Ecological Studies of *Sasa* Communities V. Influence of Light Intensity, Snow Depth and Temperature upon the Development of *Sasa kurilensis* Community*

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Sasa kurilensis is commonly distributed in the Japan Sea side region from Honshu to Hokkaido with heavy snowfall. This species often predominates in the floor synusia of deciduous forests especially of *Fagus crenata*, constituting *Fagus crenata-Sasa kurilensis* community¹⁾ or association²⁾. The light intensity at the top of *Sasa* stratum under the forest canopy falls in the range of about 7–22%^{3,4)}. The vigorous growth of *Sasa* under such considerably low light intensities may be attributable to its relatively high shade tolerance. *S. kurilensis* is scarcely distributed in the Pacific coastal region of Japan with little snow accumulation⁵⁾, and does not in warm-temperate zone of south western Japan.

In order to elucidate these distribution ranges of *Sasa kurilensis* community, the relation of its growth to environmental factors should firstly be studied. The author has already clarified the specific features in physiological functions, productive structure, matter production and the distribution of produced matter among organs of a closed *S. kurilensis* community^{6–9)}. In the present paper, the dependence of matter production of this community upon light intensity, temperature and snow depth will be analyzed, and some characteristics which are principal in matter production in relation to these environmental conditions will be discussed.

Light intensity

In the vicinity of Mt. Waisuhorun, deciduous forests of *Betula Ermani* and *B. platyphylla* are distributed here and there, and *Sasa kurilensis* grows under the forest canopies, forming the shrub stratum. The relative light intensities at the top of the *Sasa* stratum are about 14% or more in summer, except for the dense young birch forests.

For the study of light requirements of *Sasa*, two birch forests were chosen. The one is a closed forest of 30–40 years, another, an open forest of about 80 years or more. In these forests the standing crops of aerial parts and leaf amounts of *S. kurilensis* were measured in October, 1959, and relative light intensities above and under the *Sasa* stratum were also measured in August and April, 1959, using the same method as shown in a previous paper⁶⁾ (Table 1). Measurements of photosynthesis of typical one-year-old shade leaf were carried out under varying light intensities in summer, 1960, by the same method and conditions as shown in another paper⁸⁾ (Fig. 1).

The standing crop of the aerial parts of the *Sasa* stratum amounted to 2.25 kg d.w./m² in the former where mean relative light intensity of 22% was measured. This value seems to be rather high under such low light intensity as 22% (Table 1).

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Table 1. Light conditions and characteristics of *Sasa kurilensis* communities under birch forest. Sampling of *Sasa* was carried out on Oct. 17, 1959.

The numbers in parentheses indicate calculated values. Data in stand C are cited from previous papers^{7,9)} for comparison.

		Stand A Closed forest	Stand B Open forest	Stand C Open site
Mean age of birch forest		30-40 yrs.	80 yrs. or more	—
Light conditions	Above the <i>Sasa</i> -layer			
	Defoliation period (%)	76	80	100
	Foliation period			
	Mean (%)	22	41	100
	Range (%)	11-44	18-69	100
Under <i>Sasa</i> -layer (%)		4.0	4.2	3.0
Characteristics of <i>Sasa kurilensis</i> community	Leaves			
	New leaves (g/m ²) (ΔF)	90	180	295
	One-year-old leaves (g/m ²)	135	120	190
	Total leaves (g/m ²) (F)	225	305	460
	Leaf area index (m ² /m ²) ($\bar{F}$)	3.7 (3.5)	4.4 (4.1)	5.1
	Ann. gross production (g/m ²) (P_g)	(1260)	(3040)	(4760)
	Ann. respiration loss (g/m ²) (R_i)	(810)	(1990)	(3030)
	Ann. net production (g/m ²) (P_n)	(450)	(1050)	(1730)
	Standing crop of aerial part (g d.w./m ²)	2250 (2420)	5010 (5950)	7510 (8040)
	Mean longevity of culms in year	11	10	9.2
	C/ $\bar{F}$ -ratio	10.0	15.4	17.8
	$\Delta F/P_n$ -ratio	0.20	0.18	0.17
	$\bar{F}/F$ -ratio (cm ² /mg d.w.)	0.16	0.14	0.11

Discussing theoretically the growth of *Pinus* and *Picea* under shaded conditions, Monsi¹⁰⁾ has clarified that the shade tolerance is closely related not only to the specific property of photosynthesis but also to the longevity of leaves and the respiration rate of non-photosynthetic system. As discussed already in a previous paper⁹⁾, the respiration loss in *S. kurilensis* community is rather large, so this may be disadvantageous for its shade tolerance. The foliation period of birch at Waisuhorun is about 4 months from mid-June to mid-October. The attributes for the relatively high shade tolerance

of *Sasa* is surely not only to the specific property of photosynthesis (Fig. 1) but also to the 2-year longevity of the evergreen leaves with a 6-month photosynthetic period⁷⁾.

