We are IntechOpen,
the world's leading publisher of
Open Access books
Built by scientists, for scientists

6,900
Open access books available

185,000
International authors and editors

200M
Downloads

154
Countries delivered to

Our authors are among the

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

CLARIVATE ANALYTICS
BOOK CITATION INDEX
INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Growth Characteristics of Dwarf Bamboo Distributed in the Northern Part of Japan

Masazumi Kayama and Takayoshi Koike

Additional information is available at the end of the chapter

Abstract

Dwarf bamboo is a dominant forest floor species, especially in the northern part of Japan. *Sasa kurilensis*, *Sasa senanensis* and *Sasa nipponica* are widely distributed in this region. Growth characteristics of these three *Sasa* species are also different: leaf longevity of *S. kurilensis* is 3–5 years. In contrast, leaf longevity of *S. senanensis* and *S. nipponica* are 2 years and <1 year, respectively. We predicted that ecophysiological characteristics of the three *Sasa* species would reflect their leaf longevity; however, their characteristics were still not well analysed. We examined ecophysiological parameters of the three *Sasa* species grown under the same environment. Net photosynthetic rate at light saturation (P_{sat}) and nitrogen concentration (N) of S. nipponica showed high values after flushing. However, culms of *S. nipponica* were dropped after overwintering, and P_{sat} of the 2-year-old leaves drastically decreased. Meanwhile, P_{sat} of the current leaves of *S. kurilensis* was lower than the other two species. However, P_{sat} of 2-year-old leaves of *S. kurilensis* still maintained a relatively high value. P_{sat} of the current leaves of *S. senanensis* was higher than that of *S. kurilensis* even though N was the same. From these results, *S. senanensis* had a high photosynthetic nitrogen efficiency rate (P_{sat}/N).

Keywords: *Sasa*, photosynthetic capacity, nitrogen, chlorophyll, leaf thickness

1. Introduction

1.1. Dwarf bamboo in Japan

Dwarf bamboo is a small size bamboo species that distributes in Eastern Asia. On the classification of bamboo in Japan, dwarf bamboo is separated from the other bamboos. For dwarf bamboo, the sheath of culm remains until its death, whereas other bamboo species are

removed their sheath during the process of culm growth. Six genera and 72 species of dwarf bamboo are grown in Japan (**Table 1**) [1]. Moreover, the genera of *Sasa* and *Pleioblastus* are divided into several sections by their morphological characteristics [1]. The northern limit of distribution area of dwarf bamboo is considered at the middle part of Sakhalin where the genus *Sasa* distributes [3].

The habitats of dwarf bamboo in Japan are restricted by climate, especially winter [4]. The climate in Japan is divided by the coasts of the Sea of Japan and Pacific Ocean [5], and the coast of the Sea of Japan area is considered as the snowy area. The presence of snow is an important factor to restrict the distribution of dwarf bamboo, and the main genus to distribute in the snowy area is *Sasa* [1]. Among the five sections of *Sasa* genus, *Macrochlamys* and *Sasa* can distribute in snowy area, since they are adapted to the snowy environment [1]. In this article, we introduce the ecological characteristics of the three species in genus *Sasa* that grow in the northern part of Japan. We also focus on growth characteristics of the three dominant species of genus *Sasa* with an ecophysiological method.

1.2. Ecological characteristics of three *Sasa* species in Northern Japan

In Northern Japan, the dwarf bamboo is a typical and essential component of the forest floor [6, 7]. In this region, *Sasa kurilensis*, *Sasa senanensis*, and *Sasa nipponica* distributed

Genera and section	Number of species	Typical species
Sasa		
Section *Macrochlamys*	6	*Sasa kurilensis* Makino et Shibata
Section *Lasioderma*	9	*Sasa shimidzuana* Makino
Section *Monilicladae*	4	*Sasa tsuboiana* Makino
Section *Sasa*	9	*Sasa senanensis* Rehder
Section *Crassinodi*	8	*Sasa nipponica* Makino et Shibata
Sasaella	10	*Sasaella ramosa* Makino
Sasamorpha	2	*Sasamorpha purpurascens* (Hechel) Makino
Pseudosasa	2	*Pseudosasa japonica* Makino
Pleioblastus		
Subgen. Pleioblastus	4	*Pleioblastus linearis* Nakai
Subgen. Nipponocalamus		
Section *Medakea*	6	*Pleioblastus simonii* Nakai
Section *Nezasa*	11	*Pleioblastus chino* Makino
Chimonobambusa	1	*Chimonobambusa marmoreal* (Mitford) Makino

Table 1. Genera of dwarf bamboo distributed in Japan [1, 2].

widely [1, 8]. In Hokkaido Island, which is located in the most northern part of Japan, the distribution of these three species is separated (**Figure 1**, [8]). These species are separated by the snow depth. The main distribution area of *S. nipponica* is the eastern part of Hokkaido, which faces the coast of the Pacific Ocean. Snow depth of this area is lower than other areas (below 75 cm of maximum snow depth) [4]. The distribution of *S. kurilensis* is the mountain area with heavy snow (over 150 cm of maximum snow depth). The distribution of *S. senanensis* is at the middle range of maximum snow depth between *S. nipponica* and *S. kurilensis* (75–150 cm). Also, the three *Sasa* species have different freezing tolerance. The climate in the area of the coast of Pacific Ocean the minimum temperature is lower than −10°C, and soil freezing occurs due to low snow depth [5]. The freezing tolerance for the bud of *S. nipponica* (−10 to −15°C) is higher than *S. kurilensis* and *S. senanensis* (−5 to −10°C) [9]. As a result, bud of *S. nipponica* can survive soil freezing. On the other hand, the distribution area of *S. kurilensis* and *S. senanensis* is covered with deep snow during the winter [1, 4]. The culms of *S. kurilensis* and *S. senanensis* are laid on the ground by the weight of snow cover. Snow has low thermal conductivity [10], and low air temperature is not easily conducted to the soil; as a result, soil can escape freezing [11]. Thus, *S. kurilensis* and *S. senanensis* can survive under the snow cover in winter. When the leaf and culm of *S. kurilensis* and *S. senanensis* are exposed above the snow depth, these organs cannot survive [12, 13].

