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Author(s)	Sato, Tsuyoshi; Yamazaki, Haruka; Yoshida, Toshiya
Citation	Journal of Forest Research, 22(6), 336-342 https://doi.org/10.1080/13416979.2017.1381492
Issue Date	2017-09
Doc URL	http://hdl.handle.net/2115/71620
Rights	This is an Accepted Manuscript of an article published by Taylor & Francis in Journal of Forest Research on September 2017, available online: http://www.tandfonline.com/10.1080/13416979.2017.1381492 .
Type	article (author version)
File Information	Journal of Forest Research_22(6)_336-342.pdf



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Extending effect of a wind disturbance: mortality of *Abies sachalinensis* following a strong typhoon in a natural mixed forest

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Extending effect of a wind disturbance: mortality of *Abies sachalinensis* following a strong typhoon in a natural mixed forest

Strong wind constitutes the major force behind disturbance of northern Japanese forests. Canopy gaps induced by disturbance are responsible for subsequent recovery of the stand (i.e., enhancement of growth and recruitment). There is also a possibility that a sudden change in stand structure, involving significant microclimatic alterations, results in further stand degradation. We therefore examined a hypothesis proposing that wind disturbance causes indirect and delayed negative effects on the demography of *Abies sachalinensis*, a dominant conifer species of northern Japanese natural mixed forests. Data for all trees in a 3-ha study stand with diameter at breast height ≥ 10 cm were recorded for over 10 years, including the period of severe wind disturbance induced by Typhoon Songda in 2004. We found that the total amount of dead *A. sachalinensis* in the post-disturbance period was equivalent to that in the wind disturbance. The mortality of the species was generally high in larger trees. Within 1–2 years immediately after the disturbance, dead trees frequently presented the uprooted form despite there being no record of strong winds, suggesting that the physical influence of the disturbance persisted. Moreover, these dead trees showed spatial association with trees in the surrounding trees that died due to strong wind. In contrast, most *A. sachalinensis* trees that died 3–8 years later showed growth reduction after the disturbance. We conclude that a strong wind disturbance can have long-term influence on the stand dynamics, during which the possible cause of tree deaths changes gradually from physical damage to physiological stress.

Keywords: Sakhalin fir; demography; spatial patterns; windthrow; Typhoon Songda

Introduction

Natural disturbances produce structural complexity in a forest, resulting in deaths of individual trees; this plays a key role in various ecosystem processes and functions (Pickett & White 1985). Disturbances are classified according to the factors responsible for tree deaths, and strong wind is a typical agent of disturbance in many tropical and temperate forests (Boose et al. 1992; Everham & Brokaw 1996). In recent years, global warming is expected to generate extreme climatic events (IPCC 2014), which may increase the intensity and the frequency of a severe wind disturbance in forests in the future. Therefore, it is important to clarify the response pattern of a forest to strong wind when predicting future forest dynamics.

Canopy gaps, formed by partial destruction of a canopy cover, greatly change resource allocation in a forest, such as that of light and soil nutrients (Canham et al. 1994; Gray et al. 2002; Scharenbroch & Bockheim 2007). The formation of a gap generally has a positive influence on growth and survival of residual trees, especially for those that lack resources (Thorpe et al. 2007; Gray et al. 2012). However, it has also been reported that the survival of trees adjacent to the gap often falls significantly in many natural forests, known as gap expansion (Sprugel & Bormann 1981; Foster & Reiners 1986; Runkle & Yetter 1987; Worrall et al. 2005; Nagel & Svoboda 2008).

Many previous studies have examined the factors contributing to the negative influence of canopy gaps on adjacent trees. For example, the death of trees often resulted from physical damages to the crowns or trunks, which tend to be induced by larger fallen trees at the disturbance (e.g. Dittus 1985). Moreover, changes in microclimatic conditions as a result of disappearance of the surrounding trees cause a raised mortality by subsequent winds (Worrall et al. 2005). The effect of chronic wind stress, which results in a physiological degeneration in the stem (Liu et al. 2003;

Mitchell 2013), is also non-negligible. Furthermore, it has widely been reported that gap formation is often associated with a subsequent outbreak of insects or diseases, which originate from the supply of a large quantity of woody debris in the forest (Gandhi et al. 2007; Raffa et al. 2008). These patterns incorporate various temporal and spatial ranges, from direct effects of the disturbance to indirect effects through changes in forest stand structure (Everham & Brokaw 1996). It can be proposed that the influence of disturbance temporally and spatially expands in the long term (Worrall et al. 2005; Gray et al. 2012). However, the previous studies described the pattern only in limited spatial and/or coarse time scales.

The purpose of the present study was to clarify the spatiotemporal change in the pattern of deaths of surviving trees over 7 years after a strong wind disturbance in a natural forest in Hokkaido, northern Japan. In Hokkaido, strong winds constitute a typical natural force resulting in disturbance in forests (Nakashizuka & Iida 1995), and large-scale strong winds frequently occur due to large-scale typhoons that pass through at intervals of several decades, causing wind disturbance ranging from the felling of a single tree to catastrophic windthrow. The influence of typhoon disturbance on the forest dynamics is thus considered to be great, and many previous studies have been conducted on this subject, such as in the case of Typhoon Marie in 1954 (Ishizuka et al. 1998; Yoshida & Noguchi 2009). However, we believe that it is important to determine the pattern of mortality of trees, not only during the disturbance but also during the subsequent long-term period, with a comprehensive understanding of its causal factors. In the present study, we targeted the wind disturbance induced by a strong typhoon in 2004 on a natural mixed forest, with particular focus on a dominant conifer species *Abies sachalinensis* (Fr. Schm.) (Sakhalin fir) known to be especially vulnerable to strong winds (Yoshida & Noguchi 2009). We combined demographic, spatial (tree

location), and temporal (tree annual ring) data for this species, along with the observation of dead trees, to clarify the spatiotemporal pattern of the deaths triggered by the disturbance. We then examined two hypotheses: (1) the deaths of trees due to the typhoon will extend over time and space and (2) the cause of the deaths that follow the disturbance changes with time.