For the further elucidation to the mechanism of shade tolerance of *S. kurilensis*, dry matter production under low light intensity under the birch canopies was calculated from the data in Table 1 on the following assumptions: i) The foliation of birch on June 20, the completion of leaf development on July 20, and the defoliation on October 15. ii) Non-photosynthetic system of the *Sasa* always keeps in weight a constant ratio between the aerial and the

Fig. 1. Light-photosynthesis curves in sun and shade leaves of *Sasa kurilensis* (20° and 0.3% CO₂). Broken line: sun leaf of one-year-old⁸⁾. Solid line: shade leaf of one year-old.

subterranean parts. iii) Photosynthetic activities of *Sasa* leaves in stands A and B are the same as those of shade and sun leaves, respectively. Standing crop, annual gross production (Pg), annual respiration loss (Ri) and annual net production (Pn) calculated by the same method as shown in a previous paper⁹⁾ are shown in Table 1. The calculated values closely resemble the values observed (see Table 1).

The ratio in dry weight of new leaves (ΔF) to Pn and the ratio of Ri/Pg of *Sasa kurilensis* were almost unchangeable under various light conditions seen in Table 1. On the contrary, dry weight of new leaves (ΔF) was smaller under lower light intensity because of the decrease in the number of shooting culms and branches with decrease in light intensity, and the ratio in dry weight of ΔF to the whole leaves (F) was 0.40 in stand A, 0.59 in stand B, and 0.68 in stand C. This means, the longevity of leaves becomes longer when they live under weak illuminations as seen in other plants¹⁰⁻¹²⁾. The ratio of total leaf area ($\bar{F}$) to F , playing the important role in the shade tolerance of plants¹³⁾, increased with the increase of light intensity (Table 1).

If all the leaves of *Sasa* in stand A would defoliate at the end of growing period, the calculated standing crop should be decreased down to about 2/3 of the measured, and if the relative light intensity of 22% continued during the growing period, the calculated Pg and Pn should be decreased down to about 78 and 40%, respectively. These indicate that the shade tolerance of *S. kurilensis* is not merely decided by the photosynthetic characters, but also largely by the longevity of leaves, long maintenance of the active community structure, the increased $\bar{F}/F$ -ratio with the decrease of relative light intensity and the unchanged ratio of $\Delta F/Pn$ under varying light conditions.

Relative light intensity of 2-4% in average was observed on the ground surface of *Sasa kurilensis* synusiae under birch forests, and such extremely low light intensity was continued throughout the year except for the snowfall season, because of the characteristics of productive structure of the *Sasa* community⁷⁾. Plants growing accidentally under the *Sasa* stratum should tolerate such low light intensities suffering deficient matter economy, otherwise they are fated to death⁴⁾. This may be one of the most important factor for the continuation of predominance of the *Sasa* under deciduous forests.

Snow depth

On Mt. Waisuhorun, some windswept area with very little snow accumulation can be found even in winter. In such area a few sites with different snow accumulation were chosen to clarify the effect of snow on the dry matter production of *Sasa kurilensis*. The depth of snow cover was determined in mid-March and late in April, and standing crop of aerial part, amount of leaves, mean longevity of culms were measured in October, 1959. As seen in Table 2, standing crop, especially amount of one-year-old leaves decreases in proportion to the decrease in thickness of snow cover; stand D is only 1/7 of stand C in one-year-old leaves.

Dry matter production (Pg , Pn) total respiration loss (Ri) and standing crop of stands D and E were calculated from the leaf dry weight, the longevity of culms (Table 2), light-daily photosynthesis curves and respiration rate (Figs. 4, 5 and 6 of a previous paper⁸⁾) using the same method as shown in another paper⁹⁾, on following assumptions: i) A constant ratio between aerial and subterranean parts of non-photosynthetic system. ii) The time trends shown in Fig. 1 of a previous paper⁷⁾ of the dry weight of each organ of each age are also applicable to this case.

