雪田環境における高山植物の開花・結実に要する期間

メタデータ	言語: eng 出版者: 公開日: 2019-10-04 キーワード (Ja): キーワード (En): 作成者: メールアドレス: 所属:
URL	https://doi.org/10.24517/00055702

J. Phytogeogr. & Taxon.
40: 99-106, 1992

Gaku KUDO*: Pre-flowering and Fruiting Periods of Alpine Plants Inhabiting a Snow-Bed

工藤　岳：雪田環境における高山植物の開花・結実に要する期間

Abstract

Phenology of alpine plants was studied in a snow-bed along a snow-melting gradient. Pre-flowering and fruiting periods of nine species including two varieties were potentially determined by cumulative temperature of daily mean, and the data indicated that actual flowering time was affected by the timing of snow disappearance. Alpine plants could not adjust the flowering and fruiting times in accordance with the growing conditions. Hence the species having short pre-flowering and/or fruiting periods were advantageous for seed set in later exposed places where growing season was highly restricted.

Key Words: Melting gradient— Phenology— Snow— Temperature

In alpine environments where the growing season is highly restricted, plants are required to complete their annual life-cycle during short period (BILLINGS and BLISS, 1959; RAM *et al.*, 1988). Time of snow disappearance is very important factor controlling plant phenology in such environments (HOLWAY and WARD, 1963; 1965; OSTLER *et al.*, 1982; KUDO, 1991). Snow-bed is characterized by large snow cover during winter and lingering snow until summer. Here distribution of snow accumulation is variable between sites due to topographic effect, and the time of snow disappearance is very different within a narrow area. Species having a wide distribution range along the snow-melting gradient, therefore, experience quite different length of growing season between early and late exposed places. In the late exposed places, early flowering and fruiting are advantageous for successful seed set. KUDO (1991) compared flowering and fruiting conditions of many alpine plants along the gradient and indicated that species having long pre-flowering and/or fruiting periods were disadvantage for sexual reproduction in the later exposed paces. In the previous study, however, phenological variation within species along the gradient was not analyzed enough. In this study, therefore, detailed observation of flowering and fruiting phenologies were obtained during two years for nine species including of two varieties having large distribution ranges along a snow-melting gradient.

The aim of this study is to answer the following questions. (1) What determines the flowering time and the fruiting period of each species inhabiting a snow-bed ? (2) Is there any phenological variation of flowering and/or fruiting times within single species in accordance with snow conditions?

Materials and Methods

The Taisetsu Mountains are located in central Hokkaido, northern Japan (Fig. 1). Climatically, the Taisetsu Mts. have cold and snowy winters, and warm and wet summers. The annual mean temperature at an altitude of 2000m was −3.8°C, ranging from −21.3°C (January) to 13.9°C (August) in 1985 (SONE and TAKAHASHI, 1988). Because of prevailing northwesterly winds during

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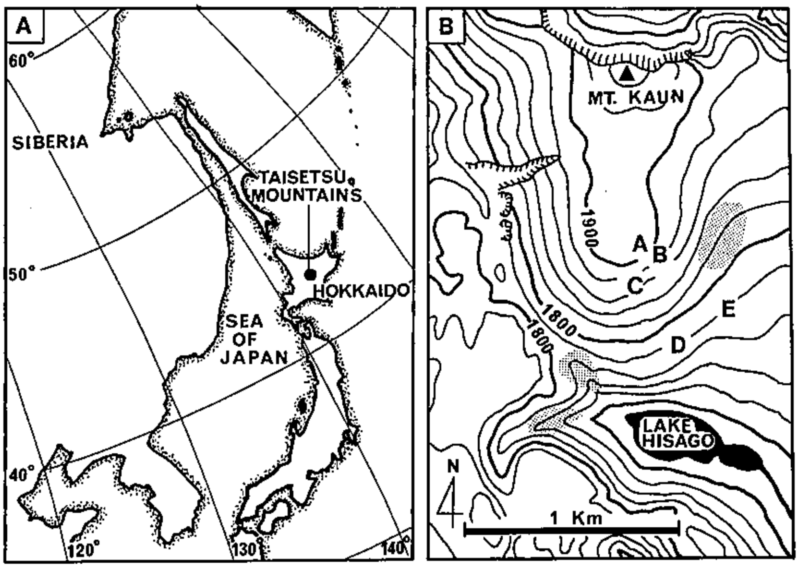

Fig. 1. (A) Location of the Taisetsu Mountatins. (B) Map of study site. A to E: Survey quadrats. Dotted areas mean perennial snow.

the winter, large snow drifts are built up on the southeast facing slopes. The time of snow disappearance varies from the late May to late September, and snow begins to cover the ground again by early to mid October.