Materials and methods

Study site

We performed field surveys in the Uryu Experimental Forest of Hokkaido University (44°22'N, 142°12'E, 280 m above sea level; Figure 1). Hokkaido Island is located in the transition zone between the temperate and boreal forests. The mean annual temperature and precipitation observed at the research station (2 km from the study site) was 4.5°C and 1,298 mm, respectively (Uryu Experimental Forest, unpublished). Snow cover occurs from November to May to a maximum depth of ca. 250 cm. The study stand was set in a primary natural mixed forest, which is a typical natural vegetation type of Hokkaido. The geology of the area is Tertiary andesite, and the main soil type is acid brown forest soil. The stand was dominated by *A. sachalinensis* (40% of total basal area), followed by *Picea glehnii* Masters, *Quercus crispula* Blume, and *Betula ermanii* Cham. (Table 1). The frequency distributions classified by DBH (diameter at breast height) demonstrated the reversed J-shape for both *A. sachalinensis* and all species combined (Figure 2). The understory was densely covered with *Sasa senanensis* (Franchet et Savatier) Rehder, with *Viburnum furcatum* Blume ex Maxim. as a major associate (Inoue et al. 2017).

During September 2004, a typhoon with very strong winds landed on Hokkaido (Figure 1a) and caused severe windthrow within forests throughout the island (e.g. Yoshida et al. 2011). A maximum momentary wind speed of 59.1 m s^{-1} was observed in the Uryu Experimental Forest (Figure 1b), which was highly exceptional as no observation of wind $>20 \text{ m s}^{-1}$ was recorded during the study period of 10 years (2002-2012).

Field survey and sample collection

We installed a 3-ha study plot (200 m \times 150 m) in the Uryu Experimental Forest during the spring of 2002. We measured DBH and the position (XY coordinates) of trees with DBH ≥ 10 cm in the plot. We repeated measurements of DBH during the spring periods of 2007 and 2012, with an assessment of survival or death at each time. The dead trees were judged visually from the absence of living leaves and buds and classified into three forms of death: (1) snapped, (2) uprooted, or (3) standing. The survival assessment was additionally conducted immediately after the disturbance (October 2004) and the subsequent spring (April 2005), where the trees confirmed dead in these supplemental censuses (except for those judged to have died before the disturbance) were designated as trees that died directly in response to the disturbance. For the periods of tree death(s), we divided the remaining dead trees (i.e., those that died during the pre-disturbance or post-disturbance period) into the following periods: April 2002–September 2004 (before the disturbance), April 2005–April 2007 (1–2 years after the disturbance), and April 2007–April 2012 (3–7 years after the disturbance).

We extracted sample cores of 30 overstory living and all dead *A. sachalinensis* trees using a borer (4.3 mm diameter) from the southern face of the stem (1.3 m height). These cores allowed us to investigate the growth in diameter with a resolution of 1 year and to specify the exact year of death for living and dead trees, respectively. The cores

were mounted and sanded with sandpaper of progressively finer grit until the rings were clearly visible. The annual ring widths were measured to the nearest 0.005 mm using a table-mounted tree-ring increment measurement system (TA Tree Ring System, Velmex, Inc.).

Data analysis

We performed a cross-dating procedure based on the annual ring data to specify the exact year of tree deaths of *A. sachalinensis*. We created the master chronology from the annual ring data of the 30 living overstory trees and estimated the year of death of dead trees using the COFECHA program (Holmes 1983), with reference to the tree census record (described above) to ensure consistency.

We calculated the mortality of *A. sachalinensis* trees. A “year” in the present study was regarded as the period starting from April (i.e., beginning of the growing period) to the following spring. The year 2004 was exceptional as it contained the pre-disturbance (April–7 September 2004) and the disturbance periods (8 September 2004–April 2005). The growth of trees was represented by the annual increment in basal area, derived from the annual ring data combined with the tree census data. The averages for the periods before and after the disturbance were used for the further analysis.

To clarify the spatial relationship among the dead trees produced during different periods, we used Ripley’s L function, which is a refinement of the K-function (Ripley 1976; Lotwick & Silverman 1982). The spatial relationship of the dead trees (all tree species combined) within a certain radius (r) from *A. sachalinensis* trees died during the post-disturbance periods (1–2 years and 3–7 years later) was analysed by the L(r) function. We obtained the 95% confidential intervals of an independent distribution (i.e. $L(r) = 0$), by using random points instead of the dead *A. sachalinensis* trees; if the

calculated $L(r)$ exceed and fall below the interval, the spatial relationship between them is judged as co-occurred ($L(r) > 0$) and exclusive ($L(r) < 0$), respectively.

