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Key-factors and key-stages that determine the leaf longevity of an evergreen broad-leaved tree, *Neolitsea sericea* (Lauraceae) at different growing sites in southern Japan

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Abstract Chronological distribution pattern of leaves is an important factor to determine plant productivity in relation to photosynthesis. Therefore, intensive studies of leaf longevity are essential in plant ecology. Leaf longevity of *Neolitsea sericea* (Lauraceae) was surveyed from 1972 to 1995. Mean leaf longevity varied from 5.6 to 53.8 months among different year classes of leaf emergence. To detect factors and stages determining the leaf longevity, we adopted the method of key-factor/key-stage analysis. We categorized *N. sericea* trees into four

groups; short and tall trees in an evergreen broad-leaved forest, short trees along the forest edge, and short trees in a Moso bamboo forest, where *N. sericea* grows as an understory plant. This categorization enabled us to realize how the factors and stages differently influenced leaf longevity at different sites. Four groups of factors (growing site, cecidomyiid gall induction, stem boring by a cerambycid, typhoon) and eight stages (every 6 month after leaf emergence until a leaf age of 48 months) were distinguished in the analysis. Effects of annual precipitation and annual mean temperature were evaluated separately. In a bamboo forest, cerambycid negatively affected leaf survival in the first year. In an evergreen broad-leaved forest, cerambycid and typhoon affected leaf survival of short and tall trees but cerambycid damage was compensated in later stages. Short trees along the forest edge suffered severe leaf fall from typhoon but were positively affected by annual precipitation. This study gives suggestions for better understanding of chronological distribution patterns of leaves.

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Introduction

In addition to the amount of leaves and their photo-
synthesis ability, the spatial and chronological distribu-
tion patterns of leaves are important in determining
plant productivity (e.g., Kikuzawa 2005; Kikuzawa and
Lechowicz 2011). The spatial distribution pattern is re-
lated to the height and shape of trees and the chrono-
logical distribution pattern includes shoot extension
module, timing of defoliation and duration of leaf per-
sistence (a synonym for “leaf longevity”). It may be ideal
for plants if they can bear leaves with a strong photo-

synthesis ability over years if possible but this ability declines with leaf age (Chabot and Hicks 1982; Kikuzawa 1991, 1995; Kikuzawa and Lechowicz 2011). To ascertain the relationship between photosynthesis ability and leaf age, we must gather more information on leaf longevity.

Leaf longevity has been calculated for various plant species, such as conifers (e.g., Kohyama 1980; Ewers and Schmid 1981; Schoettle 1990), evergreen broad-leaved trees in the warm-temperate zone (e.g., Nitta and Oh-sawa 1997; Yukawa et al. 2016b), deciduous trees (e.g., Kikuzawa 1978, 1983, 1988; Kikuzawa et al. 1979; Navas et al. 2003), understory plants in a tropical montane forest (Shiodera et al. 2008), mangrove trees (e.g., Suarez 2003) and herbs (e.g., Diemer et al. 1992; Craine et al. 1999; Navas et al. 2003). Life table data on the leaf survival rate were shown for *Glycine max* (Linnaeus) Merrill (Fabaceae) (Miyaji and Tagawa 1979) and *Pinus tabulaeformis* Carrière (Pinaceae) (Xiao 2003). However, full-scale life table data based on long-term field surveys have not been provided to analyze key-factors and key-stages that determine the leaf survival rate.

Leaf longevity is affected by various abiotic factors and growing conditions, such as light conditions (e.g., Nilsen et al. 1987; Kikuzawa 1989, 1995, 2003; Sterck 1999; Takenaka 2000; Osada et al. 2003; Reich et al. 2004; Vincent 2006), growing sites (Kai et al. 1991), leaf structural reinforcement (Mediavilla et al. 2008), precipitation (e.g., Casper et al. 2001), flooding (Terazawa and Kikuzawa 1994), temperature (Wright relationships with their host et al. 2005; van Ommen Kloeke et al. 2011), temperature-mediated favorable period duration (Kikuzawa et al. 2013) and nutrient (e.g., Lajtha and Whitford 1989; Kikuzawa et al. 2002; Ren et al. 2013; Piper and Fajardo 2014) (see Kikuzawa 2005; Kikuzawa and Lechowicz 2011 for many other references to leaf longevity).

Among biotic factors, leaf-chewing herbivores are less influential, mediated because data indicating that leaf consumption is much less than leaf production (less than 5%) have been presented on many occasions (e.g., Kikuzawa et al. 2002; Yamasaki and Kikuzawa 2003). In contrast, endophytic herbivores such as gall-inducers (Sunose and Yukawa 1979; Yukawa and Tsuda 1986; Yukawa et al. 2016b), leaf miners (e.g., Faeth et al. 1981), and stem borers (e.g., Yukawa 1977) are well known to cause leaf fall. However, a leaf miner inhibits premature abscission of leaves with mines (e.g., Oishi and Sato 2007).

In turn, the early fall of galled leaves directly or indirectly influences the population dynamics and other ecological traits of the gall inducers and their associated arthropod organisms, such as parasitoids, predators, inquiline (organisms that live in the galls together with the gall inducers) and successors (organisms that use vacated galls after the departure of gall inducers or parasitoids) (Sunose and Yukawa 1979; Yukawa 1983; Yukawa and Akimoto 2006; Yukawa et al. 2016b). A wide variety of gall inducers utilize many plant species as

hosts, and most are mono- or oligophagous having close relationships with their host plants (e.g., Yukawa and Masuda 1996). Therefore, the longevity of host leaves that is related to interaction between host plants and endophytic insects is one of the important aspects of ecological entomology. In particular, the chronological distribution patterns of leaves determine the life history strategy of leaf gall midges because some of them require 2 or more years to complete one generation on the host leaves by entering extended diapause (Redfern 1975; Maeda et al. 1982; Ohno and Yukawa 1984; Takasu and Yukawa 1984; Redfern and Hunter 2005; Yukawa et al. 2013).

Since 1970, in Kagoshima, southern Kyushu, Japan, J Yukawa has been studying the long-term population dynamics of ten cecidomyiid species (Diptera) that induce fruit or leaf galls on evergreen broad-leaved trees such as *Neolitsea sericea* (Blume) Koidzumi, *Machilus japonica* Siebold et Zuccarini (Lauraceae) and *Ligustrum japonicum* Thunberg (Oleaceae).

Moso bamboo *Phyllostachys edulis* (Carrière) J. Houz (Poaceae) commonly grows in Kyushu. Particularly, *N. sericea* and *M. japonica* are common understory trees in the bamboo forests and frequently bear cecidomyiid galls. Therefore, Moso bamboo forests are one of the important habitats for some cecidomyiids.

Pseudasphondylia neolitseae Yukawa (Diptera: Cecidomyiidae) induces leaf galls on *N. sericea* that grows in secondary forests dominated by evergreen broad-leaved trees (EBLF hereafter) and in Moso bamboo forests. Throughout the population study, JY has accumulated life table data for the leaves of *N. sericea* together with its associated herbivores in those forests.

The purpose of this paper is to identify key-factors and key-stages (= key leaf ages) that determine the leaf survival rate of *N. sericea* under different growing conditions and to assess the relative strength of abiotic and biotic effects. To identify the factors and stages, we categorized *N. sericea* trees into four groups according to their height and growing sites; short trees and tall trees in the EBLF; short trees along the forest edge; and short trees in the Moso bamboo forest. This categorization enables us to understand how the factors and stages differently influence the leaf longevity of *N. sericea* trees growing at different sites.

For this purpose, we analyzed full-scale long-term life table data on the survival rate of *N. sericea* leaves using a key-factor/key-stage analysis. This method was proposed by Yamamura (1999) to analyze long-term life table data on animal populations (see “Materials and methods” below for details of this method). This is the first attempt to use the method to analyze the long-term life table data on a plant species. The data include both abiotic and biotic factors, which have never been analyzed simultaneously. With this method, we can make suggestions for better understanding of the chronological distribution patterns of leaves, which in turn have useful implications for analyzing the survival rate and

population dynamics of associated endophytic herbivores.

Materials and methods

Study area

At the same time as field surveys on the population dynamics of the leaf gall midge, *P. neolitseae*, leaf longevity of its host plant, *N. sericea* was investigated from 1978 to 1995 in an EBLF at Shiroyama, Kagoshima City (31°35'49"N, 130°33'03"E), and 1972–1995 in a forest of Moso bamboo *Phyllostachys edulis* (Carrière) J. Houz (Poaceae) in Ono, Kagoshima City (31°61'64"N, 130°52'09"E, about 3 km from Shiroyama to the NNW). The EBLF at Shiroyama is on a hilltop, ~ 100 m a.s.l., and the bamboo forest is in a small valley, ~ 30 m a.s.l.

