Manuscript type: Original article

Title: Stand-level windthrow patterns and long-term dynamics of surviving trees in natural secondary stands after a stand-replacing windthrow event

Authors: Masato Shibuya and Satoshi Ishibashi

M. Shibuya: Research Faculty of Agriculture, Hokkaido University, Sapporo 060-8589, Japan

S. Ishibashi: Hokkaido Research Center, Forestry and Forest Products Research Institute, 7 Hitsujigaoka, Sapporo 062-8516, Japan

Corresponding author: Masato Shibuya

Research Faculty of Agriculture, Hokkaido University, Sapporo 060-8589, Japan

TEL: +81-11-706-3346, FAX: +81-11-706-2531, E-mail: shibuya@for.agr.hokudai.ac.jp

Abstract: We examined typhoon windthrow patterns in stand-scale permanent plots within three natural forests and the long-term dynamics of surviving trees in two of these plots. The aim was to verify whether pre-disturbance composition and structure affected windthrow damage and stand recovery. The stands, which were in Hokkaido, the northernmost main island of Japan, differed in pre-disturbance composition (coniferous, mixed and broadleaved stands) and structure, and the basal area losses by the windthrow event were 81–93%. Tree mortality was significantly related to tree size (diameter at breast height) and species. The windthrow patterns differed among the three stands; and, windthrow severity was affected by the pre-disturbance composition and structure. The mortality of trees that survived the windthrow event was ~60% in the two plots. The surviving trees comprised a majority of the canopy layer in the secondary stands. The relative basal area of surviving trees decreased rapidly with increasing tree density in the stand initiation stage but differed between plots. Consequently, the pre-disturbance composition and structure influenced windthrow severity, stand recovery, and secondary succession in the recovered stands.

Introduction

Wind disturbances are major events that affect the stand dynamics and ecological functions of temperate forests (Rammig et al. 2006). Evaluating wind damage risk is important for maintaining the ecological functions of forest stands and avoiding economic loss during forest management. Various factors, including tree species, size, density, and shape, disturbance history, wood characteristics, soil conditions, weather, topography, and altitude, affect the wind damage risk to trees and stands (Peterson 2004). These factors can be classified into biotic factors related to tree characteristics, stand structure, and composition and abiotic factors related to soil, weather, and topography.

Large-scale analyses at regional or landscape scales have often detected significant influences of abiotic factors on the windthrow risk of trees and stands (e.g., Boose et al. 1994; Mayer et al. 2005), along with those of biotic factors. However, the influences of abiotic factors are variable among studies due to interactions between abiotic and biotic factors and interactions among abiotic factors (Peterson 2004; Mayer et al. 2005; Evans et al. 2007). In addition, many abiotic factors (e.g., topography, slope aspect, and soil characteristics) cannot be controlled easily. In contrast, the influences of biotic factors on windthrow risk are relatively constant. For example, the variation in windthrow damage among five natural stands in Minnesota was accounted for accurately by tree size and species (Peterson 2004). Biotic factors such as tree species, density, and size and shape (e.g., slenderness ratio) can be controlled by forest management. Therefore, stand-level windthrow risk may be reduced by improving our understanding of the relationships between the windthrow risk and biotic factors, and then controlling biotic factors through forest management.

Many biotic factors influence the risk of stand-level windthrow events. For example, the windthrow risk to trees has been shown to be positively related to stem diameter (Canham et al. 2001; Rich et al. 2007) and tree height (Foster 1988; Schmidt et al. 2010). In addition, canopy trees are more vulnerable to windthrow events than are sub-canopy trees and saplings (Canham et al. 2001; Webb and Scanga 2001). Moreover, coniferous species are generally more vulnerable to windthrow events than deciduous broadleaved species (Hanson and Lorimer 2007; Schmidt et al. 2010; Albrecht et al. 2012), and conifers with slender stems (i.e., high slenderness ratio) are particularly vulnerable (Schmidt et al. 2010; Shibuya et al. 2011). Thus, the composition of forest stands affects the windthrow risk, and conifer-dominated stands are more vulnerable (Jalkanen and Mattila 2000; Valinger and Fridman 2011). Consequently, the stand-level windthrow risk is presumably influenced by the pre-disturbance forest composition and structure. Furthermore, Peterson (2000) noted that pre-disturbance composition and structure affected secondary succession after a wind disturbance.

During severe windthrows, understory trees and saplings are frequently damaged by falling canopy trees (Brokaw and Walker 1991; Clinton and Baker 2000), although many ultimately survive (Canham et al. 2001; Swanson et al. 2011). Such surviving trees and saplings contribute to rapid stand recovery (Lorimer and White 2003; Plotkin et al. 2013). Large-sized trees are advantageous for growth after a windthrow event because of their competitive advantage (Kulakowski and Veblen 2003). Most canopy trees are removed by stand-replacing windthrow events, forming large openings in the canopy, allowing the surviving trees to dominate the canopy layer (Turner et al. 1998). However, few studies have analyzed in detail the long-term survival and growth of these surviving trees after a stand-replacing windthrow event.