Furthermore, we constructed a generalized linear mixed model (GLMM) to identify contributing factors for growth and mortality of *A. sachalinensis* trees during the post-disturbance period. For the growth model, the mean annual basal area increment in the post-disturbance period was used as the response variable, assuming a Gaussian distribution with an identity link function. The growth (i.e. the mean basal area increment) before the disturbance was incorporated as an offset term in the model to evaluate the alteration of growth. In the mortality model, tree death was expressed as a dummy variable (zero: survived, one: dead), assuming a binomial distribution with a logit link function. For both models, the explanatory variables consist of the own basal area and the amount of neighbouring trees. The amount of neighbouring trees was defined as the sum of the basal areas of the trees located within the radius of 10 m (i.e., 314 m²) by living and dead trees (produced at the disturbance) separately. The radius measure was selected because it produced the smallest Akaike's information criterion (AIC) among 5, 10, and 15 m radii during the preliminary analyses. To consider the effect of spatial autocorrelation, we incorporated the ID of the grid, which divides the entire plot into 300 separate squares of 10 × 10 m, as a random effect. The model selection was based on AIC, and the Wald test was used to evaluate the variables retained in the final model. The spatial analysis and the GLMMs were performed within the statistical software package R3.2.3 (R Core Team 2016).

Results

The mortality of all tree species at the time of the typhoon disturbance in density and basal area was 7.3% and 11.0%, respectively (Table 2). In particular, *A.*

sachalinensis showed markedly high mortality (20.9% in basal area) among species. The mortality of large trees (>50 cm DBH) was particularly high, showing 27.6% at the time of disturbance (Figure 3). In contrast, the annual mortality was approximately 2–4% during the post-disturbance period, with averages of 3.5% and 2.8% during the periods of 1–2 years later and 3–7 years later, respectively, far exceeding the level recorded during the pre-disturbance period (average of 0.9%). During the post-disturbance periods, large *A. sachalinensis* trees again showed particularly high mortality. The cumulative basal area of dead *A. sachalinensis* trees during the 7-year post-disturbance period reached approximately 80% of that which occurred at the disturbance (Figure 3b).

During the pre-disturbance period, the major form of death of *A. sachalinensis* trees was standing dead (62.3% in basal area) followed by snapping (Figure 4). In contrast, at the time of disturbance, snapping accounted for 68.5%, with the other trees were uprooted. In 1–2 years after the disturbance, uprooted trees accounted for 57.1%. In contrast, standing dead trees increased gradually and reached 83.7% in 3–7 years after the disturbance.

In total, stem growth in terms of the mean annual increment of basal area of *A. sachalinensis* trees did not change considerably before and after the disturbance; the growth of trees were plotted along both sides of the equivalent line (Figure 5). However, most of the dead trees occurred in the post-disturbance period of 3–7 years later showed a reduction in growth after the disturbance (14 of 17 trees were plotted below the equivalent line; Figure 5). With regard to the linear mixed model for tree growth (Table 3), a positive effect of own basal area and a negative effect of the amount of neighbouring living trees were found. Furthermore, the increment in basal area decreased with increasing amount of neighbouring dead trees occurred at the

disturbance. In contrast, the mortality of *A. sachalinensis* trees was positively influenced by the own basal area and the amount of neighbouring dead trees, suggesting that the greater size of trees or the more locally severe the disturbance, the higher the subsequent mortality.

The result of the analysis using Ripley's L function demonstrated that the deaths of *A. sachalinensis* in 1–2 and 3–7 years after the disturbance spatially co-occurred with dead trees in the disturbance on a spatial scale of ≤ 5 and 10–25 m (Figure 6).

Discussion

In the current study, mortality of *A. sachalinensis* trees during a period of 7 years after the disturbance was considerably higher than that during the pre-disturbance period (Figure 3a). Furthermore, the total amount of deaths in the post-disturbance period ($1.7 \text{ m}^2 \text{ ha}^{-1}$) reached a level comparable (i.e., 80%) with that in the disturbance ($2.1 \text{ m}^2 \text{ ha}^{-1}$, Figure 3b). Thus, we can conclude that the subsequent deaths of trees after the disturbance have a significant influence, which is not negligible in the dynamics of a natural mixed forest. Consequently, this study indicates that the evaluation of wind disturbance clearly requires not only a measurement at the time of disturbance but also that during the period of several years to a decade after the disturbance.

The results of the GLMM and spatial analyses (Table 3; Figure 6) supported the hypothesis 1: the deaths of trees due to the typhoon will extend over time and space. More specifically, deaths of *A. sachalinensis* trees that occurred in the post-disturbance period show a spatial pattern of gradual expansion around *A. sachalinensis* trees died in the disturbance (Figure 6). This is consistent with the findings of previous studies, demonstrating “gap expansion” in natural forests dominated by *Abies* species (Marchand et al. 1986; Worrall et al. 2005; Nagel & Svoboda 2008; Suzuki 2016), including *A. sachalinensis* (Sato 1994; Yoshida et al. 2006; Noguchi & Yoshida 2009).

Our findings in this study suggest that multiple mechanisms are discernible as the driver of the gap expansion. One major mechanism would be the delayed mortality of severely damaged, but surviving trees, as indicated by many uprooted trees in 1–2 years after the disturbance (Figure 4). Another possible mechanism is the alteration of microclimatic condition, which can result in a strong wind penetration and chronic stresses in residual trees (Rizzo & Harrington 1988; Worrall et al. 2005). It is also possible that the tree deaths occurred due to physiological degeneration induced by the strong winds, which may have disrupted the water-conduction systems of trees by a temporal stem shrinking (Liu et al. 2003). On the other hand, damage caused by insects such as bark beetles can also be responsible for the gap expansion. These insects have been reported to increase significantly after the supply of large quantities of deadwoods (Gandhi et al. 2007; Raffa et al. 2008). Nevertheless, we suppose that the impact of insects was not important in this case, because there have been few reports of large-scale insect outbreaks on *A. sachalinensis*. In addition, we could find no clear supportive evidence, such as a remarkable number of holes and resin drops induced by beetles in the target trees.