The three *Sasa* species have different morphology types (**Figure 2**, [4]). The culm height of *S. kulinensis* reaches 3 m, and its longevity is estimated to be over 10 years. The upper part
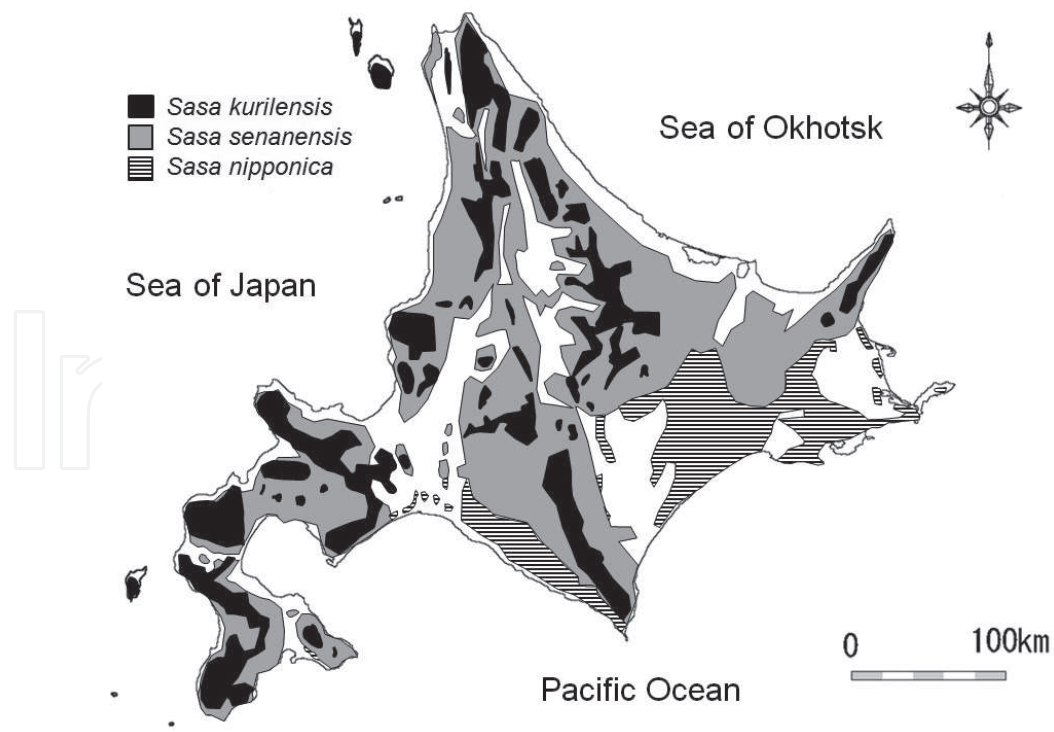
Figure 1. The distribution of the three *Sasa* species in Hokkaido Island located in Northern Japan (modification from Toyooka et al. [8]).

of the culm of *S. kulinensis* has buds on nodes and continues to bifurcate. In contrast, there are no buds at lower part of the culm of *S. kulinensis*. The leaves of *S. kulinensis* can survive for relatively longer time, and its longevity ranges from 3 to 5 years. The culm height of *S. senanensis* is about 2 m, and its longevity is 5 years. The culm of *S. senanensis* has buds on every node. The leaf longevity of *S. senanensis* is about 2 years. In contrast, the culm height of *S. nipponica* is less than 1 m, and its longevity is also about 1 year. The buds of *S. nipponica* exist at the underground of the culm. The leaf longevity of *S. nipponica* is less than 1 year.

The three *Sasa* species have well-developed rhizome systems and are dominant at the forest floor in general forests of this region [14, 15]. As a result, the light environment under the *Sasa* species is quite dark, and regeneration of other species is suppressed [16]. Moreover, the *Sasa* species has high regeneration ability after disturbances. When forests suffer from forest fires, forest cannot restore; however, dwarf bamboo is able to regenerate as ground vegetation [17, 18]. The flowering period of the *Sasa* species is estimated to be 60–100 years [4]; however, information of flowering is still limited. Based on previous information, flowering of *Sasa* species occurs synchronously and often expands over 1000 ha in area [4, 19]. After flowering, numerous seeds are produced, and all culms of the *Sasa* species dies [4, 19], as does a mono-carpic plant.
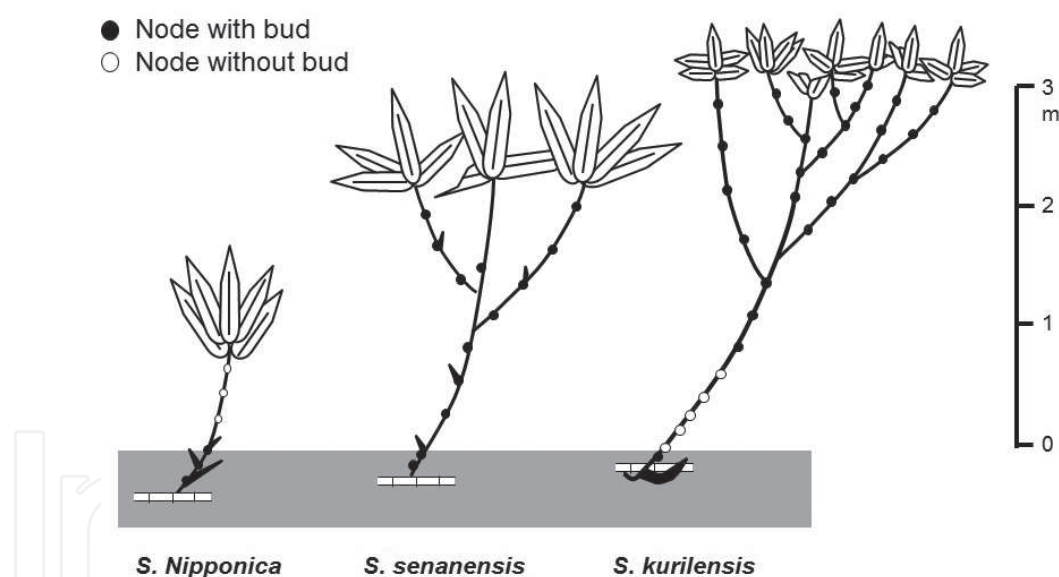

Figure 2. Morphological characteristics of the three *Sasa* species (modification from Makita [4]).