The canopy of *Castanopsis sieboldii* (Makino) Hatusima ex T. Yamazaki et Mashiba (Fagaceae) and *Cinnamomum camphora* (Linnaeus) J. Presl (Lauraceae) covered the EBLF. In addition to *N. sericea* and *C. camphora*, the following tree species of Lauraceae were growing as understory vegetation in the EBLF: *Cinnamomum tenuifolium* (Makino) Sugimoto ex H. Hara, *Litsea lancifolia* (Roxburgh ex Nees in Wallich) Bentham and Hook, *Litsea longifolia* (Nees) Alston, *Machilus thunbergii*, *Neolitsea aciculata* (Blume) Koidzumi. These lauraceous trees including *N. sericea* can be host plants of a cerambycid beetle, *Oberea hebescens* Bates (Coleoptera: Cerambycidae), details of which will be given later. In the bamboo forest, only *N. sericea* and *Machilus japonica* were growing as representatives of Lauraceae.

Neolitsea sericea and field survey

Neolitsea sericea is a flush type and medium-size evergreen broad-leaved tree up to 10 m tall and is distributed across Japan (except Hokkaido), southern Korea, China and Taiwan (including Orchid Island and Green Island).

Trees surveyed (census trees hereafter) were divided into four categories according to tree height and growing site: (1) six to 21 short trees in the bamboo forest at Ono, (2) five to 17 short trees (1.5 to 2.5 m height) in the interior of the EBLF at Shiroyama, (3) two tall trees (> 2.5 m) interior of the EBLF at Shiroyama, and (4) two to five short trees growing along the forest edge at Shiroyama. The number and height of short census trees varied interannually because those trees and their branches were occasionally killed or stunted by cerambycid attack and rarely by artificial damage, small-scale landslide and the accumulation of volcanic ash fall from Mt. Sakurajima. In such cases, we compensated next year by selecting some short trees that were growing nearby with similar height. Male and female trees were not distinguishable because they were juveniles.

Neolitsea sericea exhibits simultaneous leaf emergence from late April to early May. Therefore, we can distinguish leaves of different year classes (Fig. 1a). Newly emerged shoots of individual years were marked with different colored plastic tapes. By this marking, leaves attached to the shoots of the different year-classes were distinguished. For each year class of leaves, every early May, we recorded the number of fresh leaves emerged on newly extended shoots of the census trees. Thereafter, we repeated field surveys at 6-month intervals to record the number of all leaves remaining on the shoots of census trees in every early November (occasionally late October) and early May until all leaves of each year class fell.

To calculate leaf longevity, we assumed that the number of leaves decreased linearly with time during 6 months between two successive surveys and regarded the intermediate months (3, 9, 15, 21, 27, 33, 39, 45, 51 or 57 months) between the two surveys (0 and 6, 6 and 12, 12 and 18 months, and so on) to be the longevity of leaves that had fallen during the 6 months. By summing up longevities of each leaf and dividing the total value by the number of leaves surveyed, we calculated the mean leaf longevity for each year class.

Pseudasphondylia neolitseae

Pseudasphondylia neolitseae (Diptera: Cecidomyiidae) is a relatively large-size gall midge with female wing length 3.3–4.0 mm (Yukawa 1974). This gall midge occurs in Japan and southern parts of the Korean Peninsula (Yukawa 2014) and induces leaf galls only on *N. sericea* (Fig. 1b immature galls and 1c mature galls). One cecidomyiid larva inhabits each gall. In southern Kyushu, *P. neolitseae* is mostly univoltine (Yukawa 1974) and a few individuals exhibit the 2-year type life history pattern (Takasu and Yukawa 1984). Eggs are laid in overwintered leaf buds with lengths ranging from 22 to 38 mm, and hatched within a week (Yukawa et al. 1976). Early stage galls appear on the freshly emerged leaves. First instars pass through summer and develop to second and third stadia in October and November. Pupation takes place in the leaf galls on the host trees in early to late March. The pupal stage lasts about 2 weeks, and adults emerge in April.

Every early May, the relative abundance of galled and ungalled fresh leaves was surveyed by examining the presence or absence of early stage galls (Fig. 1b) induced by the first instars of *P. neolitseae*. We examined whether the relative abundance of galled to ungalled leaves affects leaf survival rates (see below, *Key-factor/key-stage analysis*).

Oberea hebescens

Oberea hebescens (Fig. 1d) is a cerambycid stem borer of trees of Lauraceae, such as *N. sericea*, *C. tenuifolium* and

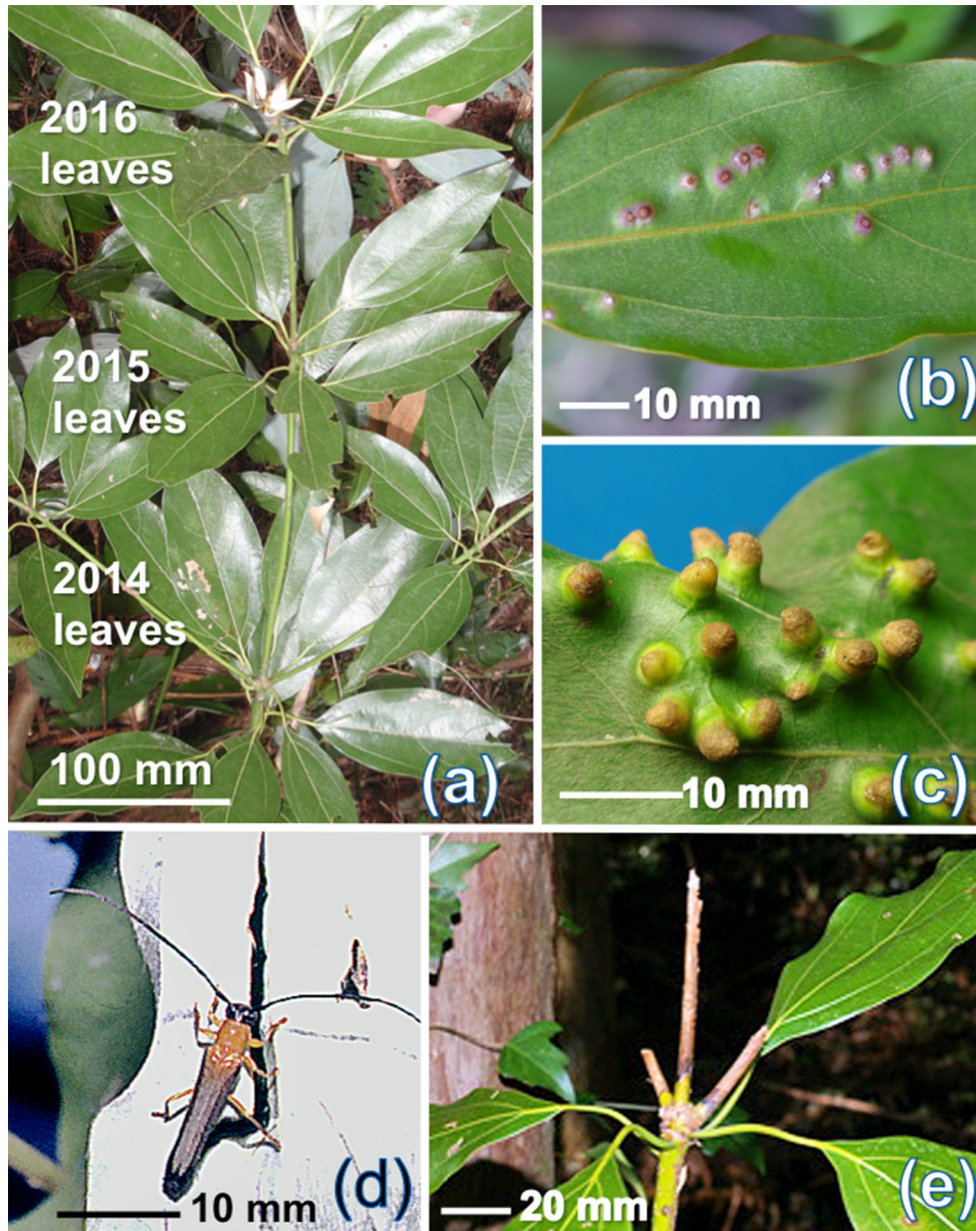


Fig. 1 **a** Leaves of *Neolitsea sericea* belonging to different-year classes of leaf emergence. **b** Young stage of leaf galls induced by *Pseudasphondylia neolitseae*. **c** mature stage of leaf galls (*ibid.*).

d adult of *Oberea hebescens* and its feeding scar on midrib of *Neolitsea sericea*. **e** stems of *Neolitsea sericea* damaged by cerambycid

Lindera praecox (Siebold et Zuccarini) Blume (Ohbayashi and Niisato 2007). In May, females of *O. hebescens* lay their eggs sequentially in the distal portion of newly extended shoots. Through mid-May to October, hatched larvae bore tunnels downward in the shoot toward the basal end of current twig and subsequently toward the 1-year-old twigs (Fig. 1e). Current leaves attached to the infested shoot dry out as a result of the original infestation. When the cerambycid larvae reach the 1-year-old twig, leaves attached to non-oviposited current shoots extending from the same 1-year-old shoot

dry out. Similarly, the leaves attached to twigs extending from the same 2- or 3-year-old twigs dry out (Yukawa 1977). At the same time, galls on these leaves dry out and cecidomyiid larvae inhabiting the galls die (Yukawa and Akimoto 2006). Adults of *O. hebescens* feed on the midribs of lauraceous plants (Fig. 1d), but this infestation was negligible in contrast to the prominent damage of shoots and twigs by larvae.

