Wind logger
3m


Nov 2016
Mar 2017
May 2017
Nov 2018
Machilus
Fraxinus
Quercus


1000
500
0
Leaf retention rate (%)
Current-year leaves
■ 2016
■ 2017
□ 2018
*
*
*
Machilus
Fraxinus
Quercus
Machilus
Fraxinus
Quercus
Machilus
Fraxinus
Quercus
2016.11
2017.11
2018.11