2. Ecophysiological characteristics of three *Sasa* species

2.1. Background

In the previous chapter, we summarized the ecological characteristics of the three dominant *Sasa* sp. in Northern Japan: *S. kurilensis, S. senanensis,* and *S. nipponica.* We showed specific

traits of leaves and culm longevity of the three species. To survive and grow under different growth conditions, the *Sasa* species have adapted to each habitat through morphological and physiological adaptation. For example, leaf and stem longevities of *S. nipponica* are 1 year, and so its leaf has to obtain large amount of photosynthetic productivity during the one growing period. In contrast, leaves and culms of *S. kurilensis* can survive for a long period. Therefore, it also may be possible for *S. kurilensis* to obtain photosynthetic productivity for a long period. In general, plant growth form can be evaluated through ecophysiological characteristics [20, 21]. Photosynthetic characteristics of three *Sasa* species have been measured by previous research [22–24]. However, characteristics cannot be compared because the measurement was done under different conditions.

There are contrasting growth characteristics, namely fast and slow [25]. Fast-growing species have short-lived leaves with a high photosynthetic capacity, whereas slow-growing species have long lived leaves with a low photosynthetic capacity that can maintain its function over long periods. The differences of photosynthetic capacity between fast- and slow-growing species are related to foliar nitrogen concentration, which is usually higher in fast-growing than in slow-growing species [25]. In contrast, photosynthetic nitrogen use efficiency is an indicator for allocation of nitrogen to photosynthetic apparatus; slow-growing species shows a high value [25]. The nitrogen use characteristic is predicted to be different according to life form. For example, the photosynthetic rate and concentration of nitrogen may be high for *S. nipponica,* since it has a short leaf longevity. We predicted, in contrary, that leaves of *S. kurilensis* may have a low photosynthetic rate and low nitrogen concentration. The long longevity of *S. kurilensis* may be compensated with low photosynthetic productivity as found in several kinds of evergreen spruce [21].

The aim of this chapter is to show ecophysiological characteristics of the three *Sasa* species in relation to their different life forms, such as leaf longevity, culm height, etc. We measured the seasonal change of photosynthetic rates, concentrations of nitrogen and chlorophyll, and leaf thickness of different aged leaves of the three *Sasa* species planted in a common garden.

2.2. Materials and methods

This research was conducted in an arboretum of the Hokkaido Research Center, Forestry and Forest products Research Institute (43°00′N, 141°23′E, 141 m a.s.l.) located in Sapporo City, Hokkaido, Japan. The annual mean, maximum, and minimum temperatures at the metrological station of this centre were 7.3, 35.7, and −22.8°C, respectively, from 1975 to 2003 [26]. The range of annual precipitation was from 581 to 1490 mm year^{-1} during 1975–2003 [26]. The maximum snow depth in winter was 130 cm [26]. In this arboretum, the subterranean stem of *S. kurilensis*, *S. senanensis*, and *S. nipponica* was planted in 1982. The size of planting area was 5 × 10 m for each *Sasa* species. Plantations of *Sasa* species were exposed to full sunlight the whole day because there were no surrounding trees around the plantation.

We measured the photosynthetic rate at light saturation (P_{sat}, μmol m^{-2} s^{-1}) from May to October 2004. The measurements were carried out at 10:00–15:00 each month. Second leaves counted from the top of culm of each *Sasa* species were used for the measurement of P_{sat}. We

selected four leaves of current and 2-year-old ones located at sunny positions. Measurements were made by using a portable gas analyzer (LI-6400, LI-COR Biosciences, Lincoln, NE, USA) under steady-state conditions (25°C, 36.0 Pa of CO_2, and 1800 µmol m^{-2} s^{-1} photosynthetic photon flux using LED), which were previously determined [27].

After measuring photosynthetic rate, we sampled the leaves and analysed the chlorophyll concentration. The fresh mass of leaves were first measured, then crushed by liquid nitrogen, and finally extracted by dimethyl sulfoxide. Measurement of chlorophyll was done by a spectrophotometer (V560, JASCO Co., Tokyo, Japan), and its concentration was calculated by an equation [28]. The remaining leaf samples were dried at 80°C, for 4 days. After drying, we measured specific leaf area (SLA = leaf area per dry mass, cm^2 g^{-1}, [29]). Leaf samples were ground to a fine powder using a sample mill (WB-1; Osaka Chemical Co., Osaka, Japan). The mass-based concentration of nitrogen (N_{mass}, mmol g^{-1}) was analysed using a NC analyser (NC-800, Sumika Chemical Analysis Service, Osaka). We also calculated the photosynthetic nitrogen use efficiency (PNUE, nmol mmol^{-1} s^{-1}, [25]) as an indicator of photosynthetic apparatus allocation. PNUE was calculated by the following Eq. (1). We also calculated area-based concentration of nitrogen (N_{area}, mmol m^{-2}) from the value of SLA Eq. (2).

$$\text{PNUE} = P_{sat} / N_{area} \times 1,000 \tag{1}$$

$$N_{area} = 10,000 / \text{SLA} \times N_{mass} \tag{2}$$

The value of P_{sat}, SLA, concentrations of chlorophyll and nitrogen, and PNUE was examined using Tukey tests. The mean values were compared among *S. kurilensis*, *S. senanensis*, and *S. nipponica*.