In this study, we used stand data from three permanent plots located in the central southern area of Hokkaido, the northernmost main island of Japan. The permanent plots had been severely disturbed by a typhoon in September 1954. Kosugi et al. (2016) and Toda and Shibuya (2017) analyzed the long-term dynamics of tree density, composition, and basal area of the permanent plots during the 60 years following the stand-replacing windthrow event. In addition, these studies suggested that surviving trees and saplings might contribute to stand recovery from windthrow damage. To understand the stand recovery process of the plots from the windthrow damage in greater detail, we analyzed the stand-level windthrow damage (reverse of tree survival) and the long-term dynamics of the survival and growth of surviving trees in relation to pre-disturbance composition and structure. Through these analyses, we examined the influences of biotic factors such as tree species and size on windthrow damage and the contribution of surviving trees to stand recovery in natural secondary stands after a windthrow disturbance.

Sites and methods

Sites

One of three plots, the Tomakomai plot (42°43´N, 141°27´E; area: 0.50 ha), established in 1956, was a coniferous stand dominated by *Picea jezoensis* Carrière and *Abies sachalinensis* Mast. before the windthrow (Kosugi et al. 2016), and lost 93% of its basal area (BA) as a result of the windthrow (Table 1). In 2014, 60 years after the windthrow, this plot was a deciduous broadleaved stand (i.e., 81% of the BA was covered by broadleaved trees) dominated by *Quercus crispula* Blume and *Magnolia obovata* Thunb. (Kosugi et al. 2016). The Jozankei plot (42°57´N, 141°12´E; area: 0.49 ha), also established in 1956, was a mixed stand that lost 86% of its BA due to the windthrow event (Table 1). In 2014, the plot was a deciduous broadleaved stand (i.e., 87% of the BA was covered by broadleaved trees) (Kosugi et al. 2016). Finally, the Tomakomai Experimental Forest (TEF) plot (42°40´N, 141°36´E; area: 0.25 ha; No. 2 plot in Toda and Shibuya 2017), established in 1958, was a deciduous broadleaved stand that lost 81% of its BA in the windthrow event (Table 1) and recovered as a deciduous broadleaved stand (i.e., almost 100% of the BA was covered by broadleaved trees) by 2014 (Toda and Shibuya 2017). The Tomakomai and TEF plots were on near-horizontal slopes with shallow soil of volcanic origin (available rooting depth: ~15 cm), while the Jozankei plot was on a slope of ~35° and had mesic brown forest soil (available rooting depth: ~50 cm). All sites had good soil drainage. The three plots were located within 50 km of one another, and the mean annual temperature and precipitation ranges were 6.7°C (Tomakomai) to 8.9°C (Jozankei) and 1107 mm (Jozankei) to 1766 mm (Tomakomai), respectively (Kosugi et al. 2016; Toda and Shibuya 2017). The windthrown trees in all three plots consisted of uprooted and snapped trees, which were grouped as “fallen trees” in this study. The stand condition before the windthrow in 1954 was reconstructed in 1956 for the Tomakomai and Jozankei plots and in 1958 for the TEF plot by measuring both surviving and fallen trees. The mean diameter at breast height (DBH, 1.3 m high) and species richness in the three plots were lower after the windthrow event (Table 1). The taxonomic nomenclature in this study follows that of Yonekura and Kajita (2003–).

Measurements

Surviving and fallen trees with a DBH ≥5 cm were tagged (only for surviving trees), identified, and measured for DBH in 1956 in the Tomakomai and Jozankei plots and in 1958 in the TEF plot. In addition, in the Tomakomai and Jozankei plots, the species and DBH of living trees (DBH ≥5 cm), including ingrowths, were measured 13 and 10 times at 2- to 13-year and 2- to 23-year intervals, respectively, until 2014. The TEF plot was measured using the same method nine times at 4- to 19-year intervals until 2014. DBH was measured to an accuracy of 2 cm in 1956–1966 and 0.1 cm in 1971–2014 in the Tomakomai and Jozankei plots. In the TEF plot, DBH was measured to an accuracy of 2 cm in 1958, and 0.1 cm thereafter. In the Jozankei plot, because of the long interval between the last and second-last measurements (23 years: 2014–1991) and the fact that most trees had lost their tags, individual data for the surviving trees were only available for 1956–1991. These data were available for the Tomakomai plot for 1956–2014. No tree-level data were available for the surviving trees in the TEF plot because of the long interval between the first and second measurements (19 years: 1958–1977). Consequently, data on windthrow damage and dynamics of surviving trees after the windthrow were available for three and two plots, respectively.