Every May to July, we recorded the number of current shoots, 1-, 2- and 3-year-old twigs of *N. sericea* that had been infested by the cerambycid.

Meteorological data

Meteorological data on monthly precipitation, monthly mean temperature and typhoons that had passed near Kagoshima City were obtained from the Japan Meteorological Agency. Annual precipitation was expressed as the sum of monthly precipitation from May (time of leaf emergence) through the following April. Annual precipitation varied tremendously, from 1175 to 3279 mm. The relative amount of annual precipitation in each year was expressed as a deviation from mean annual precipitation for the survey period. Annual mean temperature was calculated by dividing the sum of monthly mean temperature from May through the following April by 12 (months). Mean annual temperature fluctuated from 15.9° to 18.5 °C from 1972 to 1990.

The strength of each typhoon was scored according to the maximum wind velocity as follows: 1.0 (15 to 29.9 m/s), 1.33 (30 to 44.9 m/s), 1.67 (45 to 54.9 m/s) and 2.0 (> 55 m/s). Then, the typhoon scores were summed every year and arranged successively from first to fourth years after leaf emergence of each year class.

Key-factor/key-stage analysis

To analyze the long-term life table data on animal populations, a “key-factor/key-stage analysis” was proposed by integrating the conventional key-factor analyses (e.g. Varley and Gradwell 1960) and ANOVA, emphasizing the importance of discriminating between

the key-factor and the key-stage (Yamamura 1999). By discriminating factors and stages, we can avoid all problems raised by Royama (1996) as to the conventional key-factor analysis (Yukawa et al. 2016a). The effectiveness of the analysis is demonstrated by using the life table data of *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae) (Yamamura 1999). This analysis identifies the key-factor, the key-stage, and the combination of factor and stage that is most influential in determining the fluctuation of total mortality. The key-factor/key-stage analysis was further extended to analyze longitudinal data in pharmaceutical experiments (Yamamura 2012). Yukawa et al. (2016a) used the key-factor/key-stage analysis to detect density-dependent and independent forces operating on the population of fruit gall midge *Asphondylia sphaera* Monzen (Diptera: Cecidomyiidae) on *Ligustrum japonicum* and to assess the relative strength of top-down and bottom-up effects.

We adopted this method for the first time to analyze long-term data on leaf longevity of *N. sericea*. We also used the term “stage” for “leaf age”, as has been used in life table studies of insects. An “R” function to perform key-factor/key-stage analyses is available from the following web site: http://cse.naro.affrc.go.jp/yamamura/Key-factor_analysis_program.html.

Leaf longevity and survival rate

We have suspected that leaf longevity varies among different year classes of leaf emergence because of an-

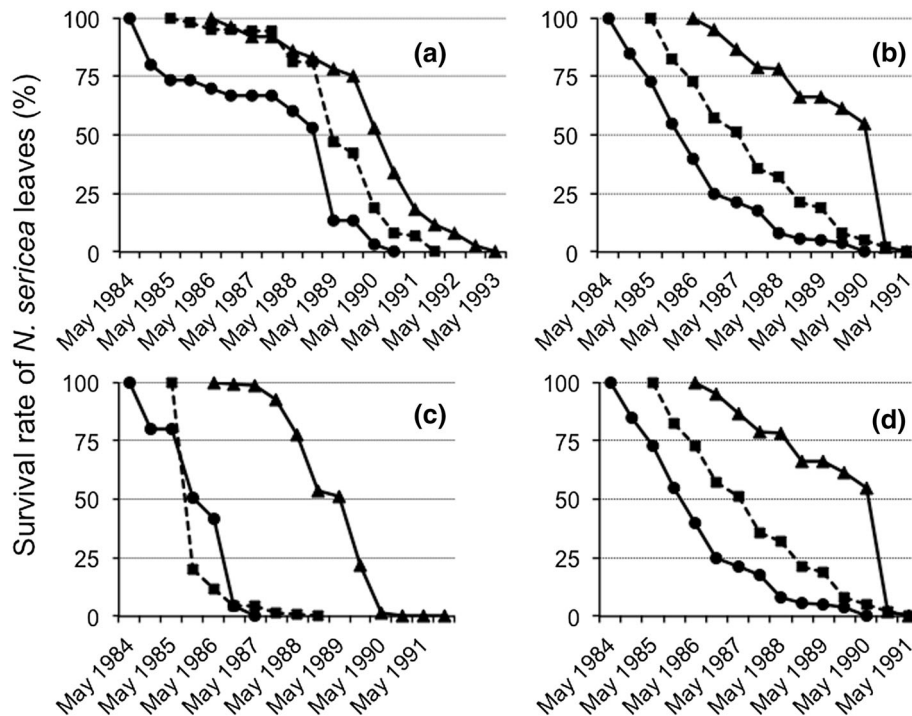


Fig. 2 Selected examples of survival curves of *Neolitsea sericea* leaves for year classes 1984 (circle with straight line), 1985 (square with dotted lines) and 1986 (triangle with straight line). **a** Short

trees in bamboo forest, **b** short trees in evergreen broad-leaved forest, **c** short trees along forest edge, **d** tall trees in the evergreen broad-leaved forest

nual variations in the factors that operate differently on leaf survival rates, resulting in an irregular end of final leaf fall. For example, all leaves fall completely before the age of 60 months (5 years) in some year classes, whereas some leaves survive more than 72 months (6 years) in other year classes. Figure 2 shows selected examples of survival curves of *N. sericea* leaves for year class 1984, 1985 and 1986 at the four growing sites. Thus, we cannot compare leaf survival rates in the final stage of leaf age among different year classes. Therefore, we tried to clarify the significant relationship between leaf longevities and leaf survival rates at the stage of 48 months, and we then used the survival rates at that stage for the key-factor/key-stage analyses.

Definition of stages

The survival rates of *N. sericea* leaves were divided into eight stages. Let N_t be the initial number of leaves emerged in May of the t th year. Let N_{8t} be the number of leaves surviving for 48 months (4 years) after leaf emergence. Then, the total survival rate, which is denoted by S_t , is given by N_{8t}/N_t . It is expressed by the multiplication of the survival rate in each stage:

$$S_t = s_{1t}s_{2t}s_{3t}s_{4t}s_{5t}s_{6t}s_{7t}s_{8t}, \quad (1)$$

where s_{it} is the leaf survival rate at the i th stage of the t th year. The survival rate at each stage is defined as follows:

s_{1t} : proportion of leaves surviving on the trees from leaf emergence to the 6th month

s_{2t} : proportion of leaves surviving on the trees from the 6th to 12th month

s_{3t} : proportion of leaves surviving on the trees from the 12th to 18th month

s_{4t} : proportion of leaves surviving on the trees from the 18th to 24th month

s_{5t} : proportion of leaves surviving on the trees from the 24th to 30th month

s_{6t} : proportion of leaves surviving on the trees from the 30th to 36th month

s_{7t} : proportion of leaves surviving on the trees from the 36th to 42th month

s_{8t} : proportion of leaves surviving on the trees from the 42th to 48th month

Equation (1) is expressed in natural logarithms as follows.

$$\log_e(S_t) = \sum_{i=1}^8 \log_e(s_{it}). \quad (2)$$

The logarithmic survival rate $\log_e(s_{it})$ is equivalent to $-k_i$ in the definition of Varley and Gradwell (1960). We added 0.5 to the number of leaves in calculating the logarithmic survival rate, to avoid $\log_e(0)$.