2.3. Results

Concerning the value of P_{sat} for the current leaves, *S. nipponica* showed high values (14 µmol m^{-2} s^{-1}) from June when its leaves flushed (**Figure 3**). In July, P_{sat} of *S. nipponica* increased to 18 µmol m^{-2} s^{-1}, and its value was significantly higher than other *Sasa* species ($P < 0.01$).
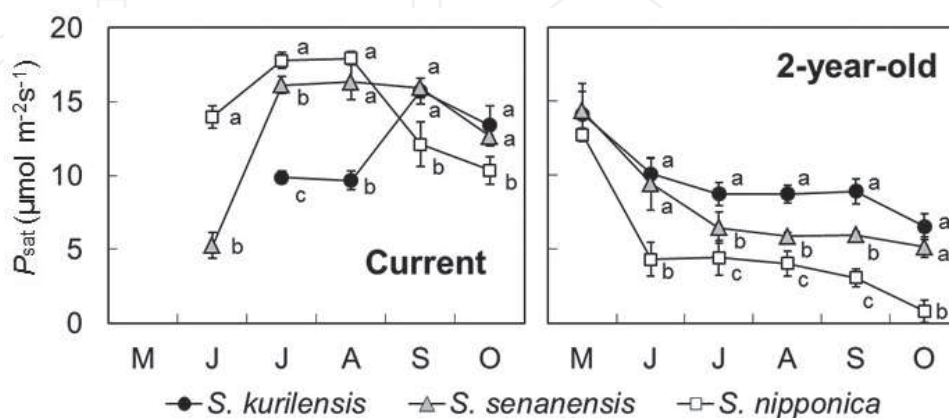

Figure 3. Seasonal change of photosynthetic rate at light saturation (P_{sat}) for current and 2-year-old leaves of the three *Sasa* species (May to October 2004, n = 4). Different letters indicate significant differences as calculated by Tukey test ($P < 0.05$).

However, P_{sat} of *S. nipponica* started to decrease from September. P_{sat} of *S. senanensis* in June was significantly lower than *S. nipponica* ($P < 0.001$); however, P_{sat} increased to 16 µmol m^{-2} s^{-1} from July to September. In contrast, flushing of leaves of *S. kurilensis* was in July, and P_{sat} was significantly lower in July and August than other *Sasa* species ($P < 0.001$). In September, P_{sat} of *S. kurilensis* increased to 15 µmol m^{-2} s^{-1}.

In 2-year-old leaves, all *Sasa* species showed high values of P_{sat} in May when all species had not yet flushed new leaves. However, P_{sat} of 2-year-old leaves was decreased from June. Especially, the culms of *S. nipponica* fell to the ground in June, and P_{sat} was drastically decreased. P_{sat} of *S. senanensis* and *S. kurilensis* was also decreased from July. However, P_{sat} of *S. kurilensis* was maintained at 8 µmol m^{-2} s^{-1} until September, and these values were significantly higher in July, August, and September than that of *S. senanensis* ($P < 0.05$).

The value of SLA was also different among the three *Sasa* species. For the current leaves, SLA in July and September showed significantly high values for *S. nipponica* than that for *S. senanensis* and *S. kurilensis* (**Figure 4**, $P < 0.05$). In contrast, SLA for current leaves of *S. kurilensis* was the lowest values from July to September. The values of SLA for current leaves decreased by time for all *Sasa* species. Compared to current and 2-year-old leaves, SLA showed low values for 2-year-old leaves for all *Sasa* species. From July, there was no significant difference in SLA of 2-year-old leaves among the three *Sasa* species.

Concentration of mass-based nitrogen (N_{mass}) in current leaves showed the highest values in June for *S. nipponica* and *S. senanensis*; however, their values decreased by time (**Figure 5**). In the case of *S. kurilensis*, the decrease of N_{mass} in current leaves was not clear. N_{mass} for current leaves was significantly higher for *S. nipponica* from June to September than those for *S. senanensis* and *S. kurilensis* ($P < 0.05$). In October, N_{mass} of *S. nipponica* showed similar value with *S. kurilensis*. As for the trend of 2-year-old leaves, all *Sasa* species decreased N_{mass} with time. N_{mass} in June of 2-year-old leaves of *S. nipponica* was significantly lower than the N_{mass} of *S. senanensis* and *S. kurilensis* ($P < 0.05$).

Compared with N_{mass}, area-based nitrogen (N_{area}) showed that its decrease by time was not obvious for current leaves. The peak of N_{area} showed in June of 2-year-old leaves for *S. kurilensis*
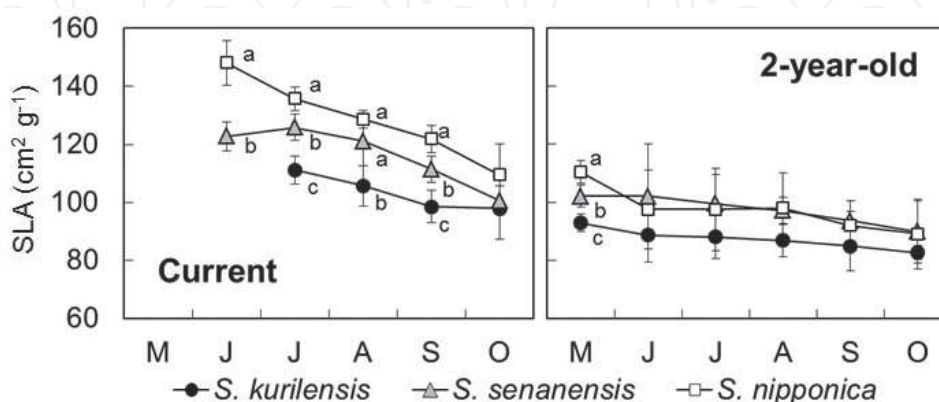