Table 2. Showing the values of leaf dry weight, annual gross production, respiration loss, net production and standing crop of *S. kurilensis* communities with different depth of snow accumulation. Data in stand C are cited from previous papers^{7,9)} for comparison. Calculating procedures are given in the text and a previous paper⁹⁾. The numbers in parentheses indicate calculated values.

	Stand D	Stand E	Stand C
Depth of snow cover (cm)			
March 14	10	80	300
April 22	0	40	190
<i>Sasa kurilensis</i> community			
Leaves			
New leaves (g/m ²)	195	240	295
One-year-old leaves (g/m ²)	22	55	190
Total leaves (g/m ²)	217	295	465
Ann. gross production (g/m ²)	(990)	(2150)	(4750)
Ann. respiration loss (g/m ²)	(480)	(1210)	(3030)
Ann. net production (g/m ²)	(510)	(940)	(1730)
Standing crop of aerial part (g/m ²)	1120 (1400)	2440 (3815)	7510
Mean longevity of culms in year	6	8	9.2

The results of calculation are also shown in Table 2. The fairly good coincidence between the standing crops calculated and observed can give some ideas on the causes of those phenomena. This decrease of snow depth brings about a remarkable decrease of *Pg* with decreasing the amount and longevity of leaves. The shortening of the life of culms and decrease of *Pg* and *Pn* are considered to be the cardinal factors for the standing crop decrease with decrease of snow coverage. In this case, the culms become shorter and thinner, but their density never decrease with decrease of standing crop, in opposition to the case under low light intensity of the forest.

Relative light intensities at the ground surface in *S. kurilensis* community where snow coverage is very thin are 20-40% in the period from the thawing to the unfolding of new leaves. Shrubs and herbs of other kinds can invade into such unstable *Sasa* community. This may suggest that *S. kurilensis* community should be rare in the Pacific coastal regions with poor snow accumulation.

Temperature

Sasa kurilensis is distributed abundantly in the upper montane and subalpine (or subarctic) zones and not in warmer regions. At higher temperatures the respiration of the bulky non-photosynthetic systems must be increased, resulting the reduction of *Pn*, and consequently the decrease of standing crop. This seems to be one of the main reasons for such specific distribution of the *Sasa* species.

For the further elucidation based on dry matter production of this distribution, the changes of standing crop of *Sasa kurilensis* community caused by temperature was calculated. Here the following assumptions were made: i) Abundant snow; with a 2° increase of annual mean temperature, snow melts 10 days earlier and starts 5 days later. ii) The rise of annual mean temperature is equally distributed to each month. iii) Mean monthly duration of bright sunshine of 38%. iv) Constant leaf amount in different to temperature change. v) A constant ratio of aerial part to subterranean part in non-photosynthetic system and mean longevity of culms of 10 years.

Standing crops of *Sasa kurilensis* communities calculated at different annual mean temperatures of -0.6 , 4.4 (annual mean temperature at 500 m of Mt. Waisuhorun), 6.4 , 9.4 and 14.4° are shown in Fig. 2. The figure represents that total dry weight at 14.4° is reduced to about $1/2$ of the maximum at 4.4° . The decrease of standing crop with increasing temperature is due to the larger increase in respiration loss against the smaller increase of gross production caused by increased growing period, while the decrease at -0.6° is due to the decrease in gross production by reduced growing period.

Increased activity caused by high temperature would shorten the mean longevity of each organ. Another assumption that the life of culms is reduced by one year with a 5° elevation of annual mean temperature was considered in further calculation of standing crop. The broken line in Fig. 2 shows the result. This appears to fit better than the former.

However, for the demonstration of this problem, the *Sasa kurilensis* communities in various localities should be surveyed more comprehensively, and seasonal changes of the photosynthetic activity and the longevity of culms should be studied under various temperature conditions.

Summary

Influence of light intensity, snow depth and temperature upon dry matter production of *Sasa kurilensis* community especially at Mt. Waisuhorun, southern Hokkaido, was analyzed.