Definition of factors

We focused on the following four groups of factors that may principally influence the survival rate of *N. sericea* leaves: (1) growing sites of *N. sericea*; (2) the proportion of galled leaves at the time of leaf emergence; (3) the number of shoots or twigs damaged by the cerambycid *O. hebescens*; (4) the impact of typhoons. The number of shoots or twigs damaged by the cerambycid is a dynamic factor that changes interannually. Such a dynamic factor can be divided into sub-factors that correspond to the influence in different years. We consider four sub-factors for the cerambycid influence: the number of shoots or twigs damaged in (3–1) the first year, (3–2) the second year, (3–3) the third year, and (3–4) the fourth year from leaf emergence. Similarly, the influence of the typhoons was divided into four sub-factors: that in (4–1) first year, (4–2) the second year, (4–3) the third year, and (4–4) the fourth year from leaf emergence. In total, we considered the following 10 factors: (1), (2), (3–1), (3–2), (3–3), (3–4), (4–1), (4–2), (4–3), and (4–4). We assume that those factors had a dominant influence when we could not discriminate the influence of two or more factors.

The logarithmic leaf survival rate that emerged in May of the t th year is expressed by

$$\log_e(S_t) = A + gG_t + \sum_{j=1}^4 c_j C_{jt} + \sum_{j=1}^4 \tau_j T_{jt} + e_t, \quad (3)$$

where A is a variable that indicates the effect of sites (area effect); it changes with the growing site. G_t is a transformed variable that indicates the proportion of galled leaves. We transformed the proportion of galled leaves using the probit transformation with mean of 5 to enhance linearity. C_{jt} is a variable that indicates the number of shoots or twigs that were damaged by the cerambycid in the j th year from leaf emergence. T_{jt} is a variable that indicates the weighted number of typhoons that occurred in the j th year from leaf emergence. It is given by the sum of the typhoon score from census fields of Kagoshima City. The score of each typhoon was set to 1.0, 1.3, 1.6 and 2.0 according to the strength of typhoon (see “[Meteorological data](#)” for the scores). g, c_j, τ_j are constants. e_t is the error that indicates the fluctuation caused by other unknown factors. Table S1 indicates the mean and standard deviation (SD) of variables. The left side of Eq. (3) is identical to $\log_e(N_{8t}) - \log_e(N_t)$. That equation is expressed on an arithmetic scale as

$$S_t = \exp(A) \times (\exp(G_t))^g \times \prod_{j=1}^4 (\exp(C_{jt}))^{c_j} \times \prod_{j=1}^4 (\exp(T_{jt}))^{\tau_j} \times \exp(e_t). \quad (4)$$

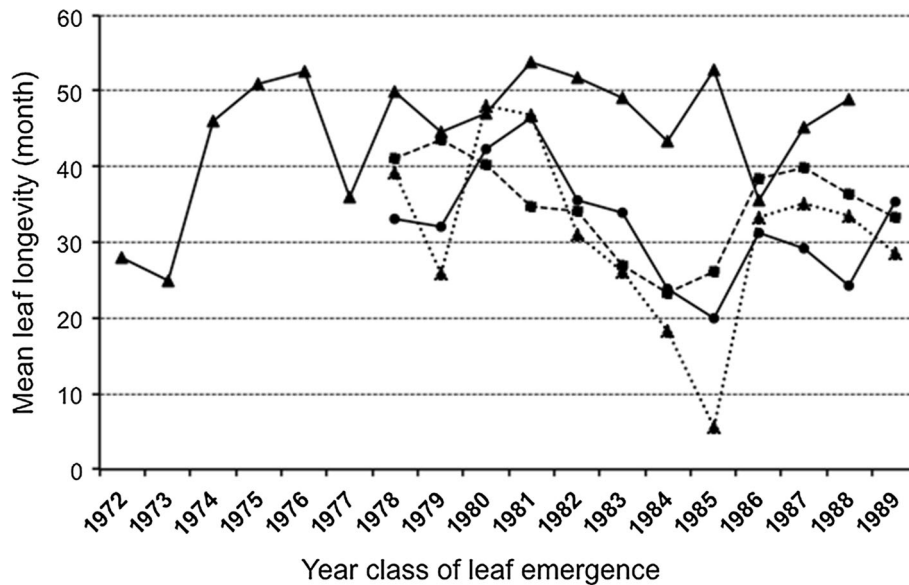


Fig. 3 Yearly changes in mean leaf longevity of *Neolitsea sericea* under different growing conditions. Short trees in bamboo forest (triangle with straight line), short trees along forest edge (square with dotted lines), tall trees in the evergreen broad-leaved forest (circle with straight line), short trees in evergreen broad-leaved

forest (triangle with dotted lines), short trees along forest edge (square with dotted lines), tall trees in the evergreen broad-leaved forest (circle with straight line)

Other climatic factors may also influence the survival rate to some extent. We can additionally use two groups of factors, precipitation and temperature. These factors are also dynamic, changing interannually, and so we can again divide the factors into the following sub-factors: annual precipitation in (5–1) the first year, (5–2) second year, (5–3) third year, and (5–4) fourth year after leaf emergence; the mean annual temperature in (6–1) the first year, (6–2) second year, (6–3) third year, and (6–4) fourth year after that emergence. If we use all factors including sub-factors in the analysis, however, key-factor/key-stage analysis (and ANOVA) does not work. This is because the number of parameters (18 in total) exceeds the number of datasets (17 in the bamboo forest and 12 in the EBLF), rendering the key-factor/key-stage analysis impossible. The influence of precipitation and temperature appears supplemental, so we performed a classical procedure for selecting parameters for those factors. We executed a preliminary multiple regression analysis for logarithmic total survival rate on these supplementary factors namely (5–1), (5–2), (5–3), (5–4), (6–1), (6–2), (6–3), and (6–4). The sub-factors that showed statistical significance ($P < 0.05$) were added to Eq. (3) for the key-factor/key-stage analysis. The results of these preliminary multiple regressions are given in Tables S2, S3, S4, S5, and S6. In the analysis including all census trees growing at four sites, no sub-factor from precipitation and temperature in the preliminary multiple regression had a statistically significant effect, so we used Eq. (3) without modification. In the subsequent analysis of trees in the bamboo forest, annual mean temperature in the second year (6–2) was statistically significant and hence it was added to Eq. (3). In the subsequent analysis of trees growing along the forest edge, annual precipitation in the first and second year

(5–1 and 5–2) was statistically significant, so these were added to Eq. (3). However, as seen later, the influence of these additional factors was negligible.

Results

Leaf longevity and survival rate

Mean leaf longevity varied tremendously from 5.6 to 53.8 months between year classes of leaf emergence and various environmental conditions at the growing sites in Shiroyama and Ono (Fig. 3). For example, mean leaf longevity decreased for the short trees along the forest edge in 1985 when a very strong typhoon impacted the census field. Key factors and key stages influencing leaf longevity will be referred to later in detail. Mean leaf longevity was significantly longer for the trees in the bamboo forest than for those in the EBLF (Table 1). The coefficient of variation indicated that the leaf longevity had less fluctuation for trees growing in the interior of the bamboo forest and EBLF than for those growing along the forest edge ($CV = 0.36$).

The longest individual leaf longevity was recorded at 108 months for the short trees in the bamboo forest, followed by 87 months for those in the EBLF and 75 months for those along the forest edge. This longevity was shortest for the tall trees in the EBLF.

The leaf survival rate between two successive stages (S_{1t} , S_{2t} , S_{3t} , S_{4t} , S_{5t} , S_{6t} , S_{7t} , and S_{8t}) and overall leaf survival rate for 48 months after leaf emergence (S_t) are shown in Tables S7, S8, S9, and S10 for all tree categories. Mean leaf longevities and overall survival rates of leaves at the stage of 48 (S_t) months were significantly correlated for all tree categories in the two census fields

Table 1 Comparison of mean leaf longevity in month among short and tall trees of *Neolitsea sericea* growing under different conditions

Tree category	No. of years surveyed	Mean leaf longevity*	Standard deviation	Minimum mean leaf longevity	Maximum mean leaf longevity	Coefficient of variance
Short trees in a Moso bamboo forest	17	44.69 a	8.41	24.94	53.80	0.19
Short trees in a broad-leaved evergreen forest	12	34.84 b	6.18	23.32	43.61	0.18
Tall trees in a broad-leaved evergreen forest	12	32.26 b	7.18	19.93	46.31	0.22
Short trees along the edge of broad-leaved evergreen forest	12	30.95 b	11.16	5.56	48.00	0.36

* Significant difference ($P < 0.0046$, ANOVA with the Bonferroni method) between mean values with different alphabetical letters