Figure 4. Seasonal change of specific leaf area (SLA) for current and 2-year-old leaves of the three *Sasa* species (May to October 2004, n = 4). Different letters indicate significant differences as calculated by Tukey test ($P < 0.05$).
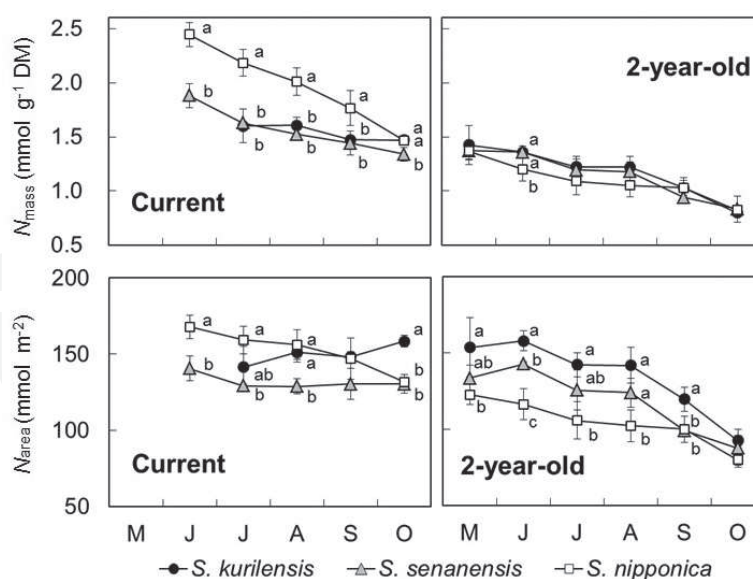
Figure 5. Seasonal change of mass-based (N_{mass}) and area-based (N_{area}) concentrations of nitrogen for current and 2-year-old leaves of the three *Sasa* species (May to October 2004, n = 4). Different letters indicate significant differences as calculated by Tukey test ($P < 0.05$).

and *S. senanensis*, whereas its peak was in June of current leaves for *S. nipponica*. N_{area} for current leaves of *S. nipponica* showed significantly higher than that of *S. senanensis* from June to August ($P < 0.01$). In contrast, N_{area} for current leaves of *S. nipponica* did not show significant difference with *S. kurilensis* from July to September. In October, N_{area} for current leaves showed significantly higher for *S. kurilensis* than those of other *Sasa* species ($P < 0.001$). Also, N_{area} for 2-year-old leaves showed significantly higher for *S. kurilensis* than that for *S. nipponica* ($P < 0.01$). N_{area} for 2-year-old of *S. senanensis* showed middle range between *S. kurilensis* and *S. nipponica*, and its trend was similar with *S. kurilensis*.

Total chlorophyll (Chl a+b) concentration showed the low value after flushing and increased in August for *S. kurilensis* and *S. nipponica* and in June for *S. senanensis* (**Figure 6**). Compared with *Sasa* species, chlorophyll concentration was significantly high value for current leaves of *S. kurilensis* in September and October (**Figure 6**, $P < 0.05$). In August, chlorophyll concentration of current leaves was significantly higher at *S. nipponica* compared to *S. kurilensis* and *S. senanensis* ($P < 0.05$).
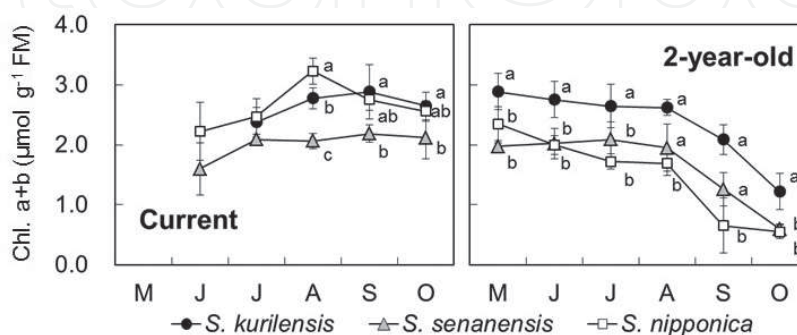

Figure 6. Seasonal change of chlorophyll (a + b) concentration for current and 2-year-old leaves of the three *Sasa* species (May to October 2004, n = 4). Different letters indicate significant differences as calculated by Tukey test ($P < 0.05$).

Chlorophyll concentration for 2-year-old leaves of *S. kurilensis* and *S. senanensis* was maintained these values compared with current leaves, whereas its value of *S. nipponica* was decreased gradually. *S. kurilensis* had a significantly higher chlorophyll concentration in all months than that of S. *nipponica* and *S. senanensis* ($P < 0.05$). Concentration of chlorophyll for 2-year-old leaves showed remarkable decrease from September.

PNUE of current leaves showed significantly high values for *S. senanensis* from July compared with the other *Sasa* species (**Figure 7**, $P < 0.05$). In contrast, PNUE of current leaves of *S. nipponica* decreased from September. PNUE of current leaves of *S. kurilensis* increased from September. PNUE of current leaves was decreased for all *Sasa* species in October.

For 2-year-old leaves, PNUE showed high in May; however, this value was decreased in June. From June to August, the value of PNUE was maintained these values for three *Sasa* species. In September, PNUE of *S. kurilensis* and *S. senanensis* was increased, whereas its value was decreased for *S. nipponica*. Compared with three *Sasa* species, PNUE for 2-year-old leaves of *S. kurilensis* was significantly higher from July to October than those for other *Sasa* species ($P < 0.05$).

