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Title: Stand recovery of a temperate hardwood forest 60 years after a stand-replacing windthrow based on a permanent plot study

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Abstract We examined the dynamics of stand structure and composition over a 60-year period in two permanent plots in a deciduous hardwood forest in Hokkaido, Japan, which were severely disturbed by a stand-replacing windthrow, to reveal trends that could be valuable to the development of a model of forest recovery after a severe windthrow. We analyzed temporal trends in tree density, species richness and diversity, successional composition, and stand development stage in the plots. Both plots recovered as hardwood stands. Tree density and species richness increased, peaking 35–40 years after the windthrow, and then decreased in both plots. Based on these results, we concluded that both plots were in the stand-initiation stage for 35–40 years after the windthrow, and then transitioned into the stem-exclusion stage. Species diversity increased with an increase in species richness during the stand-initiation stage, and then decreased slightly in both plots. In both plots, successional composition did not fluctuate greatly in the 60 years after the windthrow, and both returned to pre-disturbance composition during the stem-exclusion stage. The temporal trends observed in this study were remarkably similar to those in a previous study of permanent plots located near the plots used in this study. Therefore, this study provides valuable information that can be useful in the development of a stand recovery model in temperate forests after stand-replacing windthrows.

Keywords Permanent plot · species composition · stand development stage · stand-replacing windthrow · stand structure.

Introduction

The effects of severe disturbances on forest structure and composition are conspicuous and persist for centuries (Henry and Swan 1974). However, a general model for forest recovery after a severe disturbance, that is applicable to various forest types and climate zones, has not been established (Peterson 2000) because 1) detailed long-term studies following severe disturbances are scarce (Webb 1999, Burslem et al. 2000), 2) pre-disturbance stand structure and composition and disturbance agents (*e.g.*, wind, fire, volcanic eruption, and insect outbreak) influence post-disturbance stand structure and composition (Peterson 2000, Franklin et al. 2002, Swanson et al. 2011), and 3) climate zone and forest type (*e.g.*, early- or late-successional stands) influence recovery rate and succession (Everham III and Brokaw 1996). To improve our understanding of forest recovery after a severe disturbance, long-term permanent plot studies that include the pre-disturbance stand condition are necessary in various climate zones and forest types.

Kosugi et al. (2016) examined the dynamics of tree density, species richness and diversity, and stand development stage over a 60-year period in two stands with pre-disturbance compositions of natural coniferous and mixed forests in Hokkaido, Japan, during their recovery from a stand-replacing windthrow in a permanent plot study. They reported that tree density (diameter at breast height (DBH) ≥5 cm) and species richness peaked 37 years after the windthrow and then decreased. They concluded that the secondary stands had been in the stand-initiation stage for 37 years after the recovery from the windthrow and then transitioned into the stem-exclusion stage, following Oliver’s (1980/1981) stand development model after a stand-replacing disturbance. In addition, they showed that basal area increased over the 60 years after the windthrow, species diversity peaked in the stand-initiation stage in the both stands, and temporal trends in successional composition differed between the stands. These results are highly reliable because they were derived from permanent plot data; however, additional studies are necessary to examine their applicability to the recovery of other stands after stand-replacing windthrow.

As reviewed by Kosugi et al. (2016), the stand dynamics of secondary stands after a stand-replacing disturbance vary by climate zone and stand structure. Furthermore, Arévalo et al. (2000) showed that tree density and basal area dynamics 14 years after a catastrophic windthrow event differed between two stands with pre-disturbance compositions dominated by *Quercus* and *Pinus* species, respectively, in Minnesota, United States. This indicates the possibility that recovery after a stand-replacing windthrow may differ among stands with different pre-disturbance compositions; however, this is inconsistent with the conclusion of Kosugi et al. (2016). In this study, we aimed to verify the applicability of these inconsistent conclusions to the recovery of other natural stands following stand-replacing windthrow.