This study was conducted on the snow-bed communities developing on a block-field slope, which faces the southeast with 5-18° inclination, in the central part of the Taisetsu Mts. (43° 33'N, 142° 53'E). The five 20m x 20m quadrats, A to E, were arranged along a snow-melting gradient between 1790-1910m elevation (Fig. 1). All quadrats had large snow cover during winter, and snow disappeared from quadrat A to E every year (Table 1). It took five to seven days for complete disappearance of snow from the beginning in each quadrat. In this study, time of snow disappearance means the date of ca. 50% exposure of the quadrat. Snow-bed communities of this area were composed of dwarf shrubs, forbs and grasses (in detail see KUDO, 1991; KUDO and ITO, 1992), and vegetation height was ca. 30 cm or less.

Nine plant species including two varieties having large distribution ranges along the gradient were chosen for phenological survey. *Peucedanum multivittatum* MAXIM., *Primula cuneifolia* LEDEB., *Veronica stelleri* PALL. ex LINK var. *longistyla* KITAGAWA, *Solidago virgaurea* L. var. *leiocarpa* (BENTH.) MIQ. and *Potentilla matsumurae* TH. WOLF were deciduous perennial herbs. *Sieversia pentapetala* (L.) GREENE was deciduous dwarf shrubs, and *Rhododendron aureum* GEORGI, *Phyllodoce caerulea* (L.) BABIN-

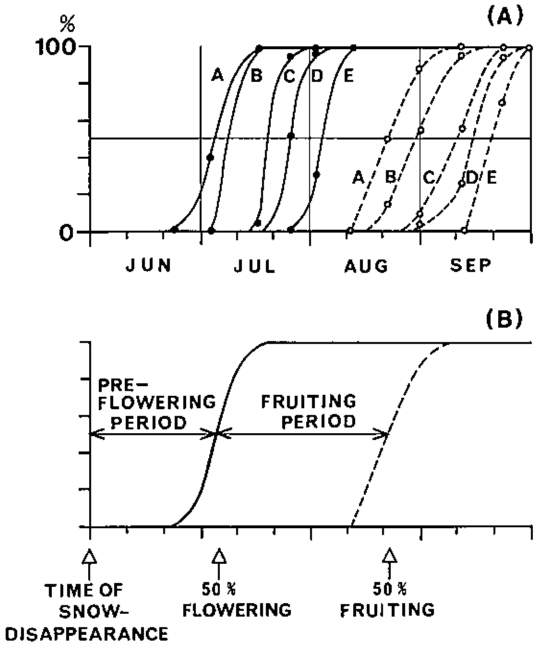

Fig. 2. An illustration of the curves of CFL (solid line) and CFR (broken line) of *Phyllodoce caerulea* in each quadrat in 1990 (A), and how to obtain the average periods (days) of pre-flowering and fruiting in quadrat A (B).

Table 1. Environmental conditions of the quadrats.

Quadrat		A	B	C	D	E
Altitude (m)		1910	1900	1880	1790	1790
Slope direction		SE	SE	SSE	SSE	SE
Inclination (°)		5	16	18	11	11
Time of snow-	1989	1 Jul	10 Jul	20 Jul	28 Jul	8 Aug
disappearance	1990	31 May	14 Jun	5 Jul	14 Jul	19 Jul
Snow-free	1989	95	80	70	60	55
period (days)	1990	130	115	95	85	80

GTON and *Phyllodoce aleutica* (SPRENG.) A. HELLER were evergreen dwarf shrubs. *P. cuneifolia* and *P. matsumurae* inhabited quadrats B to E, and other species inhabited all quadrats.