2.4. Discussion

Based on the results, the ecophysiological characteristics of the three *Sasa* species were different. The leaf of *S. nipponica* showed high P_{sat} from flushing (**Figure 3**). The leaf of *S. nipponica* also had high N (**Figure 5**), and this made it possible to maintain a high P_{sat} concentration. Furthermore, the leaf of *S. nipponica* was thin with a high value of SLA (**Figure 4**). In general, thin leaves have a low value of CO_2 diffusive conductance [25]; as a result, thin leaves show high P_{sat}. So, the relatively thin leaf of *S. nipponica* has a big advantage to obtain a high photosynthetic rate through diffusion of CO_2 in its leaves. In contrast, 2-year-old culm of *S. nipponica* was fallen in June, and its leaves were laid at a low layer of the plantation. P_{sat} of 2-year-old leaves decreased (**Figure 3**), and the photosynthetic productivity of its leaf may have been small. However, we confirmed that the leaves of *S. nipponica* could survive over 1 year, even if the culm has fallen.
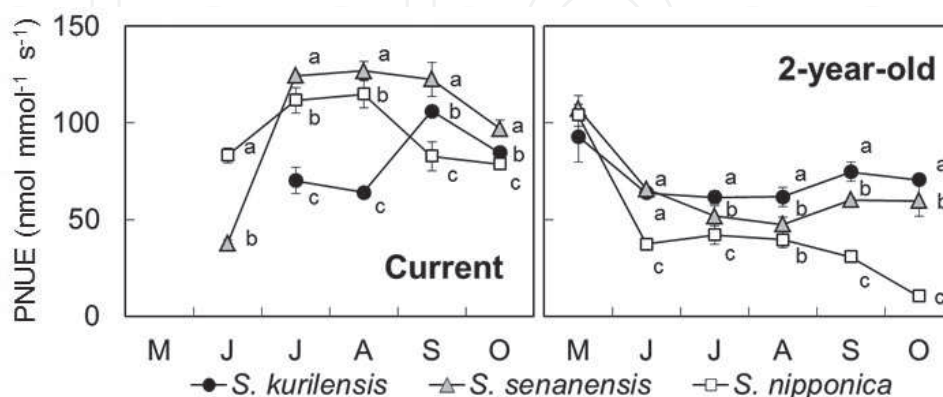

Figure 7. Seasonal change of photosynthetic nitrogen use efficiency (PNUE) for current and 2-year-old leaves of the three *Sasa* species (May to October 2004, n = 4). Different letters indicate significant differences as calculated by Tukey test ($P < 0.05$).

These characteristics that show high photosynthetic capacity and high concentration of nitrogen for younger leaf and short leaf longevity are corresponded with fast-growing species [25]. In general, fast-growing species shows that photosynthetic rate is decreased drastically by increase of leaf age [21, 30]. This trend is clear for evergreen oak compared with conifer species [30]. Moreover, there are a fast-growing species among same genus of *Picea*, and *Picea abies* and *Picea glauca* are considered as fast-growing species [21]. These species showed high photosynthetic rate for younger leaves; however, their high values were not maintained. Also, fast-growing species have a high rate of leaf turnover [31]. Woody species have a leaf turnover mechanism, and when old leaves are lost, leaf nitrogen is retranslocated to younger leaves [32]. *S. nipponica* showed continuous decrease of N_{mass} (**Figure 6**), and its trait is probably related with retranslocation of nitrogen. *S. nipponica* may be retranslocated nitrogen from old to young leaves, thus maintaining high photosynthetic capacity.

For the other *Sasa* species, the maximum value of P_{sat} for current leaves of *S. kurilensis* was lower than other species; however, its value for 2-year-old leaves was maintained for 5 months (**Figure 3**). These traits are corresponded with slow-growing species [25]. The concrete slow-growing species are *Taxus baccata*, *Picea mariana*, and *Picea rubens* [21, 30]. The leaf longevities of these species were over 5 years, and photosynthetic rates showed high value for 6-year-old leaves [21, 30]. Also, maximum leaf longevity of *S. kurilensis* is 5 years [4], and its ecophysiological characteristics are similar with other slow-growing species. Also, slow-growing species have a characteristic to maintain high value of PNUE for aged leaves [21, 30], and *S. kurilensis* showed high PNUE for 2-year-old leaves (**Figure 7**). This trait is related with the maintenance of photosynthetic rate for long period.

On other traits, slow-growing species has thick leaves [21, 25]. Leaves of *S. kurilensis* showed a low value of SLA (**Figure 4**), which was characterised by thick leaves. In general, species with a small SLA allocates nitrogen to the leaf cell wall and increases toughness of the cell [33]. This trait contributes to the extent of leaf longevity [34]. Thus, allocation of nitrogen in leaves for *S. kurilensis* is probably larger for cell wall than for protein of photosynthetic apparatus. As a result, *S. kurilensis* may make leaves with a long longevity but with a low photosynthetic rate.

P_{sat} of *S. senanensis* for current leaves showed high values in August and September (**Figure 3**). In contrast, current leaves of *S. senanensis* were thick (**Figure 4**), and N_{area} and N_{mass} were low compared with *S. nipponica* (**Figure 5**). Thus, ecophysiological characteristics of *S. senanensis* are not similar with *S. nipponica*. In contrast, leaves of *S. senanensis* were thin (**Figure 4**) and short longevity (about 2 years, [4]) compared with *S. kurilensis*. Thus, ecophysiological characteristics of *S. senanensis* are also not similar with *S. kurilensis*. Consequently, ecophysiological characteristics of *S. senanensis* are intermediate between fast- and slow-growing species. On the remarkable characteristics of *S. senanensis*, PNUE showed the highest value for current leaves (**Figure 7**). *S. senanensis* may allocate more nitrogen to protein of photosynthesis apparatus compared with other *Sasa* species. Similar ecophysiological characteristics were reported for *Pinus pinea* and *Picea jezoensis* var. *hondoensis* [21, 30].