In 1954, tree volumes of 21.1×10^6 m^3 and 652×10^3 ha of land were damaged by Typhoon No. 15 in Hokkaido (Forestry Agency of Japanese Government 1959). Extensive natural old-growth forests were damaged throughout Hokkaido. Permanent plots analyzed by Kosugi et al. (2016) had been established in the windthrown area in 1954. Two other permanent plots had been established in a deciduous hardwood forest that was severely windthrown by the 1954 typhoon in the Tomakomai Experimental Forest (TEF) of Hokkaido University. These plots are still maintained and have been measured repeatedly.

In this study, we examined the stand dynamics of these two permanent plots in the TEF. We assessed the stand dynamics in the permanent plots based on temporal changes in stand structure and composition over 60 years and determined the stand development stage following Oliver's stand development model (1980/1981) to verify the applicability of conclusions of Kosugi et al. (2016) and Arévalo et al. (2000) and to detect useful trends for the development of a stand recovery model for temperate forests after stand-replacing windthrows.

Methods

Study sites

The two permanent plots examined in this study are located in the TEF of Hokkaido University in the central southern area of Hokkaido, Japan. The topography of the TEF is mostly a flat plateau with inclines of <5° and elevations ranging from 20 to 90 m. The mean annual temperature and precipitation were 6.7°C and 1,112 mm, respectively, in 1999–2008, and the climate is characterized by a cool summer and frequent fog in summer. The soil in the TEF is typically of volcanic origin and immature, with a thin topsoil 5–10 cm thick. The natural forest in the TEF is dominated by deciduous hardwoods such as *Quercus* spp., *Acer* spp., *Ostrya japonica*, and *Tilia* spp., as well as conifers such as *Abies sachalinensis* and *Picea jezoensis*. The dominant understory vegetation includes ferns and herbaceous plants (Tomakomai Experimental Forest 2016).

The permanent 50 × 50-m plots (Plots 1 and 2; 42° 40´N, 141° 36´E) are adjacent to each other, separated by ~40 m, on an almost flat slope at 40 m above sea level. They were established in 1958 in a deciduous hardwood forest severely disturbed by a stand-replacing windthrow in 1954. Plot 1 was salvage-logged before the plot was established, while Plot 2 was not. The first measurement was conducted in the plots in 1958. Although details of the salvage logging were not recorded, it was estimated from stump-size measurements in 1958 that 6 % of the tree density and 16% of the basal area were removed from Plot 1. The pre-disturbance stand condition of Plot 2 was reconstructed from the 1958 measurements, which included both standing and fallen trees of DBH ≥5 cm. The 1954 windthrow was estimated to have reduced tree density and basal area in Plot 2 by 49 and 81%, respectively, based on the reconstruction, and we considered the windthrow stand-replacement based on this lost basal area. The pre-disturbance stand had no logging history and was presumed to be old-growth forest based on the DBH distribution reconstructed in Plot 2 (DBH distribution including fallen trees in 1958 was 6–66 cm). In total, 15 hardwood species were present in the pre-disturbance stand dominated by *Quercus crispula* (basal area ratio, 57%), *Acer* spp. (20%), *O. japonica* (7%), and *Cerasus* spp. (6%). Before the 1954 windthrow, a forest trail passed through Plot 1, which was reconstructed in 1974. The trail in Plot 1 had an area of 185 m^2 and probably influenced the dynamics of stand structure and composition of Plot 1; however, it did not have a large influence on the current stand structure and composition given that the tree density, basal area, and species richness and diversity in Plot 1 were similar to those in Plot 2, as described below. Regardless, we recognized that Plot 1 was an important reference in this study for comparison with Plot 2, which was left intact after the windthrow.

Plots 1 and 2 in this study were located ~30 and 45 km from the Tomakomai and Jozankei plots studied by Kosugi et al. (2016).

The taxonomic nomenclature followed that of Yonekura and Kajita (2003–).

Tree measurement and assessment of diversity and successional composition

Trees of DBH ≥5 cm have been tagged, mapped, identified, and measured for DBH and height in Plots 1 and 2 since 1958. Both plots were re-measured in 1977, 1984, 1989, 1994, 2000, 2004, 2010, and 2014. In addition, Plot 1 was re-measured in 1972. The height of the DBH measurement was marked on the stems of all trees. The interval between the 1958 measurement and the next was long (14 and 19 years in Plots 1 and 2, respectively); however, the stakes marking the corners of the plots remained. Multi-stemmed trees were measured separately if they ramified below breast height, 1.3 m.