We note that most of previous studies examining the gap expansion have not demonstrated a fine-scale temporal change after disturbance by monitoring. The current study confirmed the pattern of the death of *A. sachalinensis* trees (uprooted, snapped and standing dead) changed gradually within a decade after the wind disturbance (Figure 4). Therefore, the current study supports hypothesis 2: the cause of the deaths of trees following the wind disturbance changes with time. It is highly likely that direct but delayed effects of disturbance were the main contributing factors for the deaths 1–2 years later, whereas physiological or biological stresses through changes in forest stand structure was responsible for the deaths 3–7 years later (Figure 4; Figure 5). Despite the

absence of strong wind during the post-disturbance period 1–2 years later (Figure 1), an increase in the proportion of uprooted deaths (Figure 4) suggests that root systems of some trees had been severely damaged at the time of the disturbance as a result of the tree sway by strong winds (Stokes 1999). In contrast, in the post-disturbance period of 3–7 years, a notable increase in the proportion of standing death (Figure 4) and mortality of trees with lower growth rate (Figure 5) suggest that the process of growth reduction triggered by the disturbance indirectly caused higher mortality during this period.

We found a dynamic pattern in a natural mixed stand dominated by *A. sachalinensis*, where the influence of a wind disturbance not only results in direct severe windthrow but also produces a number of dead trees of various forms in a spatiotemporally extending pattern. This suggests that biodiversity and various forest ecosystem functions would also be gradually altered for a period of several years to a decade after the disturbance. Although the prediction of extreme climatic events under the global warming is still unclear (IPCC 2014; Takano et al. 2016), there are studies indicating the increase of intense tropical cyclones in the near future (Knutson et al. 2010). Therefore, it is increasingly important to evaluate a cascading impact triggered by a disturbance over the long term to evaluate the effect of a large-scale typhoon.

Acknowledgements: We sincerely thank K. Yasue for his instruction for the annual ring analysis. Thanks are extended to Y. Ohno, T. Hiura, S. Uemura and M. Kobayashi for their critical advices on this study. We also thank technical staff of the Uryu Experimental Forest, for their assistance in the field work, and members of the Nayoro laboratory (especially T. Inoue, F. Takeuchi, H. Umegane, I. Asada and N. Hyodo) for their valuable supports for this study.

Funding details: This study was supported by the research project fund from the Ministry of Education, Culture, Sports, Science and Technology of Japan (No. 26450187 and 26450205).

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Table 1. Tree species composition of the study stand at the beginning (Apr 2002) of the study period.

Table 2. Proportion of trees died at the wind disturbance in the study plot.

Table 3. Summary of the generalized linear mixed model (GLMM) to examine growth and mortality of *A. sachalinensis* trees during the post disturbance period.

Figure 1. (a) Location of the study site and the maximum momentary wind speed by Typhoon SONGDA in Hokkaido (based on the data of the Japan Meteorological Agency; only the wind records in northern Hokkaido are shown). (b) The maximum momentary wind speed recorded in the Uryu Experimental Forest during the study period

Figure 2. DBH-class distributions in the study stand at the beginning (2002) of the study period.

Figure 3. (a) Changes in mortality in terms of basal area of *A. sachalinensis* trees during the study period, and (b) cumulative basal area of dead trees during the post disturbance period (line), in comparison with that at the time of disturbance (bar). The year represents the growing season (i.e. from spring of the current year to the subsequent spring) except for 2004, which indicate only the period until the disturbance in September.

Figure 4. Proportion of the form of death in *A. sachalinensis* (in terms of basal area) in the four periods.

Figure 5. Stem growth (mean annual basal area increment) of *A. sachalinensis* trees during the period before and after the disturbance. The equivalent line is shown.

Figure 6. Spatial relationships of the distribution of dead trees at the disturbance with (a) those of *A. sachalinensis* supplied at the post-disturbance 1-2 years later and (b) 3-7 years later periods. The Ripley's L values as a function of the analysis scale (r) are shown with solid lines. The area enclosed by the two dotted lines indicate the 95% confident interval derived from the simulation assuming random distribution. See text for the details.

Table 1. Tree species composition of the study stand at the beginning (Apr 2002) of the study period.

Species	Density ha ⁻¹	Basal area cm ² ha ⁻¹	Diameter at breast height cm		
			Mean	(S.D.)	Max.
<i>Abies sachalinensis</i>	115	10.8	29.9	(16.5)	84.8
<i>Picea glehnii</i>	50	8.4	39.0	(22.7)	95.4
<i>Quercus crispula</i>	21	2.3	31.2	(20.3)	110.1
<i>Betula ermanii</i>	28	1.5	22.9	(10.4)	51.0
Other broadleaved species	97	4.3	21.7	(11.0)	63.1
Total	312	27.3	28.0	(17.1)	110.1

Tree individuals with dbh equal to or greater than 10 cm were considered.

Table 2. Proportion of trees died at the wind disturbance in the study plot.

Species	Mortality at the disturbance(%)	
	Density	Basal area
<i>Abies sachalinensis</i>	10.6	20.9
<i>Picea glehnii</i>	4.1	5.1
<i>Quercus crispula</i>	0.0	0.0
<i>Betula ermanii</i>	1.3	2.2
Other broadleaved species	5.8	7.8
Total	7.3	11.0

Trees with dbh equal to or greater than 10 cm were considered.