In 1989 and 1990, flowering and fruiting conditions were surveyed in each quadrat, every five to 10 days intervals from the time of snow disappearance to the end of September. The number of flowering buds (before flowering), flowers (actual flowering), developing fruits (before seed maturation) and ripe fruits (seed maturation) per shoot were obtained for 50 individuals of each herb species and for 50 stems of each shrub species chosen at random within each quadrat. For *Sieversia pentapetala,* having only one flower per shoot, measurements were made for 100 stems in each quadrat. When there were less than 50 (or 100 for *S. pentapetala*) flowering or fruiting individuals (or stems) within quadrats, measured numbers were reduced suitably. There were no data of 1989 for three evergreen species in quadrat A, and for *S. pentapetala* in all quadrats. Cumulative percentages of flowering (CFL) and fruiting (CFR) in each species were regularly obtained through the season in each quadrat as follows; **CFL** (%)= [(**FL**+**DF**+**RF**)/(**FB**+**FL**+**DF**+**RF**)]×100; **CFR** (%)= [**RF**/(**FB**+**FL**+**DF**+**RF**)]×100; (**FB**: total flowering-bud number of observed individuals or stems, **FL**: total flower number, **DF**: total developing-fruit number, and **RF**: total ripe-fruit number).

After drawing the cumulative flowering and fruiting curves of each species, average length of pre-flowering and fruiting periods were obtained in each quadrat as shown by Figure 2. Pre-flowering period means the days from snow disappearance to 50% **CFL,** and fruiting period means the days from 50% **CFL** to 50% **CFR.**

It is known that one of the most important environmental factors controlling flowering and fruiting times is temperature (BLISS, 1962; HOLWAY and WARD, 1965). Seasonal change of air temperature was measured at 1700m elevation from May to September in 1990 (measured by T. YAMADA and Y. KODAMA). Measurement was done at one hour intervals at the height of 1 m from the ground surface with a thermister sensor and an automatic recorder (KADEC-U). The values of daily mean were corrected with the lapse rate of temparature, −0.6°C/100m, in accordance with the elevation of each quadrat. In order to clarify the relationship between plant phenology and temperature, effective cumulative temperatures (K) of daily mean during pre-flowering and fruiting periods were calculated for each species in 1990 as follows; K (°C·day)= $\Sigma (t_5 - 5)$, where threshold temperature for plant growth was set in 5°C, and t_5 means daily mean air temperature above 5°C.

Results

Weather condition

Snow disappeared rather later in 1989 than in 1990 for all quadrats. They were early July (in quadrat A) to early August (in quadrat E) in 1989, and end of May (in A) to late July (in E) in 1990. Snow-free periods were 95 (in A) to 55 days (in E) in 1989, and 130 (in A) to 80 days (in E) in 1990 (Table 1).

Air temperature increased from early May to late June, and maintained above 10°C during July and August with the peak value (13.6°C) in early August, and abruptly decreased from mid September (Fig. 3). From mid June to mid September, daily minimum values maintained above 0°C.

Flowering and fruiting conditions

Flowering and fruiting conditions of each

Table 2. Flowering and fruiting conditions of each species in 1989 and 1990. F and M: perfect flowering and fruiting, respectively (100% **CFL** and **CFR**), f and m: 100%>CFL and **CFR**>50%, f' and m': 50%>**CFL** and **CFR**>0%. *: no flowering or fruiting.

Quadrat		A	B	C	D	E
Peucedanum multivittatum	1989	FM	FM	FM	FM	Fm'
	1990	FM	FM	FM	FM	FM
Primula cuneifolia	1989		FM	FM	FM	Fm
	1990		FM	FM	FM	FM
Veronica stalleri var. longistyla						
	1989	FM	FM	Fm	Fm	Fm'
	1990	FM	FM	FM	FM	FM
Solidago virgaurea var. *leiocarpa*						
	1989	Fm	Fm	Fm'	f*	f'*
	1990	Fm	Fm	Fm'	Fm'	Fm'
Potentilla matsumurae	1989		FM	FM	FM	Fm
	1990		FM	FM	FM	FM
Sieversia pentapetala	1990	FM	FM	FM	FM	FM
Rhododendron aureum	1989	FM	FM	Fm'	F*	**
	1990	FM	FM	FM	FM	**
Phyllodoce caerulea	1989	FM	FM	Fm	Fm	F*
	1990	FM	FM	FM	FM	FM
Phyllodoce aleutica	1989	FM	FM	Fm	Fm'	F*
	1990	FM	FM	FM	FM	FM