In this study, we examined the temporal dynamics of tree density, species richness and diversity, and successional composition in a similar manner to Kosugi et al. (2016).

Species diversity was estimated with the Shannon index (H'):

$$H' = -\sum p_i ln p_i$$

where p_i is the relative basal area of species i.

Successional composition was expressed as the relative importance (RI; White et al. 2015) of early-, intermediate-, and late-successional species.

RI = relative density + relative dominance (relative basal area)

Trees were classified as early-, intermediate-, and late-successional species based on Kikuzawa (1983), Koike (1988), Hanada et al. (2006), Nonoda et al. (2008), and Iwasaki and Shibuya (2013) using photosynthetic characteristics, leaf emergence pattern, suitable regeneration site, and shade tolerance (Table 1).

Results

Stand structure and composition

In Plot 2, tree density increased after the windthrow in 1954 and peaked at 2,020/ha in 1989, 35 years after the windthrow. Then, tree density decreased to 1,316/ha in 2014, 60 years after the windthrow (Fig. 1). The dynamics of tree density in Plot 1 were very similar to those in Plot 2, but the peak occurred 40 years after the windthrow (Fig. 1). The basal area continued to increase over the 60 years after the windthrow in both plots, and was 27–28 m^2/ha in 2014 (Fig. 1). The basal area in Plot 2 in 2014 was slightly larger than the pre-disturbance value (105%).

Density dynamics differed among species (Table 1). In Plot 2, temporal trends in *Q. crispula* and *Magnolia obovata* density were parallel to the overall density dynamics of the plot, but those of *Carpinus cordata* and *Acer pictum* were not. The early-successional species, *Cerasus* spp., and *Tilia japonica* contributed to the decrease in density after 1989 (Table 1). Similarly, the density dynamics in Plot 1 differed among species (Table 1). The early-successional species, *Fraxinus lanuginosa*, *Cerasus* spp., and *Q. crispula* strongly influenced the decrease in density after the peak (Table 1).

Before the 1954 windthrow, Plot 2 had a species richness of 15, which increased to 25 in 1984–1989, 30–35 years after the windthrow, and then decreased to 18 by 2014 (Fig. 2). In Plot 1, species richness increased until 40 years after the windthrow and then decreased (Fig. 2). The temporal trends in species richness were similar between the plots (Fig. 2). In the final measurement in 2014, although three *Pinus koraiensis* were present in Plot 1, all other trees in both plots were hardwood species (Table 1), indicating that these permanent plots recovered as deciduous hardwood stands after the 1954 windthrow. The number of intermediate- and late-successional species was stable 23–60 years after the windthrow (6–7 and 9–10 species, respectively) in both plots, while the number of early-successional species decreased in 2014 in the plots, 60 years after the windthrow, compared to that in 1977 (Table 1).

Species diversity and successional composition

Species diversity increased until 30 and 35 years after the 1954 windthrow in Plots 2 and 1, respectively (Fig. 2). Species diversity decreased slightly after these peaks in both plots, and increased with the increase in species richness in both plots (Fig. 2).

The RI by successional category (*i.e.*, successional composition) did not fluctuate greatly during the 60 years after the windthrow in both plots (Fig. 3). The RIs of intermediate- and late-successional species slightly increased and decreased, respectively, during the recovery from the windthrow. The RI of late-successional species began to increase 40 and 50 years after the windthrow in Plots 2 and 1, respectively, and successional composition tended to revert to the pre-disturbance composition (Fig. 3).

We examined the influence of the forest trail in Plot 1 on the dynamics of stand structure and composition after the windthrow, and determined it to be insignificant because the dynamics of tree density, species richness, and basal area were surprisingly similar between the two plots (Figs. 1 and 2).