In addition, the trait of chlorophyll concentration also concerns with ecophysiological characteristics. The concentration of chlorophyll showed high values for *S. kurilensis*, especially 2-year-old leaves (**Figure 6**). In general, chlorophylls have light harvesting complex proteins

(LHCP) at thylakoids in the chloroplast [35]. As an increase of chlorophyll contributes to an increase in photon absorption, chlorophyll concentration shows a positive relationship with photosynthetic rate within the same species [35]. In the case of 2-year-old leaves of *S. kurilensis*, P_{sat} showed a high value despite not having a high nitrogen concentration (**Figures 3** and **5**) and small SLA (**Figure 4**). There is a possibility that 2-year-old leaves of *S. kurilensis* allocate nitrogen to chlorophyll (Chl/N) and reinforce the absorption and transferring capacity of photon. Consequently, *S. kurilensis* may use absorbed photo efficiently for increasing photosystem by decreasing CO_2 diffusion in its leaf. Leaf longevity of *S. kurilensis* is 3–5 years [4]. Therefore, aged leaves of *S. kurilensis* are considered to be shaded by new leaves that flushed later on; therefore, mutual shading occurs. High concentration of chlorophyll in 2-year-old leaves of *S. kulinensis* may have had the advantage under shady conditions.

3. Conclusion

Sasa species regenerates at the same place with clonal development, and these traits cannot be simply classified into fast- and slow-growing species as other species. We regard the *Sasa* species as follows: *S. nipponica* is classified as a fast-growing species, whereas *S. kulinensis* are slow-growing species. Indeed, ecophysiological characteristics of *Sasa* sp. are the same as slow- and fast-growing species as found in other plant species. *S. senanensis* cannot be classified as two growing types and showed intermediate characteristics between fast- and slow-growing species.

Related to the habitat of the three *Sasa* species, edaphic habitat of *S. nipponica* is considered to be the deep humus layer and A-horizon [36]. The characteristics of a fast-growing species is to have an advantage in a fertile habitat, and the growth trait of *S. nipponica* shows a rapid turnover of leaves and culms [4], which is considered to be suitable for the habitat. We conclude that ecophysiological characteristics of *S. nipponica* are adapted to fertile habitats. The distribution area of *S. nipponica* is classified as low altitudes, facing to the coast of Pacific Ocean where the summers are relatively cloudy with high humidity and the high photosynthetic performance of *S. nipponica* is kept [8]. Moreover, although the snowy period there is short, the soil freezes with cold climate [5]. *Sasa* cannot keep evergreen leaves during winter; hence, the *Sasa* species must produce new leaves from spring after the death of leaves of previous year. Its high photosynthetic rate may be compensating short leaf longevity.

In contrast, the distribution of *S. kurilensis* is hillsides and slope of valley sides where soil depth is shallow [36]. In general, these locations restrict plant growth. The leaves and culms of *S. kurilensis* can survive for several years [4], and these traits may exist to compensate for low photosynthetic productivity. *S. kurilensis* showed high concentration of chlorophyll and PNUE for 2-year-old leaves (**Figures 6** and **7**). This characteristic is suitable for conditions where resources are limited. Thus, we conclude that ecophysiological characteristics of *S. kurilensis* reflect the adaptability to infertile habitats. *S. kurilensis* distributes at high mountain areas in Hokkaido Island (**Figure 1**). The area of *S. kurilensis* probably corresponds with deep snow and harsh environmental conditions.

The habitat of *S. senanensis* is similar to the soil condition of *S. nipponica* [36]. Leaf longevity of *S. senanensis* is about 2 years [4], and this characteristic is probably suitable for relatively good environmental conditions, such as high soil fertility. Compared with *S. nipponica*, N_{mass} and N_{area} in current leaves were lower for *S. senanensis* (**Figure 5**). Thus, the nutrient requirement of *S. senanensis* is also lower than that of *S. nipponica*, and *S. senanensis* can adapt to infertile habitats or resources limited conditions. Moreover, the longevity of culm of *S. senanensis* is about 5 years, which is different from its leaves. Its culm has buds at every node (**Figure 2**), and the leaves can flush during the latter period of the culm life-span. Based on these results, we conclude that the growth characteristics of *S. senanensis* may be high flexibility, and it is also able to adapt to different nutrient and environmental conditions. In fact, the distribution area for *S. senanensis* in Hokkaido Island is the largest (**Figure 1**). The flexibility of *S. senanensis* may be enabling this species to grow in a broad distribution range.

Acknowledgements

Author details

Masazumi Kayama[1,2]* and Takayoshi Koike[3]

*Address all correspondence to: kayama@affrc.go.jp

1 Hokkaido Research Center, Forestry and Forest Products Research Institute, Sapporo, Japan

2 Japan International Research Center for Agricultural Sciences, Tsukuba, Japan

3 Silviculture and Forest Ecological Studies, Hokkaido University, Sapporo, Japan

References

[1] Suzuki S. Illustrations of Japanese Bambusaceae. Funabashi: Jukai Shorin; 1996. p. 271. (in Japanese)

[2] Uchimura E. Bamboo Guide Book. Tokyo: Soshinsha; 2014. p. 269. (in Japanese)

[3] Ohrnberger D. The Bamboos of the World. Amsterdam: Elsevier Science; 1999. p. 596

[4] Makita A. The characteristics of life history for dwarf bamboo. In: Koike T editor. Tree Physiological Ecology. Tokyo: Asakura Publishing Co.; 2004. pp. 199-214. (in Japanese)

[5] Japan Meteorological Agency. General Information on Climate of Japan [Internet]. 2017. Available from: http://www.data.jma.go.jp/gmd/cpd/longfcst/en/tourist.html

[6] Ishibashi S. The relationship between natural regeneration and land/forest description in natural cool-temperature and boreal forests. Journal of the Japanese Forest Society. 1998;**80**:74-79. (in Japanese and English summary)

[7] Noguchi M, Yoshida T. Factor influencing the distribution of two co-occurring dwarf bamboo species (*Sasa lurilensis* and *S. senanensis*) in a conifer-broadleaved mixed stand in northern Hokkaido. Ecological Research. 2005;**20**:25-30