Table 3. Summary of the generalized linear mixed model (GLMM) to examine growth and mortality of *A. sachalinensis* trees during the post disturbance period.

period	AIC	Explanatory variables			Inter- cept	S.D. of the random effect
		Own basal area	Living neighbors	Dead neighbors		
Mean basal area increment	542.6	0.01 (<0.01)	-4.85 (<0.01)	-12.40 (0.02)	10.30 (0.08)	0.88
Mortality	51.0	0.003 (0.01)	3.64 (0.09)	9.49 (0.01)	-5.00 (0.50)	6.42

Values in parentheses show the p-value. See text for the details.

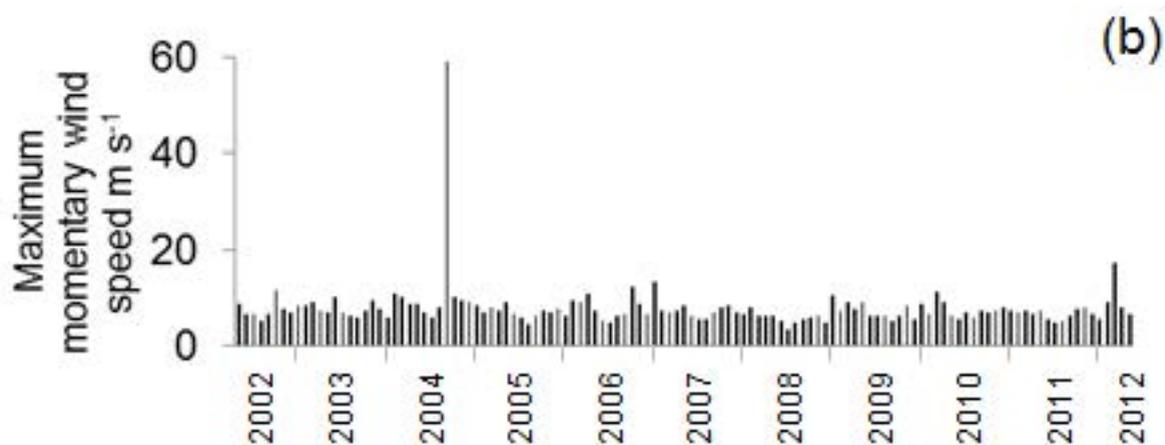
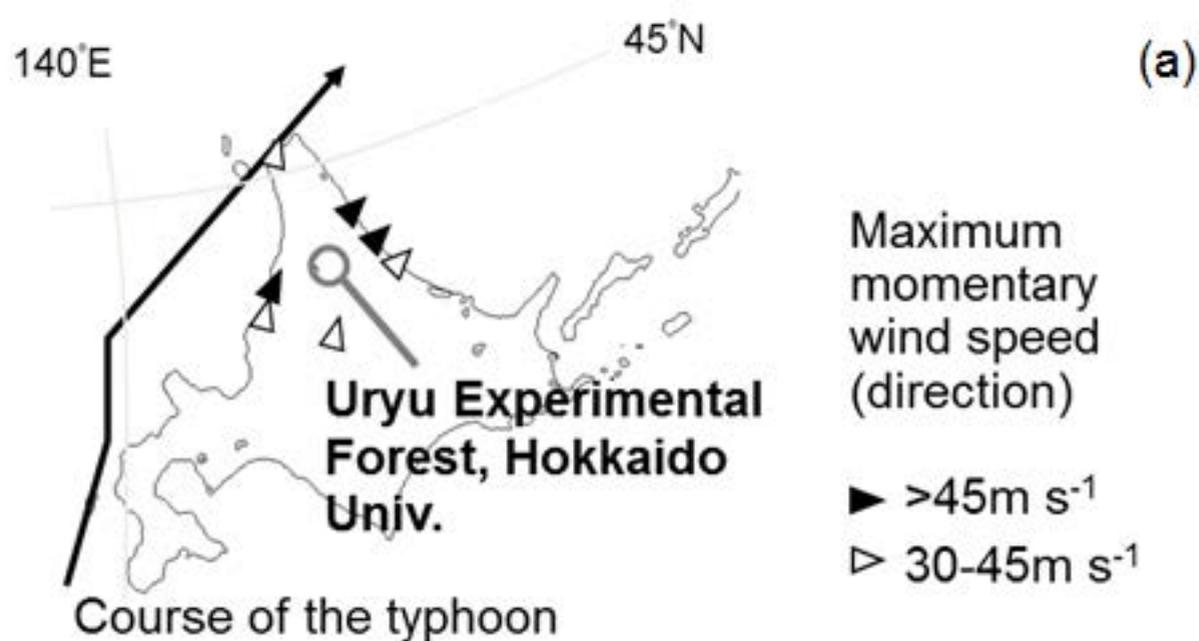


Figure 1. (a) Location of the study site and the maximum momentary wind speed by Typhoon SONGDA in Hokkaido (based on the data of the Japan Meteorological Agency; only the wind records in northern Hokkaido are shown). (b) The maximum momentary wind speed recorded in the Uryu Experimental Forest during the study period.