Discussion

Tree density and species richness increased in the first 35–40 years, and basal area continued to increase during the 60 years after the windthrow in both plots. In Oliver’s model (1980/1981), tree density and species richness increase in the stand-initiation stage and begin to decrease in the stem-exclusion stage. Based on the tree density and species richness results, the secondary stands in Plots 2 and 1 were inferred to have been in the stand-initiation stage for 35 and 40 years after the windthrow, respectively, thereafter transitioning to the stem-exclusion stage.

The temporal trends in tree density, species richness, and basal area in this study were remarkably similar to the results of Kosugi et al. (2016). Therefore, it might be possible to apply these trends to secondary stands established after late-successional stands disturbed by a stand-replacing windthrow in central Hokkaido irrespective of the pre-disturbance forest type (*e.g.* coniferous, mixed, and hardwood stands). This conclusion differs from that of Arévalo et al. (2000), possibly because the permanent plots in Kosugi et al. (2016) and this study were late-successional stands based on their composition before and after the windthrow (Fig. 5 in Kosugi et al. 2016, Fig. 3 in this study).

We reviewed several long-term permanent plot studies on stand structure and composition after severe wind disturbances, including Crow (1980; study period, 33 years), Hibbs (1983; 40 years), Weaver (1989; 49 years), Mabry and Korsgren (1998; 53 years), and Fisher and Fisher (2012; 25 years). Excluding Crow (1980), these studies could not precisely determine the duration of the stand development stages because of the long intervals between measurements. In a rainforest in Puerto Rico, tree density, species richness, and diversity peaked in 1946 and then decreased (Crow 1980). Before establishing the permanent plot (Crow 1980), the study forest had been disturbed by three windthrows and one selective cutting, and the peak in 1946 occurred 14 years after the last windthrow. Therefore, the stand-initiation stage in Crow’s plot was inferred to have lasted at least 14 years. Crow (1980) measured tree size for trees with DBH >4 cm. The difference in the durations of the stand-initiation stage between Crow (1980; at least 14 years) and this study (35–40 years) may be attributable to differences in measurement size (DBH >4 cm versus DBH ≥5 cm), location (Puerto Rico versus Hokkaido), and disturbance history. It is possible that tree measurement size affects the duration of the stand-initiation stage of secondary stands after a stand-replacing disturbance. However, measurement size varies among studies, *e.g.*, height ≥1.3 m in Hibbs (1983), DBH ≥4.1 cm in Weaver (1989), and DBH ≥2.54 cm in Mabry and Korsgren (1998). In studies using smaller measurement sizes, the duration of the stand-initiation stage may be shorter.

The temporal trends in species diversity in both plots (Fig. 2) were extremely similar to those in the permanent plots of Kosugi et al. (2016). Species diversity increased with increasing species richness and peaked in the stand-initiation stage, thereafter decreasing slightly in both studies irrespective of differences in their pre- and post-disturbance stand structures and compositions. These trends might be applicable to the recovery of a forest stand after a stand-replacing windthrow in central Hokkaido. In this study, successional composition tended to revert to the pre-disturbance composition (Fig. 3). To address the recovery of a forest stand after a disturbance, Abrams and Scott (1989) proposed a disturbance-mediated accelerated succession model. However, in northeastern USA, late-successional species generally dominate the understory sapling layer of late-successional stands (Leak et al. 1987), and a dominance of late-successional species is maintained before and after wind disturbance in natural old-growth stands (Fraver et al. 2009). Our results (Fig. 3) are consistent with the latter case. Including the two permanent plots of Kosugi et al. (2016), all four plots in central Hokkaido were in late succession before and after the 1954 stand-replacing windthrow. This could indicate the importance of advance regeneration to stand recovery after a severe windthrow, because many advance-regeneration saplings survive windthrows (Canham et al. 2001; Swanson et al. 2011). Notably, early-successional species were apparently decreased 46 years after the windthrow in both plots, and only three trees were present in Plot 2 in 2014, 60 years after the windthrow (Table 1). This indicates that early-successional species had been minor components of the secondary stands recovered after the 1954 windthrow when more than 80 % of the basal area was lost, and that most early-successional trees disappeared by 60 years after the windthrow.