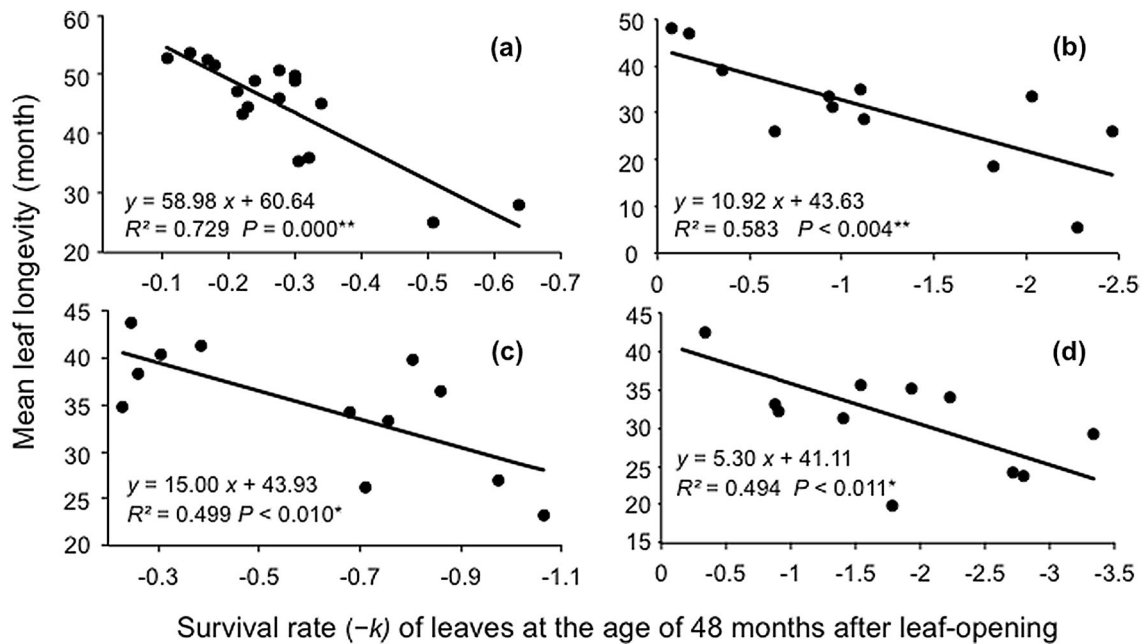


Fig. 4 Relationship between leaf survival rate at age 48 months after leaf emergence and mean leaf longevity of *Neolitsea sericea*. Leaf survival rate ($-k$) was calculated as follows: $-k = \text{Log}_e(\text{number of leaves surviving} + 0.5) - \text{Log}_e(\text{number of leaves emerged} + 0.5)$. In transforming original numbers to natural

logarithms, 0.5 was added to avoid number 0. **a** Short trees in bamboo forest, **b** short trees along the forest edge, **c** short trees in evergreen broad-leaved forest, **d** tall trees in the evergreen broad-leaved forest. * $P < 0.05$; ** $P < 0.01$; *** $P \leq 0.000$

(Fig. 4). These results allowed us to use the survival rates of leaves at the stage of 48-month within the key-factor/key-stage analyses, instead of leaf longevity that showed an irregular end of final leaf fall among the year classes of leaf emergence.

Key-factor/key-stage analysis

All trees

First, we analyzed leaf survival data including all census trees growing at the four sites. Table 2 indicates that the different conditions of growing site (A) was most influential in determining total survival rate (S_t); the relative amount of influence of the site was 42.9% as indicated by the ' S_t (total)' column in Table 2. The "Site" row of the " S_{8t} (42–48)" column in the table indicates that the influence of site was strongest in the period from 42 to

48 months (20.0%). The divided coefficients are shown in Table 3. The S_t (total) column in Table 3 indicates the overall coefficients of factors, which are identical to the estimates calculated by conventional ANOVA with a corner-point restriction. By comparing the overall coefficients of sites, we found that the survival rate in the EBLF was smallest (-3.52), whereas that in the bamboo forest was largest (0).

The S_t (total) column in Table 2 indicates that a typhoon in the third year (T3) was also influential in determining total survival rate (10.3%). Table 3 indicates that the divided coefficients for typhoons (T1, T2, T3, and T4) were almost negative for most stages, which indicated that the typhoon reduced the leaf survival rate through most stages.

The relative influence of site became very large upon analyzing all trees simultaneously. The influence of other factors became obscure in this overall analysis. Therefore, we next analyzed the leaf survival data separately

Table 2 Key-factor/key-stage table (in percentage) (factors include growing sites of *Neolitsea sericea*)

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
Site	– 0.537	0.043	0.942	1.464	2.260	8.356	10.422	19.988	42.938	1.31e–07***
GL	– 0.741	– 0.261	– 0.128	0.425	0.788	2.001	1.693	2.846	6.624	0.006**
C1	0.309	0.060	– 0.027	0.022	0.005	– 0.082	– 0.025	0.252	0.513	0.424
C2	– 0.006	– 0.001	– 0.024	– 0.003	0.015	0.010	0.001	0.034	0.025	0.859
C3	– 0.013	0.000	0.001	0.002	0.000	0.011	0.017	– 0.001	0.017	0.882
C4	0.017	0.006	0.009	0.008	0.042	– 0.001	0.007	0.019	0.109	0.711
T1	0.742	0.260	0.715	0.328	0.701	– 0.323	0.192	– 0.458	2.155	0.105
T2	0.225	0.264	0.554	0.414	1.633	3.775	– 0.473	– 0.722	5.670	0.010*
T3	– 0.455	0.228	– 0.103	0.391	0.546	0.806	4.115	4.791	10.320	0.001***
T4	– 0.059	0.001	– 0.023	0.025	– 0.006	0.045	– 0.045	0.275	0.212	0.606
Residuals	2.183	0.626	0.923	0.021	1.500	5.543	9.772	10.849	31.417	–
Total	1.666	1.227	2.840	3.098	7.484	20.140	25.674	37.872	100.000	–

Site: growing sites of *Neolitsea sericea*; GL: the proportion of galled leaves at the time of leaf emergence, C1, C2, C3 and C4: the number of shoots or twigs damaged by the cerambycid beetle in first, second, third and fourth years, respectively, T1, T2, T3 and T4: typhoon impacts in first, second, third and fourth years, respectively. S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t} and S_{8t}: proportion of leaves surviving on trees during period indicated, respectively, with leaf age (month) in parentheses, Pr: Probability from Type I ANOVA at the final stage (the total of all stages). Bold numbers mean that these data are paid special attention in the text

* $P < 0.05$; ** $P < 0.01$; *** $P \leq 0.000$

Table 3 Estimated coefficient at each stage (factors include growing sites of *Neolitsea sericea*)

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
(Intercept)	– 0.2618	– 0.1146	– 0.0728	0.1419	0.1704	0.4361	0.4280	0.9974	1.7245	0.077
Site2	0.0628	– 0.0008	– 0.0294	– 0.0311	– 0.1056	– 0.1075	– 0.1870	– 0.3537	– 0.7523	0.170
Site3	0.0995	0.0108	– 0.0420	– 0.1328	– 0.1301	– 0.6895	– 0.8310	– 1.8093	– 3.5243	0.000
Site4	– 0.0630	0.0145	– 0.0905	– 0.0954	– 0.2859	– 0.4837	– 0.6934	– 0.8635	– 2.5609	0.000
GL	0.0401	0.0244	0.0123	– 0.0306	– 0.0378	– 0.0681	– 0.0987	– 0.2149	– 0.3735	0.087
C1	– 0.0341	– 0.0060	0.0000	– 0.0015	– 0.0051	0.0084	0.0089	– 0.0019	– 0.0314	0.610
C2	– 0.0097	– 0.0058	– 0.0216	– 0.0094	– 0.0131	– 0.0187	– 0.0109	– 0.0011	– 0.0904	0.273
C3	0.0686	0.0027	0.0183	– 0.0061	– 0.0155	– 0.1128	– 0.0476	– 0.0664	– 0.1587	0.671
C4	0.0297	0.0146	0.0311	0.0203	0.0685	0.0547	0.0077	0.0007	0.2273	0.199
T1	– 0.1830	– 0.0802	– 0.1965	– 0.1082	– 0.2361	– 0.0320	– 0.1262	– 0.0036	– 0.9658	0.010
T2	– 0.0102	– 0.0487	– 0.0782	– 0.0809	– 0.2691	– 0.6145	– 0.0656	– 0.0966	– 1.2639	0.001
T3	0.0431	– 0.0241	0.0089	– 0.0394	– 0.0586	– 0.0816	– 0.4409	– 0.4846	– 1.0772	0.001
T4	0.0296	– 0.0004	0.0116	– 0.0125	0.0030	– 0.0226	0.0228	– 0.1377	– 0.1062	0.606

See explanations in Table 2 for Site, GL, C1, C2, C3, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, and S_{8t}. Pr: Probability from Wald test. Bold numbers mean that these data are paid special attention in the text

for each of the four sites. The term A dealing with the site effect in Eq. (3) was dropped in the following analyses.