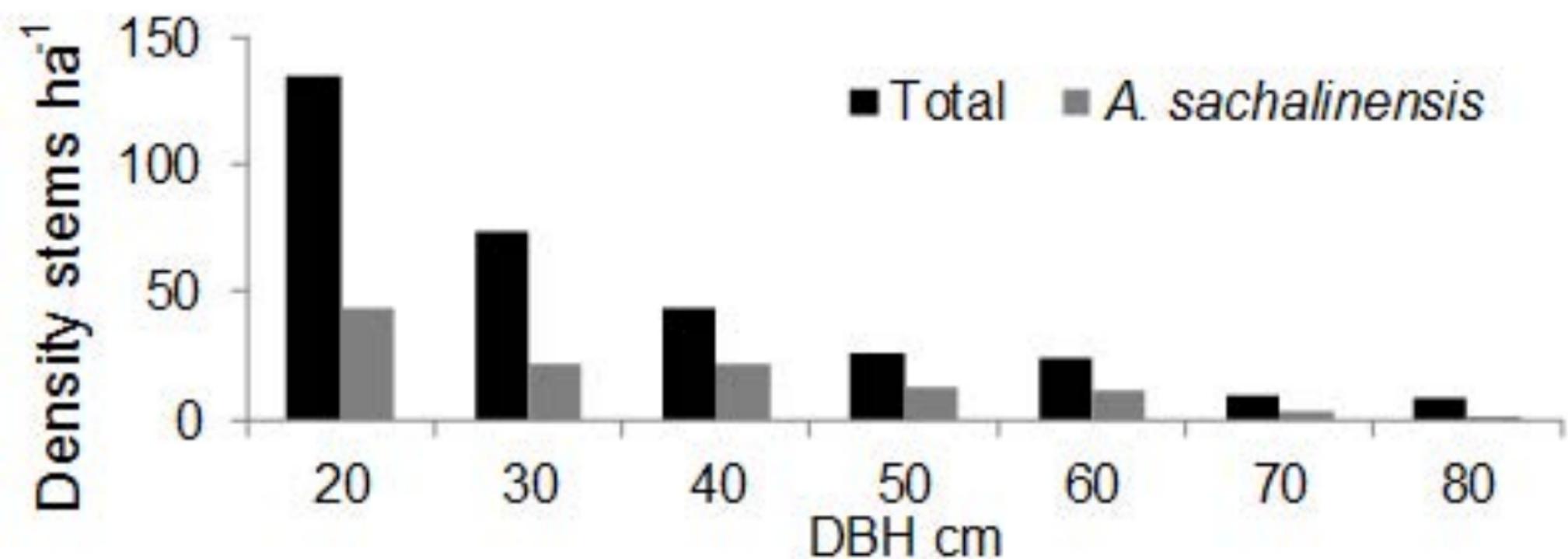


Figure 2. DBH-class distributions in the study stand at the beginning (2002) of the study period.

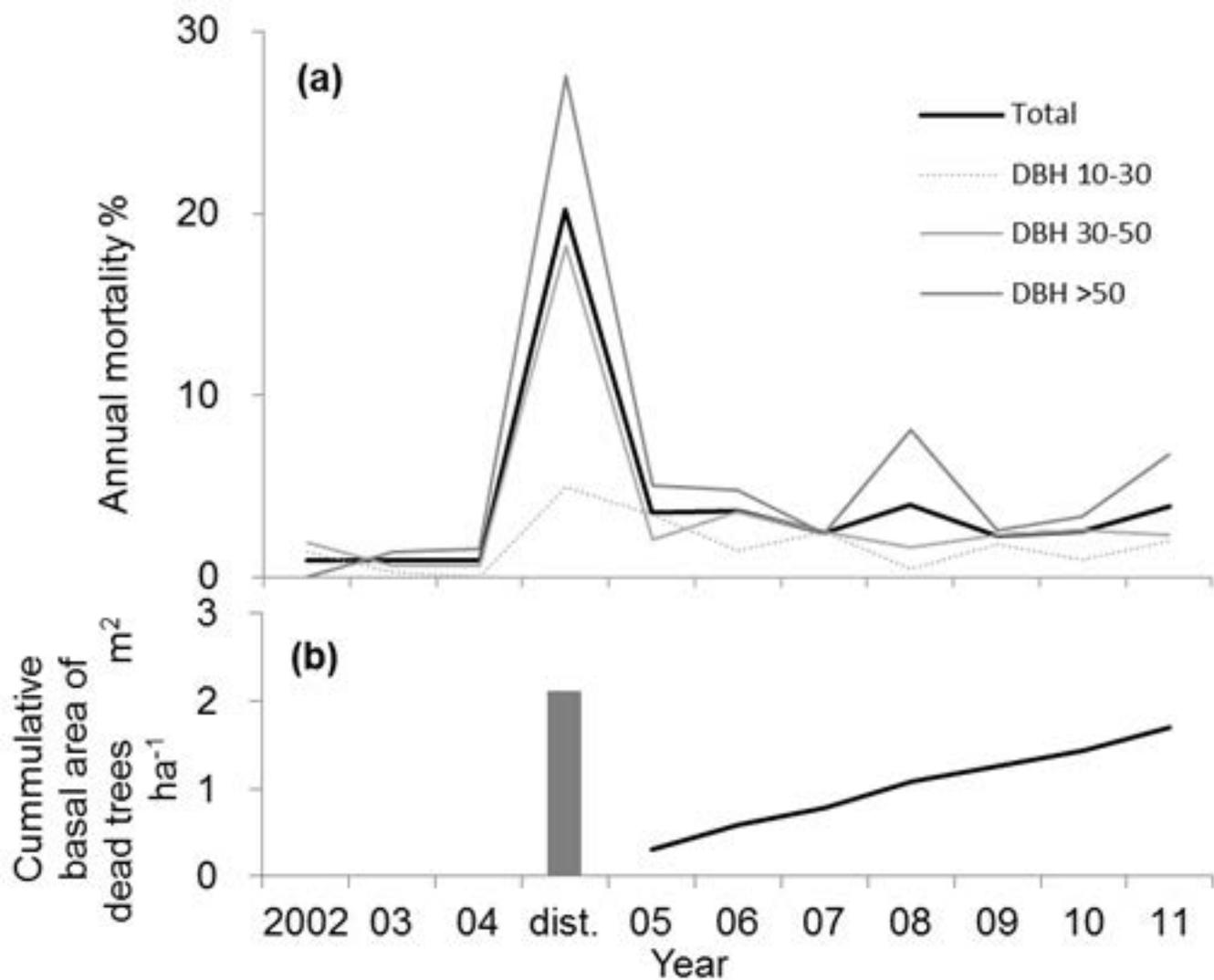


Figure 3. (a) Changes in mortality in terms of basal area of *A. sachalinensis* trees during the study period, and (b) cumulative basal area of dead trees during the post disturbance period (line), in comparison with that at the time of disturbance (bar). The year represents the growing season (i.e. from spring of the current year to the subsequent spring) except for 2004, which indicate only the period until the disturbance in September.