Analyses

Logistic regression was used to analyze the windthrow patterns of the three permanent plots. A binary variable for tree status (surviving: 0, fallen: 1) was analyzed by logistic regression using species and DBH as explanatory variables. Tree species with fewer than 20 individuals before the windthrow were grouped into an “Others” category. No interaction term between DBH and species was included in the logistic regressions because the DBH distributions differed considerably among species in the plots. The analyses were performed using R i386 3.0.2 (R Core Team 2013).

In the Tomakomai plot, 10 coniferous and 41 broadleaved trees in a 0.5-ha plot survived the windthrow event in 1954. In the Jozankei plot, 48 coniferous and 50 broadleaved trees in a 0.49-ha plot survived. We examined the survival rates and DBH distributions in the Tomakomai and Jozankei plots in 2014 and 1991, respectively, as well as temporal trends in the relative BA of the surviving trees. The relative BA of surviving trees, which represents the quantitative contribution of the trees to the stand BA, is defined as follows:

$$\text{Relative BA (\%)} = \frac{\textit{Total basal area of alive surviving trees}}{\textit{Stand basal area}} \times 100.$$

We examined the similarity in species composition between pre- and post-disturbance stands to determine whether the pre-disturbance stand condition affected secondary succession after the disturbance. We tested the compositional similarity between 1954 and 2014 for the three permanent plots using the similarity index (S) as follows:

$$S = 1 - BC$$

$$BC = \frac{\sum |x_{1i} - x_{2i}|}{\sum (x_{1i} + x_{2i})},$$

where BC is the Bray-Curtis dissimilarity, x_{1i} is the relative BA of species i in 1954, and x_{2i} is the relative BA of species i in 2014.

Results

Windthrow patterns

Tree mortality by density was highest in the Tomakomai plot (85%), followed by the Jozankei (82%) and TEF (49%) plots (Table 1). Many small trees were damaged and killed by falling canopy trees in the Tomakomai and Jozankei plots (Takei 1958), but no quantitative data were recorded. The same situation might have occurred for small trees in the TEF plot. The windthrow patterns differed among the three plots (Fig. 1). In the Tomakomai plot, DBH was not a significant variable, and mortality was significantly greater for coniferous species (conifers: 96%, broadleaved species: 71%) (Table 2a). Mortality by DBH class ranged from 50 to 100% (Fig. 1a), and was greater than ~90 % among all DBH classes except the 6–8- and 58–60-cm classes.

In the Jozankei plot, mortality depended significantly on DBH and species (Table 2b). The mortality of *A. sachalinensis* was 86%, significantly greater than that of the other species (mortality: 69%) (Table 2b), and was higher for *A. sachalinensis* than for other species in most DBH classes (Fig. 1b).

Mortality in the TEF plot was significantly and positively related to DBH, and did not differ among species (Table 2c, Fig. 1c), although the mortality by species ranged from 25 to 83%. The mortality by DBH class was scattered, and that of the 6–12-cm class was low, 30~40%. No conifers occurred in the TEF plot before the windthrow.

Survival, growth, and relative BA of surviving trees

In the Tomakomai plot, 10 conifer and 41 broadleaved trees survived the 1954 windthrow (Table 3a). However, only one conifer and 21 broadleaved trees were alive in 2014 (Table 3a); thus, the total mortality of the surviving trees in the 60 years following the windthrow was 56%. Nine of the surviving conifers died after the windthrow by 1959 (Table 4). Trees were distributed in the 6–42-cm-DBH classes in the Tomakomai plot in 2014, and the surviving trees were in the 14–40-cm classes (Table 3a). In addition, 82% of the surviving trees (18 trees) were in the large DBH class (≥26 cm) (Table 3a).

In the Jozankei plot, 48 conifer and 50 broadleaved trees survived the windthrow, and 19 conifer and 20 broadleaved trees remained alive in 1991 (Table 3b); thus, the mortality of the surviving trees was 60% between 1956 and 1991. Meanwhile, 24 conifer and 17 broadleaved trees died after the windthrow by 1959 (Table 4). In 1991, DBHs of trees were distributed in the 6–76-cm classes, and there were 18 trees in the large DBH class (≥26 cm). Overall, surviving trees accounted for 61% of the density and 76% of the BA of large trees in 1991.

Tree density increased after the windthrow in 1954 and was most abundant in 1991 in the Tomakomai and Jozankei plots (Kosugi et al. 2016). The relative BA of the surviving trees decreased rapidly with increasing tree density in the plots (Fig. 2). After 1991, the relative BA of the surviving trees in the Tomakomai plot remained stable (~10%) (Fig. 2), although the stand BA continued to increase from 1991 to 2014 (Kosugi et al. 2016). The relative BA was greater in the Jozankei plot than in the Tomakomai plot, where surviving trees accounted for 19.4% and 11.6% in 1991, respectively (Fig. 2).