Short trees in Moso bamboo forest

The number of shoots or twigs damaged by the cerambycid in the first year (C1) was most influential in determining S_t , as indicated by the S_t (total) column in Table 4 (59.5%). The C1 row of S_{1t} (0–6) column in Table 4 indicates that the influence of C1 emerged mostly through s_{1t} , namely mostly through the first 6 months (49.6%). The coefficient division (Table 5) indicates that the element of column S_{1t} (0–6) of the C1 row in Table 5 was negative (– 0.046). Thus, we see that the cerambycid in the first year reduced the survival rate mostly through the early season of the first year. The S_t (total) column in Table 4 also indicates that the influence of cerambycid damage in the second year (C2) was

strong (13.8%). The S_{3t} (12–18) column of row C2 in Table 4 indicates that the effect of C2 arose mostly through s_{3t} , i.e., mostly through the period from 12 to 18 months (6.1%). Thus, cerambycid damage in the second year emerged mostly in the early season of the second year.

Short trees in the EBLF

The influence of the cerambycid in the first year (C1) was greatest (37.7% in S_t (total) in Table 6), similar to the result from the Moso bamboo forest. However, row C1 in Table 6 indicates that C1 was influential throughout all stages, in contrast to the Moso bamboo forest where the influence of C1 was mostly during the first year. The overall coefficient of C1 was positive (0.219 in column S_t (total) in Table 7), that is, damage caused by the cerambycid in the first year increased the overall leaf survival rate. If we closely inspect row C1 in Table 7, we see

Table 4 Key-factor/key-stage table for short trees of *Neolitsea sericea* in bamboo forest (in percentage)

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
GL	0.351	0.399	0.550	– 0.495	– 0.742	0.092	0.933	0.483	1.571	0.455
C1	49.571	9.040	4.375	0.321	– 2.590	1.497	0.811	– 3.574	59.450	0.003**
C2	– 1.722	0.296	6.116	1.748	– 0.196	– 0.175	5.769	1.920	13.757	0.056
C3	1.491	– 0.204	– 0.589	– 0.172	1.620	– 0.041	0.292	1.328	3.724	0.265
C4	1.007	0.372	0.322	0.185	0.862	– 0.732	– 0.818	– 0.275	0.923	0.563
T1	– 1.039	0.933	0.087	0.572	0.086	1.232	0.297	2.451	4.618	0.220
T2	0.090	0.588	0.089	0.049	– 0.127	0.035	– 0.749	0.225	0.199	0.786
T3	– 0.414	0.256	– 0.229	0.168	0.309	0.091	– 0.141	0.095	0.136	0.822
T4	– 0.644	– 0.048	0.479	– 0.080	0.191	0.053	0.090	0.780	0.822	0.585
Temp2	– 0.030	– 0.007	– 0.013	0.024	– 0.001	– 0.015	– 0.009	0.053	0.001	0.984
Residuals	3.488	– 0.951	– 1.381	1.964	3.704	– 0.021	0.976	7.019	14.798	–
Total	52.148	10.674	9.806	4.283	3.117	2.017	7.450	10.506	100.000	–

See explanations in Table 2 for GL, C1, C2, C3, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, S_{8t} and Pr. Temp2: annual mean temperature in the second year. Bold numbers mean that these data are paid special attention in the text

** $P < 0.01$

Table 5 Estimated coefficient at each stage for short trees of *Neolitsea sericea* in bamboo forest

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
(Intercept)	– 2.362	– 0.592	– 0.941	1.986	– 0.361	– 1.467	– 0.876	4.702	0.089	0.985
GL	– 0.054	– 0.006	– 0.046	– 0.002	0.053	0.038	– 0.015	– 0.105	– 0.137	0.404
C1	– 0.046	– 0.012	– 0.002	0.005	0.000	– 0.004	0.005	0.012	– 0.042	0.039*
C2	0.010	– 0.001	– 0.005	– 0.013	– 0.001	0.009	– 0.002	– 0.021	– 0.024	0.343
C3	0.025	– 0.019	– 0.003	– 0.023	0.012	0.010	0.028	– 0.006	0.025	0.716
C4	0.036	0.019	0.014	– 0.012	0.014	– 0.004	– 0.021	– 0.038	0.008	0.856
T1	– 0.098	– 0.035	– 0.016	0.064	– 0.006	– 0.010	0.029	0.196	0.126	0.475
T2	– 0.016	– 0.093	0.011	– 0.008	0.001	– 0.016	0.098	0.013	– 0.010	0.929
T3	– 0.016	– 0.057	0.027	0.018	– 0.044	– 0.044	0.007	0.116	0.008	0.959
T4	– 0.016	0.004	0.047	– 0.030	0.014	0.019	0.016	0.002	0.057	0.630
Temp2	0.142	0.035	0.059	– 0.112	0.004	0.073	0.043	– 0.249	– 0.005	0.984

See explanations in Table 2 for GL, C1, C2, C3, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, and S_{8t}. Pr: Probability from Wald test. Temp2: annual mean temperature in the second year. Bold numbers mean that these data are paid special attention in the text

* $P < 0.05$

Table 6 Key-factor/key-stage table for short trees of *Neolitsea sericea* in the secondary forest of evergreen broad-leaved trees (in percentage)

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
GL	– 0.732	0.004	– 0.782	– 0.341	0.119	0.226	0.476	2.393	1.363	0.529
C1	1.957	4.579	1.649	3.647	10.603	1.710	10.911	2.623	37.678	0.058
C2	– 1.775	0.205	0.956	0.113	0.707	1.112	0.970	4.946	7.233	0.224
C3	0.006	– 0.078	– 0.301	– 0.338	– 0.241	0.177	0.675	0.250	0.149	0.826
C4	– 0.398	0.224	0.493	– 0.933	1.090	– 0.359	1.777	3.592	5.486	0.269
T1	– 0.017	– 0.001	– 0.009	0.015	– 0.006	– 0.005	– 0.047	0.074	0.003	0.973
T2	0.349	– 1.059	1.273	2.118	3.423	5.204	0.053	20.727	32.087	0.067
T3	– 0.556	0.085	– 0.625	0.152	– 0.901	1.956	0.187	5.056	5.355	0.273
T4	0.257	0.022	– 1.529	– 0.111	0.599	– 0.286	3.548	3.373	5.874	0.257
Residuals	0.365	0.070	0.088	0.531	– 0.145	0.051	2.613	1.198	4.771	–
Total	– 0.543	4.051	1.213	4.854	15.247	9.785	21.163	44.231	100.000	–

See explanations in Table 2 for GL, C1, C2, C3, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, S_{8t} and Pr. Bold numbers mean that these data are paid special attention in the text

that the influence of C1 was negative in the earlier stages (before 30 months) and that it turned to positive in later stages. This indicated a type of compensation, i.e., damage caused by the cerambycid reduced the leaf survival rate at first, but this damage was later overcompensated to produce a higher leaf survival rate.

Typhoon in the second year (T2) was also influential in determining S_t (32.1% in column S_t (total) in Table 6). The T2 row in Table 7 indicates that the coefficient for the typhoon was negative after 18 months, which confirmed that the typhoon reduced the leaf survival rate. The T2 row in Table 6 indicates that the

Table 7 Estimated coefficient at each stage for short trees of *Neolitsea sericea* in the secondary forest of evergreen broad-leaved trees

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
(Intercept)	0.005	0.144	– 0.121	0.220	– 0.206	– 0.171	– 0.208	– 0.756	– 1.092	0.447
GL	– 0.020	– 0.051	– 0.015	– 0.062	0.024	0.034	0.033	0.170	0.114	0.729
C1	– 0.004	– 0.026	– 0.050	– 0.028	– 0.025	0.039	0.089	0.223	0.219	0.190
C2	– 0.059	0.008	0.055	– 0.007	0.015	0.011	– 0.017	0.040	0.046	0.784
C3	– 0.217	0.142	0.155	0.254	– 0.258	0.047	– 0.947	– 0.253	– 1.077	0.455
C4	– 0.058	0.033	0.108	– 0.114	0.065	– 0.110	0.017	– 0.008	– 0.067	0.892
T1	– 0.052	0.012	0.048	0.006	– 0.088	– 0.097	– 0.300	– 0.373	– 0.845	0.118
T2	– 0.017	0.028	0.080	– 0.057	– 0.125	– 0.171	– 0.250	– 0.938	– 1.451	0.060
T3	0.064	– 0.013	0.168	– 0.016	0.095	– 0.259	– 0.212	– 0.885	– 1.058	0.188
T4	– 0.014	– 0.001	0.085	0.006	– 0.033	0.016	– 0.197	– 0.188	– 0.327	0.257

See explanations in Table 2 for GL, C1, C2, C3, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, and S_{8t}. Pr: Probability from Wald test. The bold numbers mean that these data are paid special attention in the text

Table 8 Key-factor/key-stage table for tall trees of *Neolitsea sericea* in the secondary forest of evergreen broad-leaved trees (in percentage)