The timing of the peaks of tree density and species richness differed by only 5 years between the plots and was longer in Plot 1. This difference might have resulted from the salvage logging conducted in Plot 1; however, tree density, species richness, and basal area were almost equivalent between the plots 60 years after the windthrow, and the trail and logging had little influence on the current stand structure and composition.

After comparing dynamics in stand structure and composition dynamics over a 60-year period after a stand-replacing windthrow in the permanent plots of Kosugi et al. (2016) and this study, we found surprising similarities in the dynamics of tree density, basal area, species richness and diversity, and the duration of the stand-initiation stage. These results may be valuable for establishing a general model of stand recovery of late-successional temperate forests after a stand-replacing windthrow.

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Figure Legends

Fig. 1. Tree density and basal area dynamics during the 60 years after a windthrow.

Values at year 0 indicate the pre-disturbance values in Plot 2.

Fig. 2. Temporal trends in species richness and diversity (Shannon index) during the 60 years after

a windthrow.

Values at year 0 indicate the pre-disturbance values in Plot 2.

Fig. 3. Temporal trends in relative importance by successional category.

Relative importance: see text, successional category: see Table 1.

Toda and Shibuya Table 1

Table 1 Tree frequency (1/0.25 ha) by species

Plot 1

Species＼Year	1958	1972	1977	1984	1989	1994	2000	2004	2010	2014
Years from windthrow	4	18	23	30	35	40	46	50	56	60
Early-successional species										
Alnus hirsuta	1	2	2	1	1	1	1	1	1	0
Betula platyphylla	0	0	1	1	1	1	1	1	1	0
Salix caprea	0	3	4	6	6	3	1	0	0	0
Toxicodendron trichocarpum	0	3	2	3	4	4	1	0	0	0
Intermediate-successional species										
Chengiopanax sciadophylloides	0	5	14	16	15	13	11	10	8	8
Cornus controversa	1	2	4	3	2	2	2	2	1	1
Cercidiphyllum japonicum	4	4	5	6	5	5	5	5	5	4
Fraxinus lanuginosa	3	23	44	77	96	119	127	124	113	92
Kalopanax septemlobus	3	1	2	3	3	2	2	2	2	2
Magnolia obovata	2	3	12	12	12	11	11	10	9	9
Morus australis	4	5	8	7	2	2	3	1	0	0
Late-successional species										
Acer amoenum	–	–	15	14	12	12	11	11	11	11
Acer pictum	35	34	7	9	10	12	14	15	13	15
Carpinus cordata	12	45	51	55	52	53	55	53	55	56
Ostrya japonica	19	28	27	29	28	25	22	20	18	16
Acer japonicum	0	1	0	1	0	0	0	0	0	0
Cerasus sargentii	14	24	16	17	19	17	16	13	13	11
Cerasus maximowiczii	–	2	9	17	18	19	14	10	8	6
Quercus crispula	14	24	43	52	50	51	48	44	39	36
Aria alnifolia	1	19	27	32	32	34	33	33	32	31
Tilia japonica	10	13	11	11	11	11	11	11	7	7
Undetermined										
Euonymus sieboldianus	0	2	0	0	0	2	2	2	0	0
Hydrangea paniculata	0	2	2	3	3	2	1	0	0	0
Weigela hortensis	0	0	0	1	1	1	0	0	0	0
Pinus koraiensis	0	0	0	0	0	1	2	2	3	3
Pourthiaea villosa	0	0	0	0	0	1	0	0	0	0
Total (/0.25ha)	123	245	306	376	383	404	394	370	339	308

(To be continued)

(Continued)