The similarities (*S*) in species composition between 1954 and 2014 in the Tomakomai, Jozankei, and TEF plots were 0.25, 0.34, and 0.75, respectively.

Discussion

The windthrow patterns analyzed by logistic regression differed among the three permanent plots (Table 2); however, the influences of tree species and DBH on mortality were qualitatively invariable (i.e., a high mortality of conifers and a positive effect of DBH on tree mortality) among the plots, irrespective of differences in pre-disturbance composition and structure (Table 1). The high vulnerability of conifers to windthrow (e.g., Schmidt et al. 2010; Albrecht et al. 2012) and a positive effect of DBH on tree mortality (Canham et al. 2001; Rich et al. 2007) have been observed frequently, and the results shown in Fig. 1 are consistent with previous studies. Moreover, data on these biotic factors are readily available to estimate the stand-level windthrow risk in central southern Hokkaido.

Density- and BA-based mortality increased with pre-disturbance conifer-dominance and mean DBH (Table 1). Therefore, pre-disturbance composition and structure influenced the windthrow severity in the three permanent plots. Notably, many small trees survived in the deciduous broadleaved TEF plot (Table 1) because surviving trees would be expected to contribute to stand recovery after a stand-replacing windthrow event. For example, in a tree-pulling experiment in a hardwood stand in the northeastern United States, more than half of the trees survived the experimental hurricane disturbance (Cooper-Ellis et al. 1999). Therefore, a high survival rate may be characteristic of windthrows in temperate broadleaved forests.

Although the mortality varied among broadleaved species (25–83%) in the TEF plot, no significant interspecies differences were observed (Table 2c). The vulnerability of tree species to windthrow varies depending on the wood density (or strength) and the shade tolerance of the species (Zimmerman et al. 1994; Everham III and Brokaw 1996), and windthrow severity sometimes differs among broadleaved species (Peterson 2007; Rich et al. 2007). However, the variation in vulnerability to windthrow among broadleaved species diminished under a severe wind disturbance (Peterson 2007), probably similar to the stand-replacing windthrow event in this study.

The mortality rate of the surviving trees from the 1954 windthrow was ~60% in both the Tomakomai and Jozankei plots by 2014 and 1991, respectively (Table 3). Because few surviving trees died after 1991 in the Tomakomai plot, excluding windthrown trees in 2004 (Kosugi et al. 2016), it is likely that few surviving trees died during 1991–2014 in the Jozankei plot. The mortality of the surviving trees was particularly high during the 5 years following the windthrow event, especially for conifers; 9 of 10 conifers in the Tomakomai plot and 24 of 48 in the Jozankei plot died during this period (Table 4). In addition, 17 broadleaved trees had died by 1959 in the Jozankei plot (Table 4). Consequently, mortality was high in the 5-year-period following the windthrow. Similarly, Turner et al. (1997) described tree mortality during several years following hurricanes (i.e., delayed mortality). For example, after a cyclone disturbance in Sri Lanka, delayed mortality in the 42 months following the disturbance accounted for 20% of the total tree mortality caused by the disturbance (Dittus 1985). Furthermore, 82% of this delayed mortality occurred in the 18 months following the disturbance, and trees with substantial crown damage (≥40% of crown lost) exhibited high mortality (Dittus 1985). Many of the surviving trees in the Tomakomai and Jozankei plots were likely damaged in the crown or stem during the windthrow event, subsequently resulting in delayed mortality. In addition, insect damage might have driven delayed mortality, especially in conifers. Therefore, our findings agree with Turner et al. (1997) that delayed mortality is an important feature of wind disturbances.

In the Tomakomai plot, 82% of the surviving trees still alive in 2014 had a DBH within the ≥26-cm class, accounting for 30% of the BA of large trees. In the Jozankei plot, 46% of the surviving trees (18 of 39 trees) had a DBH within the ≥26-cm class, accounting for 76% of the BA of large trees in 1991 (Table 3b). Consequently, the surviving trees were important to stand recovery after the stand-replacing windthrow in 1954 and were major constituents of the canopy layer in the secondary stands. Compared with the Tomakomai plot, surviving trees were abundant in the Jozankei and TEF plots (Table 1). The Jozankei and TEF plots were less dominated by conifers and had smaller mean DBHs before the windthrow in 1954 (Table 1). The relative BA of surviving trees decreased rapidly with increasing tree density in the stand initiation stage in the Tomakomai and Jozankei plots (Kosugi et al. 2016), and it remained stable in the stem exclusion stage in the Tomakomai plot (Fig. 2). This indicates that surviving trees were extremely important to stand recovery in the stand initiation stage. The relative BA was greater in the Jozankei plot (19.4% in 1991) than in the Tomakomai plot (11.6% in 1991) (Fig. 2), probably because of the abundance of surviving trees in the Jozankei plot (Table 3). Furthermore, the similarity in species composition between 1954 and 2014, assessed using the similarity index (S), was greater in the TEF plot (S = 0.75) than in the Jozankei (S = 0.34) and Tomakomai (S = 0.25) plots, and the similarity was greater in stands with a greater dominance of broadleaved species in pre-disturbance composition. Consequently, pre-disturbance composition and structure affected both stand recovery and secondary succession after the windthrow in 1954 via variations in tree survival.