[8] Toyooka H, Sato A, Ishizuka M. Distribution Map of the *Sasa* Group in Hokkaido. Sapporo: Hokkaido Branch, Forestry and Forest Products Research Institute; 1983. p. 36. (in Japanese)

[9] Sakai A. Plant Cold Hardiness and Adaptation to Cold Climate. Tokyo: Center for Scientific Publisher; 1982. p. 469. (in Japanese)

[10] Sturm M, Perovich DK, Holmgren J. Thermal conductivity and heat transfer through the snow on the ice of the Beaufort Sea. Journal of Geophysical Research. 2002;**107**(C21):8043. DOI: 10.1029/2000JC000409

[11] Kayama M. Study on the adaptation capacity of spruce species grown on serpentine soil and its application for forest rehabilitation. Research Bulletin of the Hokkaido University Forests. 2006;**60**:33-78. (in Japanese and English summary)

[12] Sasa K, Satoh F, Komiya K, Fujiwara K. Possibility of *Sasa* grassland structure as an environmental indicator in mid winter season at cold and strong wind region. Translocation of the Meeting in Hokkaido Branch of the Japanese Forest Society. 1994;**42**:50-52. (in Japanese)

[13] Ishikawa M, Oda A, Fukami R, Kuriyama A. Factors contributing to deep supercooling capability and cold survival in dwarf bamboo (*Sasa senanensis*) leaf blades. Frontiers in Plant Science. 2015;**5**:791

[14] Yajima T, Watanabe N, Shibuya M. Change in biomass of above- and under-ground parts in *Sasa kurilensis* and *Sasa senanensis* stands with culm height. Journal of the Japanese Forest Society. 1997;**79**:234-238. (in Japanese and English summary)

[15] Takeda K, Ito T. Effect of the rhizomes of *Sasa nipponica* on the slope reinforcement for preventing surface failure II. Field survey of the structure of *Sasa nipponica* population. Journal of the Japanese Society of Revegetation Technology. 2003;**28**:431-437. (in Japanese and English summary)

[16] Noguchi M, Yoshida T. Tree regeneration in partially cut conifer-hardwood mixed forests in northern Japan: Roles of establishment substrate and dwarf bamboo. Forest Ecology and Management. 2004;**190**:335-344

[17] Takaoka S, Sasa K. Landform effects on fire behavior and post-fire regeneration in the mixed forests of northern Japan. Ecological Research. 1996;**11**:339-349

[18] Kayama M, Nomura M, Sugishita Y, Satoh F, Sasa K, Koike T. Growth and survival of Sasa (*Sasa senanensis*) community grown under cold and strong windy environment in northern Japan. Bamboo Journal. 2000;**17**:20-26

[19] Makita A. Survivorship of a monocarpic bamboo grass, *Sasa kurilensis*, during the early regeneration process after mass flowering. Ecological Research. 1992;**7**:245-254

[20] Mediavilla S, Escudero A. Photosynthetic capacity, integrated over the lifetime of a leaf, is predicted to be independent of leaf longevity in some tree species. New Phytologist. 2003;**159**:203-211

[21] Kayama M, Kitaoka S, Wang W, Choi DS, Koike T. Needle longevity, photosynthetic rate and nitrogen concentration of eight spruce taxa planted in northern Japan. Tree Physiology. 2007;**27**:1585-1593

[22] Agata W, Hakoyama S, Kuwamitsu Y. Influence of light intensity, temperature and humidity on photosynthesis and transpiration of *Sasa nipponica* and *Arundinaria pygmaea*. Botanical Magazine Tokyo. 1985;**98**:125-135

[23] Lei TT, Koike T. Functional leaf phenotypes for shaded and open environments of a dominant dwarf bamboo (*Sasa senanensis*) in northern Japan. International Journal of Plant Science. 1998;**159**:812-820

[24] Ohshima T. Ecological studies of Sasa communities III. Photosynthesis and respiration of *Sasa kurilensis*. Botanical Magazine Tokyo. 1961;**74**:349-356

[25] Lambers H, Chapin FS III, Pons TL. Plant Physiological Ecology. New York: Springer-Verlag; 1998. p. 540

[26] Hokkaido Research Center. Forestry and Forest Products Research Institute. Annual Report 2004. Sapporo: Hokkaido Branch, Forestry and Forest Products Research Institute; 2005. p. 116. (in Japanese)

[27] Kayama M, Yamanaka T. Growth characteristics of ectomycorrhizal seedlings of *Quercus glauca*, *Quercus salicina*, and *Castanopsis cuspidata* planted on acidic soil. Trees. 2014;**28**:569-583

[28] Barnes JD, Balaguer L, Manrique E, Elvira S, Davison A. A reappraisal of the use of DMSO for the extraction and determination of chlorophylls a and b in lichens and higher plants. Environmental and Experimental Botany. 1992;**32**:85-100

[29] Reich PB, Walters MB, Ellsworth DS. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monograph. 1992;**62**:365-392

[30] Escudero A, Mediavilla S. Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. Journal of Ecology 2003;**91**:880-889

[31] Aerts R, Chapin FS III. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. Advance of Ecological Research. 2000;**30**:1-67

[32] Killingbeck KT. Nutrient resorption. In: Noodén LD, editor. Plant Cell Death Processes. San Diego: Elsevier-Academic Press; 2004. pp. 215-226

[33] Takashima T, Hikosaka K, Hirose T. Photosynthesis or persistence: Nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. Plant, Cell and Environment. 2004;**27**:1047-1054

[34] Onoda Y, Hikosaka K, Hirose T. Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency. Functional Ecology. 2004;**18**:419-425

[35] Lawlor DW. Photosynthesis. 3rd ed. Oxford: BIOS Scientific Publishers Ltd.; 2001. p. 386

[36] Sakai A. The Distributions of Plants and Adaptation to Environments, from Tropical Region to Polar or Desert Region. Tokyo: Asakura Publishing Co.; 1995. p. 164. (in Japanese)