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
GL	– 0.382	0.299	0.816	0.719	1.499	6.245	8.317	9.285	26.797	0.077
C1	– 0.149	– 0.077	– 0.071	0.110	– 0.338	– 1.073	0.891	4.498	3.791	0.441
T1	0.000	– 0.002	– 0.023	– 0.035	– 0.030	0.042	0.047	0.005	0.002	0.986
T2	0.115	0.298	0.310	1.613	0.967	15.075	3.114	– 5.354	16.138	0.145
T3	– 0.145	– 0.167	– 0.134	0.054	0.285	– 0.442	8.268	16.764	24.482	0.087
T4	0.013	– 0.036	– 0.211	0.014	– 0.051	0.222	– 0.206	1.900	1.646	0.606
Residuals	0.175	0.676	0.394	– 0.160	1.209	3.571	6.352	14.929	27.145	–
Total	– 0.373	0.991	1.081	2.315	3.541	23.638	26.782	42.025	100.000	–

See explanations in Table 2 for GL, C1, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, S_{8t} and Pr. Bold numbers mean that these data are paid special attention in the text

Table 9 Estimated coefficient at each stage for tall trees of *Neolitsea sericea* in the secondary forest of evergreen broad-leaved trees

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
(Intercept)	– 0.149	– 0.019	0.033	– 0.001	0.000	0.091	0.614	0.551	1.121	0.670
GL	0.028	– 0.012	– 0.039	– 0.009	– 0.043	– 0.124	– 0.376	– 0.478	– 1.054	0.216
C1	0.011	– 0.005	– 0.042	– 0.022	0.008	0.063	0.013	0.258	0.283	0.685
T1	0.001	– 0.025	– 0.220	– 0.382	– 0.314	0.152	0.286	– 0.268	– 0.770	0.496
T2	– 0.010	– 0.024	– 0.012	– 0.167	– 0.101	– 1.548	– 0.476	0.035	– 2.302	0.073
T3	0.011	0.016	0.026	– 0.006	– 0.020	0.022	– 0.681	– 1.541	– 2.173	0.080
T4	– 0.004	0.011	0.064	– 0.004	0.016	– 0.068	0.063	– 0.581	– 0.504	0.606

See explanations in Table 2 for GL, C1, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, and S_{8t}. Pr: Probability from Wald test. The bold numbers mean that these data are paid special attention in the text

influence strengthened in S_{6t} (30–36) and S_{8t} (42–48) (5.2 and 20.7%, respectively). This indicates delayed effects, i.e., the typhoon in the second year reduced the leaf survival rate through the third and fourth years.

Tall trees in EBLF

The sub-factors C2, C3 and C4 were excluded in the analysis of tall trees in the EBLF because damage by the cerambycid was not recognized in second, third or fourth years. Column S_t (total) in Table 8 indicates that the effect of cecidomyiid galls was stronger than those of other factors for tall trees (26.8%). Row GL in Table 8

indicates that the influence of galls generally increased with stage progress. This influence largely appeared after 30 months, i.e., mostly through third and fourth years. The division of coefficients (Table 9) confirmed that the galls reduced the leaf survival rate, because the elements in row GL in Table 9 were generally negative.

The influence of typhoons in the third year (T3) was also great (24.5%). Row T3 in Table 8 indicates that the influence of typhoons in the third year arose through the fourth year (until the 48 month stage). The negative coefficients in Table 9 lead us to conclude that typhoons reduced the leaf survival rate.

Residual variability was 27.1% as seen in column S_t (total) in Table 8, and was the largest among the four

Table 10 Key-factor/key-stage table for short trees of *Neolitsea sericea* along an edge of the secondary forest of evergreen broad-leaved trees (in percentage)

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
GL	– 3.620	– 1.371	– 1.629	1.349	2.898	5.666	3.252	9.212	15.756	0.336
C1	– 1.223	0.107	0.585	0.353	1.128	1.367	2.707	0.743	5.766	0.488
C2	0.822	0.297	– 0.418	0.047	1.714	2.062	3.379	2.492	10.395	0.396
C4	2.514	0.876	1.552	0.023	0.939	0.244	2.174	0.166	8.487	0.427
T1	10.736	3.311	6.574	– 0.031	8.011	3.493	10.236	– 0.915	41.415	0.219
T2	0.115	– 0.069	0.425	– 0.124	2.083	2.121	– 2.423	– 0.934	1.194	0.719
T3	– 0.197	0.196	0.096	1.077	0.761	2.693	3.783	0.002	8.413	0.428
T4	– 0.106	– 0.088	– 0.150	0.048	0.038	– 0.368	1.259	0.446	1.079	0.731
P1	0.209	– 0.050	– 0.080	0.054	– 0.366	0.235	1.116	0.723	1.842	0.662
P2	– 0.079	0.024	– 0.132	– 0.161	– 0.681	0.009	– 0.254	1.586	0.313	0.849
Residuals	– 0.270	– 0.125	– 0.365	0.716	– 0.265	0.761	2.542	2.346	5.339	–
Total	8.903	3.109	6.458	3.351	16.261	18.281	27.770	15.868	100.000	–

See explanations in Table 2 for GL, C1, C2, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, S_{8t} and Pr. P1 and P2: annual precipitation in first and second years, respectively. Bold numbers mean that these data are paid special attention in the text

Table 11 Estimated coefficient at each stage for short trees of *Neolitsea sericea* along an edge of the secondary forest of evergreen broad-leaved trees

Factors	S _{1t} (0–6)	S _{2t} (6–12)	S _{3t} (12–18)	S _{4t} (18–24)	S _{5t} (24–30)	S _{6t} (30–36)	S _{7t} (36–42)	S _{8t} (42–48)	S _t (total)	P
(Intercept)	0.532	– 0.113	0.076	0.283	0.422	0.308	2.145	– 0.955	2.698	0.717
GL	– 0.156	0.030	– 0.056	– 0.116	– 0.300	– 0.039	– 0.806	0.278	– 1.165	0.560
C1	– 0.090	0.005	– 0.021	– 0.032	– 0.097	– 0.030	– 0.086	0.270	– 0.081	0.884
C2	– 0.041	0.000	– 0.013	0.021	0.298	– 0.076	– 0.042	– 0.471	– 0.324	0.804
C4	– 0.662	0.136	– 0.029	– 0.341	– 0.242	– 0.539	– 2.945	0.813	– 3.808	0.710
T1	– 1.089	– 0.205	– 0.475	– 0.118	– 0.411	– 0.390	– 2.022	0.057	– 4.653	0.413
T2	– 0.029	– 0.010	0.008	0.113	0.120	– 1.151	0.483	– 1.739	– 2.204	0.508
T3	0.127	– 0.053	0.110	0.005	0.510	– 0.358	– 0.224	– 1.471	– 1.354	0.553
T4	– 0.077	– 0.002	– 0.075	– 0.063	– 0.232	– 0.096	0.021	0.661	0.138	0.891
P1	0.000	0.000	0.000	0.000	0.001	0.000	– 0.001	– 0.003	– 0.003	0.643
P2	0.000	0.000	0.000	0.000	0.002	0.000	0.001	– 0.005	– 0.001	0.849

See explanations in Table 2 for GL, C1, C2, C4, T1, T2, T3, T4, S_{1t}, S_{2t}, S_{3t}, S_{4t}, S_{5t}, S_{6t}, S_{7t}, and S_{8t}. Pr: Probability from Wald test. P1 and P2: annual precipitation in the first and second year, respectively. The bold numbers mean that these data are paid special attention in the text

sites. Thus, we surmise that the leaf survival rate on tall trees was shaped by other unknown factors.

Short trees along edge of EBLF

Sub-factor C3 was excluded from the analysis because damage by the cerambycid was not recognized in the third year. The influence of typhoons in the first year (T1) was stronger than that of other factors for the trees growing along the forest edge. The influence was 41.4% as seen in the column S_t (total) in Table 10. Row T1 in Table 10 indicates that the impact of T1 appeared through nearly all stages from the first year through fourth year. Row T1 in Table 11 indicates that the influence of T1 was generally negative; the typhoon in the first year reduced the leaf survival rate through all stages.

The influence of galls (GL) was also strong on the trees along the edge (15.8%). The influence increased with stage progress as seen in row GL in Table 10. The

negative elements in row GL in Table 11 confirmed that the galls generally reduced the leaf survival rate.

Discussion

Leaf longevity and survival rate

The present work supports the conclusion that evergreen trees can grow on the forest floor, whereas deciduous trees cannot survive there (Miyashita and Tateno 2014). One of advantages of evergreen leaves is long life of a single leaf, which compensates low productivity under an evergreen canopy. Evergreen leaves are costly, but their longevity can manage to compensate the cost, even in low light conditions.