Conclusion

From our results, we conclude that pre-disturbance composition and structure significantly affect both the windthrow severity of natural stands, and the secondary succession of recovered stands. Surviving trees contribute greatly to stand recovery, especially in the initial stage of secondary succession. To our knowledge, this is the first detailed report of the long-term dynamics of trees following a stand-replacing windthrow event that shows that surviving trees contribute greatly to stand recovery.

However, given that surviving trees accounted for only 3% of the tree density in the recovered stands (Table 3), the dynamics of ingrowth trees, and factors influencing them, are also important to the composition and structure of recovered secondary stands.

References

Albrecht, A., Hanewinkel, M., Bauhus, J. and Kohnle, U. 2012 How does silviculture affect storm damage in forests of southern-western Germany? Results from empirical modeling based on long-term observations. *Eur. J. Forest Res.* **131**, 229–247.

Boose, E.R., Foster, D.R. and Fluet, M. 1994 Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monographs* **64**, 369–400.

Brokaw, N.V.L. and Walker, L.R. 1991 Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* **23**, 442–447.

Canham, C.D., Papaik, M.J. and Latty, E.F. 2001 Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Can. J. For. Res.* **31**, 1–10.

Clinton, B.D. and Baker, C.R. 2000 Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. *For. Ecol. Manage.* **126**, 51–60.

Cooper-Ellis, S., Foster, D.R., Carlton, G. and Lezberg, A. 1999 Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* **80**, 2683–2696.

Dittus, W.P. 1985 The influence of cyclones on the evergreen forest of Sri Lanka. *Biotropica* **17**, 1–14.

Evans, A.M., Camp, A.E., Tyrrell, M.L. and Riely, C.C. 2007 Biotic and abiotic influences on wind disturbance in forests of NW Pennsylvania, USA. *For. Ecol. Manage.* **245**, 44–53.

Everham III, E.M. and Brokaw, N.V.L. 1996 Forest damage and recovery from catastrophic wind. *Bot. Rev.* **62**, 113–185.

Foster, D.R. 1988 Species and stand response to catastrophic wind in central New England, U.S.A. *J. Ecol.* **76**, 135–151.

Guisan, A. and Zimmerman, N.E. 2000 Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186.

Hanson, J.J. and Lorimer, C. 2007 Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. *Ecol. Appl.* **17**, 1325–1340.

Jalkanen, A. and Mattila, U. 2000 Logistic regression models for wind and snow damage in northern Finland based on the National Forest Inventory data. *For. Ecol. Manage.* **135**, 315–330.

Kosugi, R., Shibuya, M. and Ishibashi, S. 2016 Sixty-year post-windthrow study of stand dynamics in two natural forests differing in pre-disturbance composition. *Ecosphere* **7**, e01571.10.1002/ecs2.1571.

Kulakowski, D. and Veblen, T.T. 2003 Subalpine forest development following a blowdown in the Mount Zirkel Wilderness, Colorado. *J. Veg. Sci.* **14**, 653–660.

Lorimer, C.G. and White, A.S. 2003 Scale and frequency of natural disturbances in northeastern US: implications for early successional forest habitats and regional age distributions. *For. Ecol. Manage.* **185**, 41–64.

Mayer, P., Brang, P., Dobbertin, M., Hallenbarter, D., Renaud, J.P., Walthert, L. and Zimmermann, S. 2005 Forest storm damage is more frequent on acidic soils. *Ann. For. Sci.* **62**, 303–311.

Peterson, C.J. 2000 Catastrophic wind damage to North American forests and the potential impact of climate change. *Sci. Total Environ.* **262**, 287–311.

Peterson, C.J. 2004 Within-stand variation in windthrow in southern boreal forests of Minnesota: Is it predictable? *Can. J. For. Res.* **34**, 365–375.

Peterson, C.J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. *For. Ecol. Manage.* **250**, 96–108.

Plotkin, A.B., Foster, D., Carlson, J. and Magill, A. 2013 Survivors, not invaders, control forest development following simulated hurricane. *Ecology* **94**, 414–423.

R Core Team. 2013 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http//www.R-project.org.

Rammig, A., Fahse, L., Bugmann, H. and Bebi, P. 2006 Forest regeneration after disturbance: a modelling study for the Swiss Alps. *For. Ecol. Manage.* **222**, 123–136.