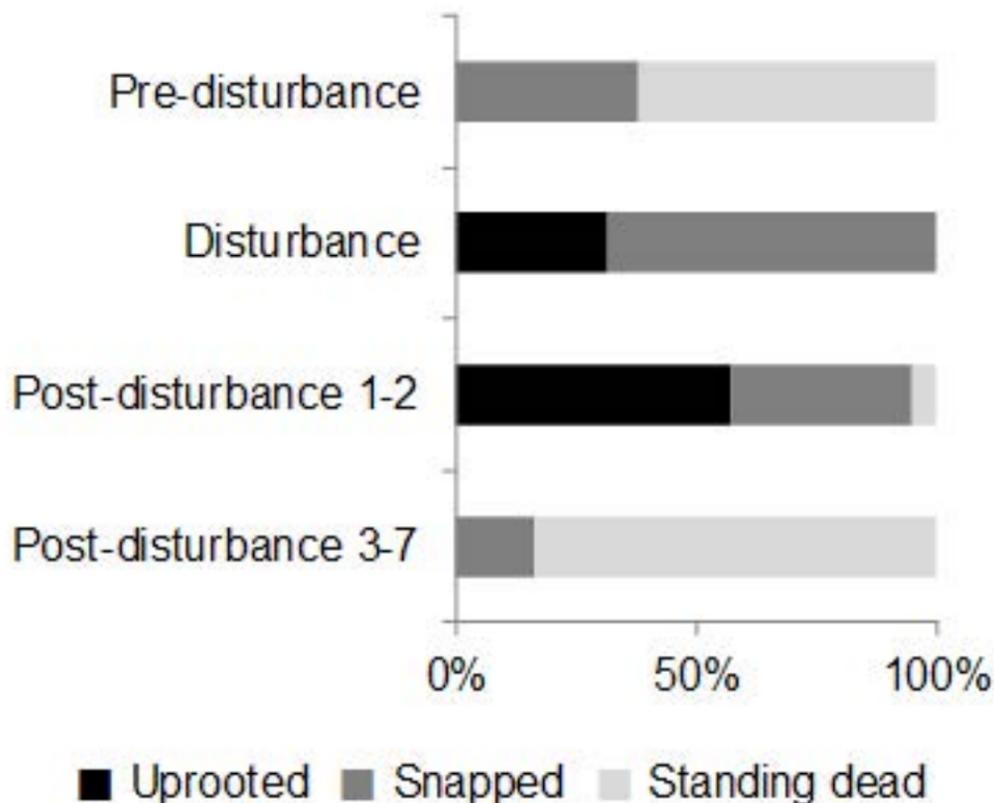


Figure 4. Proportion of the form of death in *A. sachalinensis* (in terms of basal area) in the four periods.