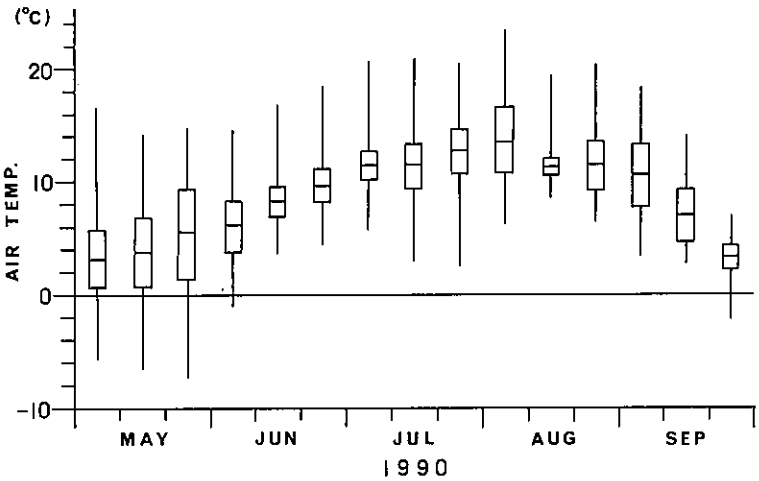

Fig. 3. Seasonal change of air temperature of stydy area in 1990. Each column indicates the mean value and S.D. The vertical bars indicate the ranges during each 10 or 11 days.

species in both the years are shown in Table 2. In 1989, there was no species succeeded in full fruiting (100% **CFR**) in quadrat E, indicating that every species reduced, more or less, their reproductive output under the condition of short snow-free period. *Solidago virgaurea* var. *leiocarpa* did not attain even full flowering (100% **CFL**) in quadrats D and E in 1989, and the **CFR**s were less than 50% in quadrats C, D and E in both the years. *Rhododendron aureum* had no flowers in quadrat E in both the years and failed to mature the fruits in quadrat D in 1989. Other species succeeded in full fruiting in all quadrats in 1990.

Flowering and fruiting characters

In 1989, there were less differences in the

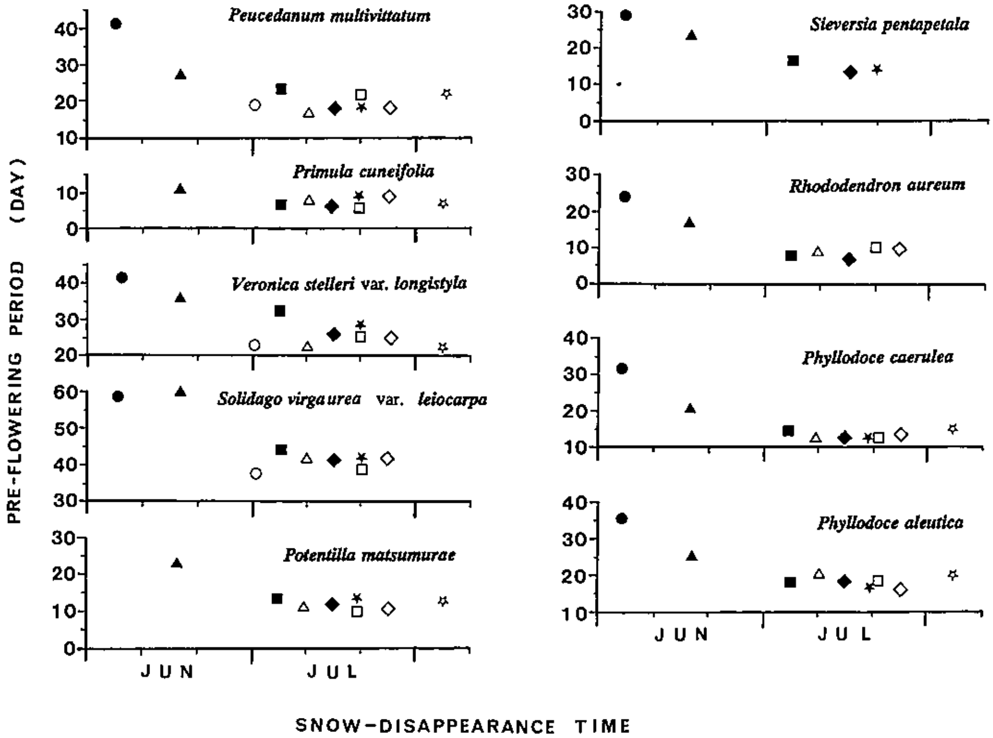

Fig. 4. Relationship between the time of snow disappearance and pre-flowering period in each species. Circles denote quadrat A, triangles B, squares C, diamonds D, and stars E. Open symbols mean the values in 1989, and closed ones in 1990.