1. The relatively high shade tolerance of *Sasa kurilensis* is attributable to the characters of photosynthesis, the increased longevity of leaves and the increased ratio of total leaf area to total leaf weight with decrease of light intensity, the constant distribution ratio for new leaves independent of light conditions, and the maintenance of active productive structure for full utilization of growing season, though the species has a disadvantageous character of large respiration loss.

2. The standing crop of the community was decreased with the decrease in snow depth. This is mainly caused by the shortening of the life of culms and the depression of gross and net production caused by the shortening of the life and decrease in amount of leaves.

3. The maximum standing crop is expected at the locality where the annual temperature is 4.4° , which is really observed at the station concerned. If higher than 4.4° , the standing crop decreases with increase of respiration loss, and if lower than this temperature, it decreases with decreases of gross production caused by short growing period.

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Fig. 2. Relation between dry weight of aerial part of *Sasa kurilensis* community and annual mean temperature. Solid circles: the dry weight calculated by the assumption that the mean longevity of culms is 10 years regardless of the temperature. Open circle: by the assumption that the mean longevity of culms is reduced by 1 year with rising of annual mean temperature of 5° .

The broken line in Fig. 2 shows the result. This appears to fit better than the former.

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References

- 1) Yoshioka, K., Bull. Soc. Ecol. 2: 72 (1952). 2) Suzuki, T., Journ. Jap. For. Soc. 31: 139 (1949). 3) Monsi, M., and Saeki, T., Jap. J. Bot. 14: 22 (1953). 4) —, and Oshima, Y., ibid. 15: 60 (1955). 5) Suzuki, S., Ecol. Rev. 15: 131 (1961). 6) Oshima, Y., Bot. Mag. Tokyo 74: 199 (1961). 7) —, ibid. 74: 280 (1961). 8) —, ibid. 74: 349 (1961). 9) —, ibid. 74: 473 (1961). 10) Monsi, M., ibid. 73: 81 (1960). 11) Kuroiwa, S., ibid. 73: 133, 165 (1960). 12) Oka, G., Rept. Natural Monument, Bot. 16: 51 (1936). 13) Nomoto, N., Iwaki, H., and Monsi, M., Bot. Mag. Tokyo 74: 386 (1961).

摘 要

大 島 康 行: ササ群落の生態学的研究 V.
チシマザサ群落の発達にたいする、積雪量、温度の影響

チシマザサ群落の分布要因を解析する第一歩として、光、積雪量および温度条件のちがいが現存量におよぼす影響を物質生産の面から解析した。北海道ワイスホルン山の林内照度を異にする 2 つのカバ林、チシマザサにおよぼす光条件の影響がしらべられた。その結果、チシマザサには生産された物質のうち呼吸によって消費される割合が大きいという耐陰性に不利な性質があるにもかかわらず⁹⁾、光が弱くなるほど、葉の寿命が長くなり、また葉面積一葉重比が大きくなること、光条件の変化にかかわらず生産された物質の葉への分配の割合が一定であること、葉が常緑で約 6 か月の生育期間中その生産構造が一定の活動的な状態に維持されていること⁷⁾、などの特性が光合成の特性とともに弱光の条件下で比較的高い現存量が維持されている原因となっていることが認められた。また落葉樹林下でチシマザサが下層群落として、しばしば割合に安定な状態を維持しているのは、その生産構造がほぼ一定の状態に維持され、地表面附近の相対照度が非常に低くその変動の幅が小さいことが一つの重要な原因となっている。

またワイスホルン山のチシマザサの純群落で、積雪量と現存量の関係を解析した。チシマザサ群落の現存量は積雪量が少なくなると低下するが、これはおもに積雪量が少なくなると桿の寿命が低下すること、および葉の寿命が短くなることによって葉量が減少し、そのため物質生産が低下することに原因していることが明らかになった。

温度条件とチシマザサ群落の生育との関係を明らかにするため、年平均気温の変化にともなう物質生産量と現存量の変化を計算した。その結果、年平均気温 4.4° (ワイスホルン山の海拔 500 m の地点) で最大の現存量が期待された。平均気温の 4.4° より高い地域では呼吸による生産物の消費の増加が物質生産による生産物の増加をいちじるしく上まわり、また 4.4° 以下の地域では生育期間の減少が現存量の低下のおもな要因になっていることが明らかになった。(東京都立大学理学部生物学教室)