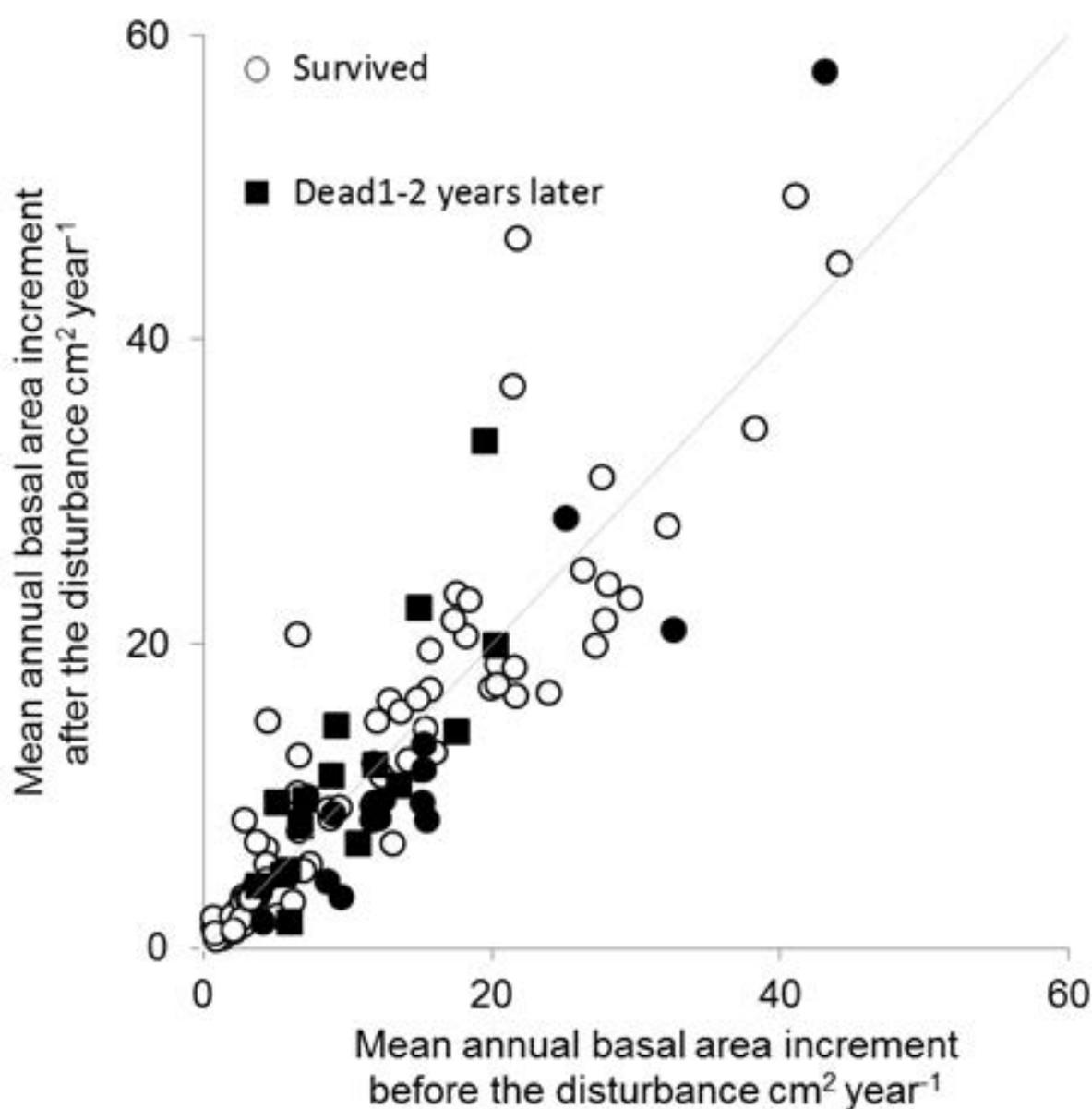


Figure 5. Stem growth (mean annual basal area increment) of *A. sachalinensis* trees during the period before and after the disturbance. The equivalent line is shown.

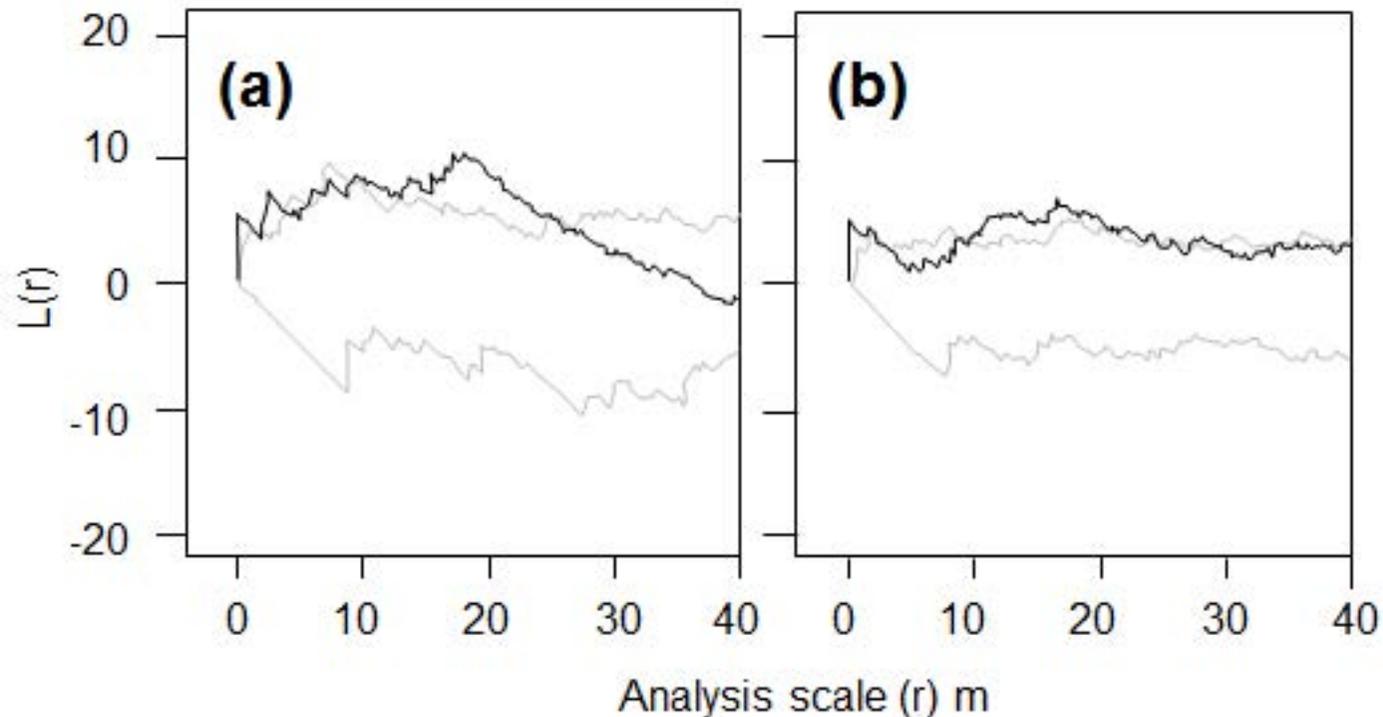


Figure 6. Spatial relationships of the distribution of dead trees at the disturbance with (a) those of *A. sachalinensis* supplied at the post-disturbance 1-2 years later and (b) 3-7 years later periods. The Ripley's L values as a function of the analysis scale (r) are shown with thick (black) lines. The area enclosed by the two thin (gray) lines indicate the 95% confident interval derived from the simulation assuming random distribution. See text for the details.