Rich, R.L., Frelich, L.E. and Reich, P.B. 2007 Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. *J. Ecol.* **95**, 1261–1273.

Schmidt, M., Hanewinkel, M., Kändler, G., Kublin, E. and Kohnle, U. 2010 An inventory-based approach for modeling single-tree storm damage–experiences with the winter storm of 1999 in southwestern Germany. *Can. J. For. Res.* **40**, 1636–1652.

Shibuya, M., Urata, T., Torita, H. and Iijima, H. 2011 Windthrow damage and tree shape in coniferous plantations in central Hokkaido, northern Japan. *Jpn. J. For. Environ.* **53**, 53–59.

Swanson, M.E., Franklin, J., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B. and Swanson, F.J. 2011 The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front. Ecol. Environ.* **9**, 117–125.

Takei, T. 1958. Investigation report on wind-damaged forests. *Sapporo-Rinyu* **48**: 2–17.

Toda, M. and Shibuya, M. 2017 Stand recovery of a temperate hardwood forest 60 years after a stand-replacing windthrow based on a permanent plot study. *J. For. Res.* **22**, 303–308.

Turner, M.G., Dale, V.H. and Everham III, E.H. 1997 Fires, hurricane, and volcanoes: comparing large disturbances. *BioScience* **47**, 758–768.

Turner, M.G., Baker, W.L., Peterson, C.J. and Peet, R.K. 1998 Factors influencing succession: lessons from large, infrequent natural disturbance. *Ecosystems* **1**, 511–523.

Valinger, E. and Fridman, J. 2011 Factors affecting the probability of windthrow at stand level as a result of Gudrun winter storm in southern Sweden. *For. Ecol. Manage.* **262**, 398–403.

Webb, S.L. and Scanga, S.E. 2001 Windstorm disturbance without patch dynamics: twelve years of change in a Minnesota forest. *Ecology* **82**, 893–897.

Yonekura, K. and Kajita, T. 2003– BG plants (YList). http://ylist.info.

Zimmerman, J.K., Everham III, E.M., Waide, R.B., Lodge, D. J., Taylor, C. M. and Brokaw, N.V.L. 1994 Response of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life history. *J. Ecol.* **82**, 911–922.

Table 1 Stand description before and after stand-replacing windthrow

Site	Forest type	Relarive BA of conifers (%)[*]	Density (1/ha)			Basal area (m^2/ha)			Mean DBH[**] (cm)		Species richness	
			Before	After	Loss (%)	Before	After	Loss (%)	Before	After	Before	After
Tomakomai	Coniferous forest	93	700	102	85	34.9	2.3	93	21.2	12.3	17	12
Jozankei	Mixed forest	57	1096	200	82	30.4	4.3	86	16.2	13.5	19	11
TEF[***]	Broadleaved forest	0	756	388	49	26.7	5.0	81	16.0	10.3	15	13

[*] Relative basal area of conifers before the windthrow in 1954.

[**] DBH: diameter at breast height (1.3 m high).

[***] Toamkomai Experimental Forest of Hokkaido University.

For Tomakomai and Jozankei, stand conditions before and after the windthrow are in 1954 and 1956, respectively, and in 1954 and 1958 for TEF.

Table 2 Results of windthrow patterns in permanent plots

a) Tomakomai plot

Variable	Coefficient	Mortality (%) [1]
Intercept (*Abies sachalinensis*)	3.272***	98
Magnolia obovata	-2.526**	76
Picea jezoensis	-1.301	94
Quercus crispula	-3.493***	52
Others	-2.372**	78
DBH	0.033	

D^2=0.195 [2]

b) Jozankei plot

Variable	Coefficient	Mortality (%) [1]
Intercept (*Acer pictum*)	-0.638´	64
Abies sachlinensis	1.521***	86
Picea spp.	0.223	71
Others	0.601	75
DBH	0.068***	

D^2=0.089 [2]

c) TEF plot

Variable	Coefficient	Mortality (%) [1]
Intercept (*Acer pictum*)	-1.704**	60
Chengiopanax sciadophylloides	0.359	41
Carpinus cordata	-0.184	25
Ostrya japonica	-0.246	31
Prunus spp.	-0.049	40
Quercus crispula	-0.894	83
Others	1.020	57
DBH	0.110***	

D^2=0.160 [2]

***: p <0.001, **: p <0.01, ´: 0.05<p <0.1.

[1] Mortality in density by a stand-replacing windthrow in 1954.

[2] D^2: 1-(residual deviance/null deviance) (Guisan and Zimmermann 2000).