Plot 2

Species＼Year	1954	1958	1977	1984	1989	1994	2000	2004	2010	2014
Years from windthrow	0	4	23	30	35	40	46	50	56	60
Early-successional species										
Aralia elata	0	0	1	1	1	0	0	0	0	0
Alnus hirsuta	0	0	10	4	3	2	1	1	1	0
Betula platyphylla	0	0	2	2	2	2	2	2	2	2
Phellodendron amurense	0	0	3	4	5	4	0	0	0	0
Salix caprea	0	0	20	23	22	17	5	4	2	1
Toxicodendron trichocarpum	6	1	12	12	12	7	0	0	0	0
Intermediate-successional species										
Chengiopanax sciadophylloides	16	10	23	24	23	21	19	17	13	12
Cornus controversa	10	0	6	7	7	7	6	5	5	5
Cercidiphyllum japonicum	1	1	2	3	4	4	4	4	3	3
Fraxinus lanuginosa	2	2	11	20	23	23	29	29	30	23
Kalopanax septemlobus	1	0	2	4	4	3	0	0	0	0
Morus australis	1	1	0	0	0	0	0	0	0	0
Magnolia obovata	4	0	44	50	51	48	41	39	39	37
Late-successional species										
Acer amoenum	–	–	9	7	7	7	7	7	8	9
Acer pictum	42	17	19	26	32	32	33	33	35	31
Carpinus cordata	30	21	60	63	64	62	65	67	75	72
Ostrya japonica	29	20	30	24	18	17	14	12	11	11
Acer japonicum	0	0	0	0	0	0	0	0	1	1
Cerasus sargentii	16	5	24	26	25	22	20	16	16	13
Picea jezoensis	0	0	1	1	1	0	0	0	0	0
Cerasus maximowiczii	–	–	40	53	56	45	33	24	20	12
Quercus crispula	23	4	54	67	75	73	62	56	54	49
Aria alnifolia	11	10	37	39	40	40	40	38	33	32
Tilia japonica	6	5	25	28	27	25	20	18	17	15
Undetermined										
Euonymus sieboldianus	0	0	0	0	1	1	1	0	0	0
Euonymus oxyphyllus	0	0	0	1	1	1	1	1	0	0
Hydrangea paniculata	0	0	1	1	1	1	0	0	0	0
Pourthiaea villosa	0	0	1	1	1	1	1	1	1	1
Total (/0.25ha)	198	97	437	491	506	465	404	374	366	329

–: *Acer amoenum* and *Cerasus maximowiczii* are included in *A. pictum* and *C. sargentii*, respectively.

Tada and Shibuya Fig. 1

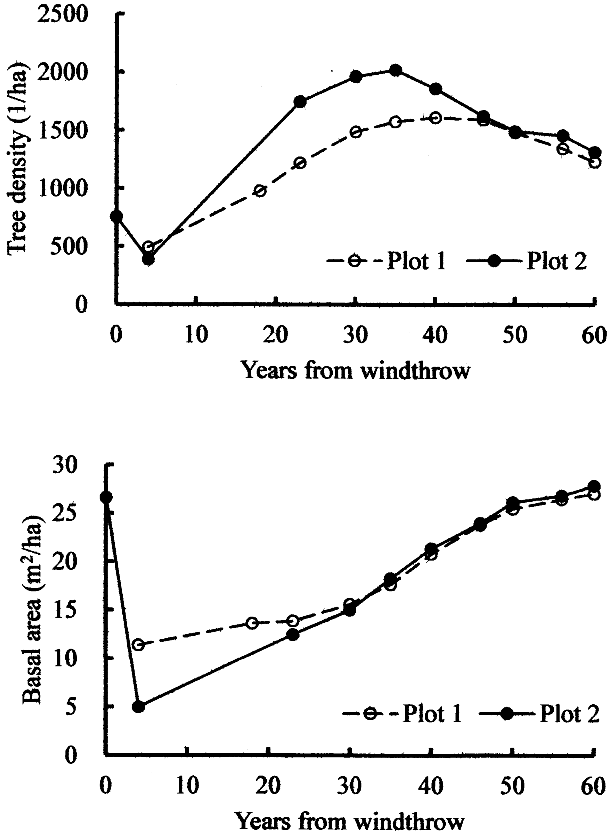

Fig. 1. Tree density and basal area dynamics during the 60 years after a windthrow.

Values at year 0 indicate the pre-disturbance values in Plot 2.