Mean leaf longevity of *N. sericea* varied greatly by year classes of leaf emergence (Fig. 3). Such variation has not been demonstrated precisely based on long-term field data although leaf longevity has been calculated for various plant species on the relatively short term (see

examples in Kikuzawa 2005; Kikuzawa and Lechowicz 2011). To analyze the chronological distribution patterns of leaves, the accumulation of long-term field data is essential. However, it should be emphasized here that the mean leaf longevity and the leaf survival rate at the 48-month stage were significantly correlated for all tree categories in the two census fields (Fig. 4). These results allow us to use the leaf survival rates of evergreen broad-leaved trees at the 48-month stage for the key-factor/key-stage analyses instead of actual leaf longevity data. Therefore, this relationship between leaf longevity and the leaf survival rate in certain months may be worth testing using leaf longevity data of other evergreen broad-leaved trees.

Key-factor/key-stage analysis

The present work is the first attempt to use the method of key-factor/key-stage analysis to study the long-term life table data of leaves with a mixture of abiotic and biotic factors operating on a plant species. We successfully identified key-factors and key-stages that determine the leaf survival rate of *N. sericea* under different growing conditions and assessed the relative strength of abiotic and biotic effects. We revealed the key-factor/key-stage analysis could be applied not only to animal ecology but also to plant ecology.

Abiotic factors

Annual precipitation

Annual precipitation varied yearly from 1175 to 3279 mm, so the growing sites of *N. sericea* in southern Kyushu may be categorized as within the humid subtropical climate zone of the Köppen Climate Classification. Therefore, *N. sericea* do not suffer leaf drop from severe dry conditions unlike plants growing in dry areas, for which leaf longevity sometimes becomes longer to compensate non-efficient photosynthesis (e.g., Casper et al. 2001).

The current survey showed that annual precipitation had no significant effect on leaf survival rate when all census trees growing at the four different sites were considered (Table S2). However, annual precipitation in the first and second years positively affected that rate for the short trees along the forest edge (Table S6). This can be naturally explained by drier conditions along the forest edge than in the interior of the bamboo forest or EBLF. Very weak significant correlation was found between annual precipitation in the fourth year and leaf survival in the bamboo forest, but this was almost negligible.

Mean annual temperature

At global scale, the relationship of leaf longevity to mean annual temperature is positive for deciduous spe-

cies but negative for evergreen species (Kikuzawa et al. 2013). However, the relationship of leaf longevity of each plant species with mean annual temperature has not been analyzed intensively based on long-term field data. Unlike the tremendous fluctuation in annual precipitation, the mean annual temperature did not vary much from year to year (from 15.9 to 18.5 °C in Kagoshima). Therefore, as a whole, no remarkable influence on leaf survival was detected (Tables S2, S3, S4, S5, and S6).

Typhoon

Typhoon, hurricane and cyclone are catastrophic events for organisms and their environment. However, the effects of strong wind on a particular plant species have not been intensively evaluated, although these effects have been roughly evaluated at large scale in ecosystems (e.g., Tanner et al. 1991; Mabry et al. 1998; Xi et al. 2012).

Of course, strong wind had varying effects at the different growing sites of *N. sericea*. Typhoon had the most harmful direct effects in the first year on the leaf survival of short trees, particularly along the forest edge (Table 10). Typhoon also caused considerable harm to leaf survival of the short and tall trees in the EBLF (Tables 6 and 8). These effects became stronger in the second or third years, which means that damages by strong wind carried over into subsequent years. This is the first finding of such a response by a plant species to strong wind. No typhoon effects were recognized in the bamboo forest, which is in a valley where the wind force was possibly weakened (Table 4).

Biotic factors

Among biotic factors, leaf-chewing herbivores are less influential on the survival rate of host leaves (e.g., Kikuzawa et al. 2002; Yamasaki and Kikuzawa 2003) than endophytic herbivores (e.g., Sunose and Yukawa 1979; Faeth et al. 1981; Yukawa and Tsuda 1986). The current study revealed that leaf-gall induction by *P. neolitseae* and stem boring by *O. hebescens* had a strong impact on the survival rate of their host leaves.

Pseudasphondylia neolitseae

Gall induction by cecidomyiids has a deleterious effect on host plants by altering plant architecture and reducing leaf longevity, photosynthesis, seed production and biomass. Such deleterious effects become severe when gall density is high (e.g., Yukawa and Rohfritsch 2005). For example, mean longevity of leaves heavily galled by *Masakimyia pustulae* Yukawa and Sunose (Diptera: Cecidomyiidae) on *Euonymus japonicus* Thunberg (Celastraceae) is considerably shortened, whereas ungalled and lightly galled leaves are seldom

shed within a year (Sunose and Yukawa 1979). Gall induction by *Contarinia* sp. (Diptera: Cecidomyiidae) along the midrib of evergreen *Quercus glauca* Thunberg (Fagaceae) also caused an earlier drop of galled leaves in April–May, whereas ungalled leaves survived more than 26 months on average (Yukawa and Tsuda 1986). Similarly, galled leaves induced by *Illiciomyia yukawai* Tokuda (Diptera: Cecidomyiidae) on *Illicium anisatum* usually fell earlier than ungalled leaves (Yukawa et al. 2016b).

The current survey revealed for the first time that gall induction by *P. neolitseae* had a negative effect on leaf survival of the tall trees of *N. sericea* in the EBLF (Table 8) and short trees along the EBLF edge (Table 10). The influence was accelerated toward later stages, in contrasted to the case of leaf-chewing herbivores in which young leaves suffered much greater feeding damage than mature leaves (e.g., Coley 1980). This seems natural because gall midges that induce leaf galls on evergreen broad-leaved trees require their host leaves to remain attached to the twigs for at least 12 months to complete their univoltine annual life cycle on host trees (Yukawa 1987). It may be worth confirming in the future if the cecidomyiid larvae manipulate the host plant to prevent the petiole from detaching in the first year, because there are some instances of cecidomyiid fruit galls that remain on host trees longer than normal fruit. Examples are fruit galls induced by *A. sphaera* Monzen on *Ligustrum* spp. (Oleaceae) (Yukawa and Miyamoto 1979) and those by *Asphondylia aucubae* Yukawa and Ohsaki on *Aucuba japonica* Thunberg (Aucubaceae) (Yukawa and Ohsaki 1988).

The gall induction by *P. neolitseae* did not much affect leaf survival for short trees in the bamboo forest (Table 4) or short trees in the EBLF (Table 6). This might be caused by relatively dark growing sites.

Oberea hebescens

There are at least 800 species of cerambycid (Coleoptera) in Japan. Larvae of many species live in fallen or decayed plants and the remainder in living plants (Kojima and Nakamura 1986). In the latter case, some species are of economic importance, and affect beneficial trees in various ways. For example, larvae of *Anoplophora malasiaca* (Thomson) bore twigs of various species of *Citrus*, chestnut, mulberry, fig and many other forest trees, and *Xylotrechus pyrrhoderus* Bates infests vines of vitaceous plants (Kojima and Nakamura 1986). *Monoctonus alternatus* Hope, a vector of *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle (Nematoda: Aphelenchoididae) is a major pest of pine trees (e.g., Togashi et al. 2008).

Stem boring by the cerambycid, *O. hebescens* modulated leaf survival of short trees in the bamboo forest (Table 4) and the EBLF (Table 6), but was less influential for tall trees (Table 8) and short trees along the forest edge (Table 10). These results can be contrasted

with the effects of gall induction by *P. neolitseae*. The adults of *O. hebescens* may prefer relatively dark sites. In addition, we have no data at the moment to explain differences (if any) between tall and short trees regarding defense mechanism against the borer.

The stem boring was more influential on leaf survival in the bamboo forest (Table 4) than in the EBLF (Table 6). This was possibly caused by the concentration of damages to *N. sericea* in the bamboo forest where alternative host trees, such as *Cinnamomum tenuifolium*, *Lindera praecox* and *Machilus thunbergii*, were not growing (in contrast to the EBLF). In the bamboo forest, some short trees of *Machilus japonicus* were growing but larvae of the cerambycid have never been observed boring its shoots and twigs. The main shoot of *M. japonicus* is very short and the side shoots are not thick enough for the cerambycid larvae to bore.

For the short trees in the EBLF, stem boring (C1) had a negative effect on leaf survival particularly during early stages. However, its effect became positive during later stages (Table 7). Such a weak tendency was found for the short trees in the bamboo forest (Table 5). Thus, the key-factor/key-stage analysis clearly demonstrated for the first time a compensatory reaction by a plant species to the deleterious influence of the cerambycid. This finding is remarkable in the study of the chronological distribution patterns of leaves (Kikuzawa 2005; Kikuzawa and Lechowicz 2011).

Residual variability

Residuals are almost inevitable in field surveys, but they were unusually large in the analysis of the tall trees in the EBLF. This might have been caused by difficulties in gathering detailed data from higher branches of the tall trees surveyed. We need to discover unknown important factors operating on tall trees.

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