Table 3 Dynamics of survived trees

a) Tomakomai

DBH distribution of surviving trees in 1956			Dead trees until 2014		DBH distribution in 2014		
					Surviving trees in 1956		
DBH (cm)*	Coni-fers	Broad-leaved	Coni-fers	Broad-leaved	Coni-fers	Broad-leaved	Ingrowths**
6	5	14	4	8			121
8	1	12	1	4			95
10		5		4			119
12		1		0			90
14		1		1		1	78
16							67
18		3		0		2	60
20		1		1			34
22		1		0			34
24		2		1		1	23
26						2	10
28	1		1			3	12
30	1		1		1	3	7
32						1	6
34						1	6
36						4	1
38						2	3
40						1	1
42		1		1			1
52	1		1				
60	1		1				

Frequency: trees/0.5ha.

* DBH class by 2 cm-interval.

** ingrowth trees after windthrow in 1954.

b) Jozankei

DBH distribution of surviving trees in 1956			Dead trees until 1991		DBH distribution in 1991		
					Surviving trees in 1956		
DBH (cm)*	Coni-fers	Broad-leaved	Coni-fers	Broad-leaved	Coni-fers	Broad-leaved	Ingrowths**
6	8	11	4	7		1	252
8	16	8	10	3			406
10	7	4	5	1	1	3	265
12	7	4	4	2	1	1	160
14	1	5	0	4	3	3	72
16	2	3	2	3	2	3	41
18	2	3	0	2	1	1	25
20	2		2		5	1	9
22		3		3	2		7
24	1	1	1				2
26	2		1		1	1	4
28					3		2
30		1		1			1
32		2		2		1	
34		1		0		2	
36		2		1		1	
42		1		1		1	
70		1		0			
76						1	

Frequency: trees/0.49ha.

*: DBH class by 2 cm-interval.

**: ingrowth trees after windthrow in 1954.

Table 4 Survival of trees by species that survived a windthrow in 1954

a) Tomakomai plot

Species \ Year	1956	1959	1961	1966	1971	1977	1981	1986	1991	2004	2009	2012	2014
Picea jezoensis Carrière	9	2	2	2	1	1	1	1	1	1	1	1	1
Abies sachalinensis Mast.	1	0	0	0	0	0	0	0	0	0	0	0	0
Magnolia obovata Thunb.	15	13	13	12	11	8	7	7	7	7	7	7	7
Quercus crispula Blume	14	14	14	14	13	13	13	13	13	12	11	10	10
Phellodendron amurense Rupr.	3	3	3	2	2	2	2	2	2	2	1	1	1
Ulmus davidiana Planch. var. *japonica* Nakai	3	3	3	3	3	3	3	3	3	2	1	1	1
Acer pictum subsp. *mayrii*	2	2	2	2	2	2	2	1	1	1	1	0	0
Kalopanax septemlobus Koidz.	2	2	1	1	1	1	1	1	1	1	1	1	1
Betula ermanii Cham.	1	1	1	1	1	1	1	1	1	0	0	0	0
Cercidiphyllum japonicum Siebold et Zucc. ex Hoffm. Et Schult.	1	1	1	1	1	1	1	1	1	1	1	1	1
Total	51	41	40	38	35	32	31	30	30	27	24	22	22

b) Jozankei plot

Species \ Year	1956	1959	1961	1966	1971	1977	1981	1986	1991
Abies sachalinensis Mast.	43	23	23	23	23	22	22	21	18
Picea jezoensis Carrière	3	0	0	0	0	0	0	0	0
Picea glehnii Mast.	2	1	1	1	1	1	1	1	1
Acer pictum Thunb. subsp. *mono* H.Ohashi	24	10	10	10	10	5	5	5	5
Quercus crispula Blume	5	5	5	5	5	5	5	4	4
Tilia japonica Simonk.	5	5	5	5	5	3	3	3	3
Acer japonicum Thunb.	4	4	4	4	4	4	4	4	3
Acer pictum Thunb. subsp. *mayrii* H.Ohashi	4	4	4	4	4	4	4	4	2
Chengiopanax sciadophylloides C.B.Shang et J.Y.Huan	3	1	1	1	1	1	1	1	1
Sorbus commixta Hedl.	3	2	2	2	2	1	1	1	1
Kalopanax septemlobus Koidz.	1	1	1	1	1	0	0	0	0
Styrax obassia Siebold et Zucc.	1	1	1	1	1	1	1	1	1
Total	98	57	57	57	57	47	47	45	39

Figure legends

Fig. 1. Mortality by diameter at breast height (DBH) class.

The white and striped bars represent the surviving and fallen trees after the windthrow in 1954, respectively: (a) ○: conifer mortality, +: broadleaved tree mortality; (b) ○: *Abies sachalinensis* mortality, +: mortality of trees other than *A. sachalinensis*; (c) ○: mortality of all species.

Fig. 2. Temporal trends in the relative basal area of surviving trees.