Tada and Shibuya Fig. 2

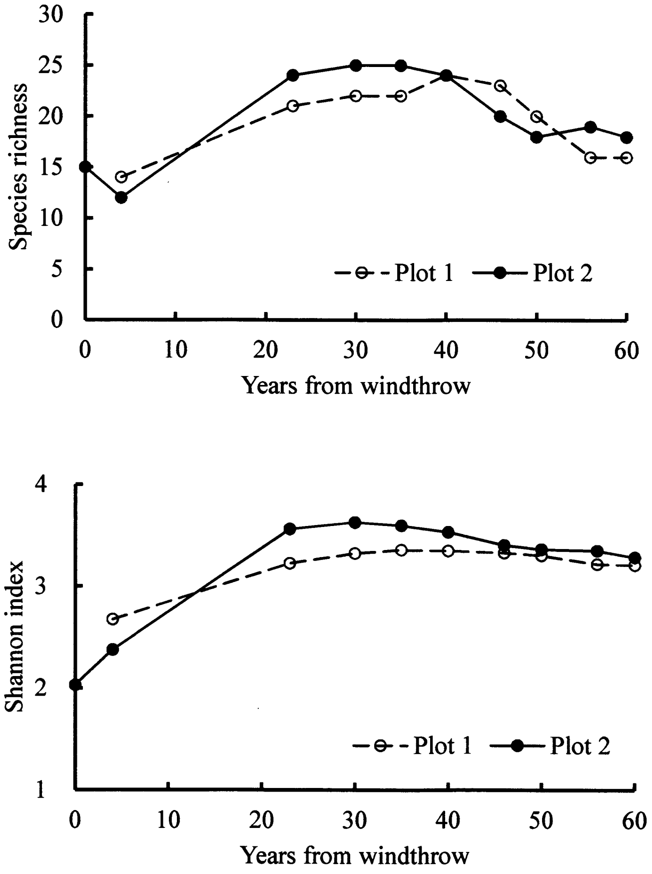

Fig. 2. Temporal trends in species richness and diversity (Shannon index) during the 60 years after a windthrow.

Values at year 0 indicate the pre-disturbance values in Plot 2.

Tada and Shibuya Fig. 3

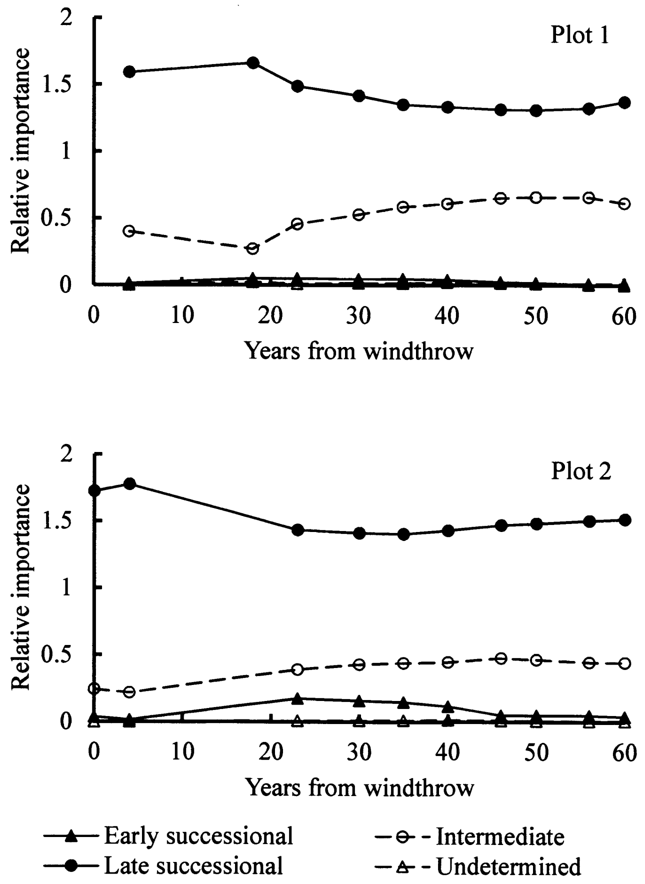

Fig. 3. Temporal trends in relative importance by successional category.

Relative importance: see in text, successional category: see Table 1.

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