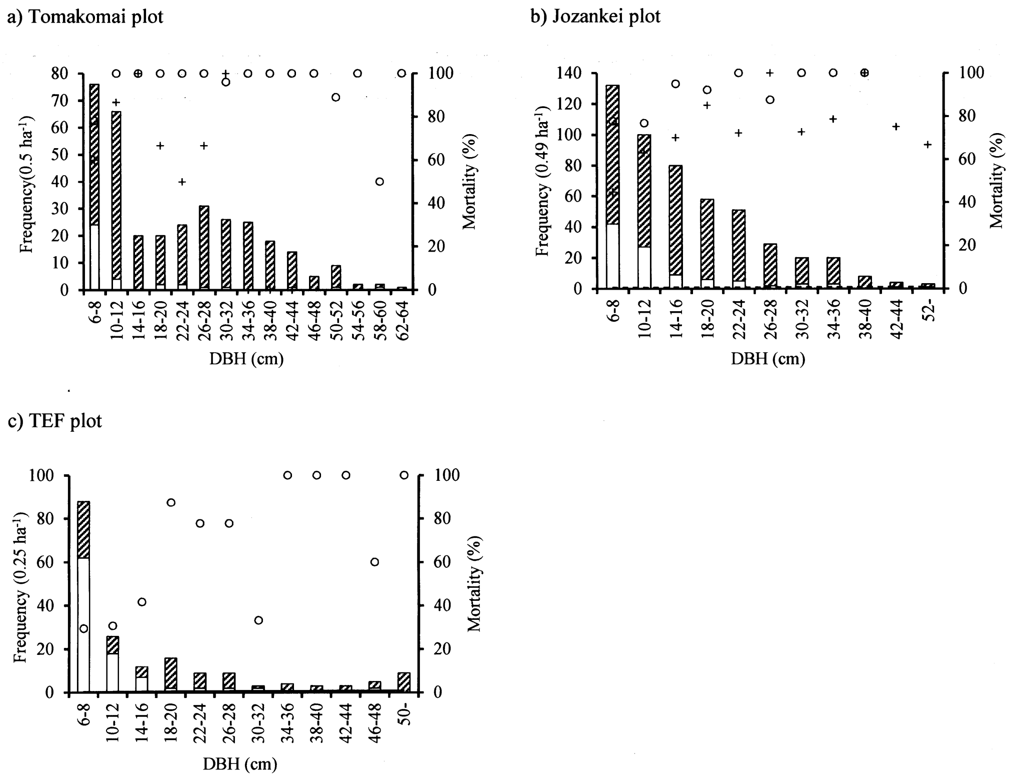
a) Tomakomai plot
Frequency(0.5 ha-1)
Mortality (%)
DBH (cm)
6-8
10-12
14-16
18-20
22-24
26-28
30-32
34-36
38-40
42-44
46-48
50-52
54-56
58-60
62-64
b) Jozankei plot
Frequency (0.49 ha-1)
Mortality (%)
DBH (cm)
6-8
10-12
14-16
18-20
22-24
26-28
30-32
34-36
38-40
42-44
52-
c) TEF plot
Frequency (0.25 ha-1)
Mortality (%)
DBH (cm)
6-8
10-12
14-16
18-20
22-24
26-28
30-32
34-36
38-40
42-44
46-48
50-

Fig. 1.

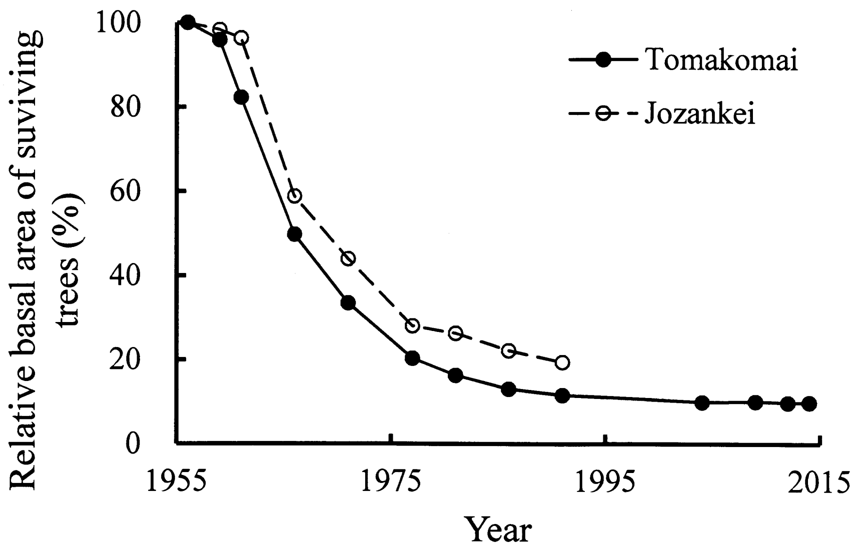
Relative basal area of suviving trees (%)
100
80
60
40
20
0
1955
1975
1995
2015
Year
Tomakomai
Jozankei

Fig. 2