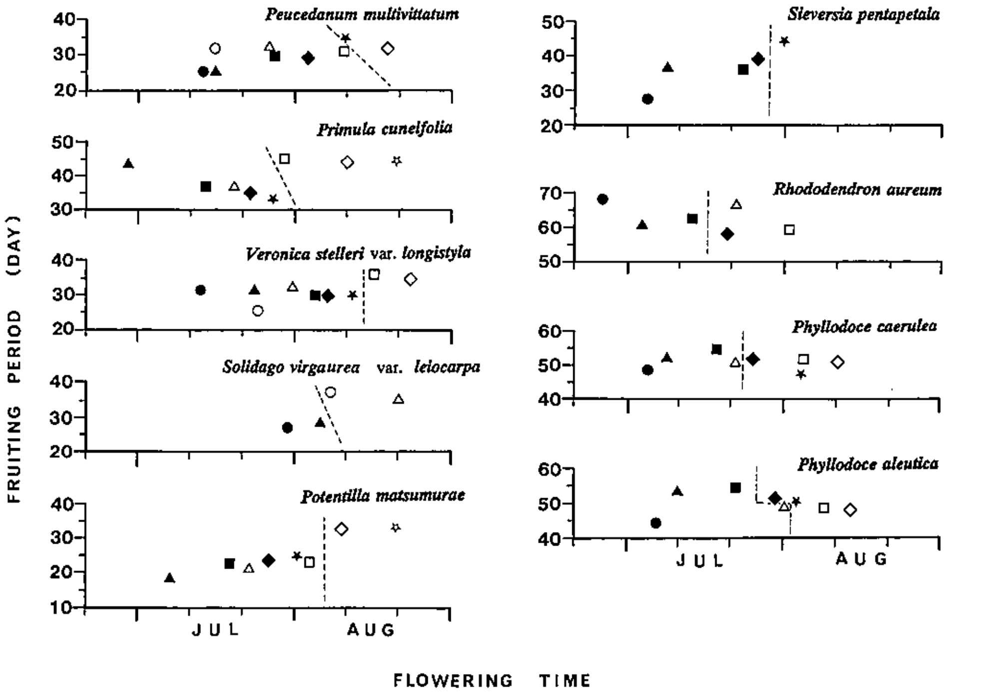

Fig. 5. Relationship between the time of flowering (50% CFL) and fruiting period in each species. Right side of broken line means that seeds matured after mid September. For symbols, refer Figure 4.

pre-flowering periods within species among quadrats; whereas, in 1990, pre-flowering periods of most species were apparently longer in quadrats A and B in comparison with other quadrats (Fig. 4). In other words, the patterns of pre-flowering period were different between before and after late June in the time of exposure; when snow disappeared before late June, pre-flowering periods increased with the accelerated time of exposure. When snow disappeared after late June, on the other hand, there was no relationship between pre-flowering period and snow disappearance time in any species (KENDALL's rank correlation test, $p>0.10$). The late June corresponded to the time in which daily mean temperature rose near 10°C (Fig. 3). This warm condition might bring about the stable pre-flowering period in each species, when snow disappeared after late June. Thus cumulative temperature for flowering after winter dormancy, seemed to be physiologically determined in each species, and actual flowering time was affected by the timing of exposure. In the Taisetsu Mountains, budding of plants did not occur until early June, in which mean air temperature was 6.1°C, even in early exposed places where snow disappeared before mid May. This means that the threshold temperature for the beginning of growth is around 5°C.

Within quadrats, flowering occurred sequentially as follows; *Primula cuneifolia* → *Rhododendron aureum* → *Potentilla matsumurae* → *Phyllodoce caerulea* → *Sieversia pentapetala* → *Phyllodoce aleutica* → *Peucedanum multivittatum* → *Veronica stelleri* var. *longistyla* → *Solidago virgaurea* var. *leiocarpa.*

Relationships between flowering time and fruiting period are shown in Figure 5. When plants bloomed after middle season due to later exposure, most of developing fruits were aborted by freezing injury by late September. Thus shortened fruiting periods are effective for avoidance of frost and snow, when plants bloom in later season. However, there was no negative correlation between flowering time and fruiting period (KENDALL's rank correlative test, $p>0.10$) within species, indicating absence of phenological adjustment for successful seed maturation under short growing conditions. When fruit matured after mid September because of later flowering followed by later exposure, the fruiting periods in herbs and deciduous shrubs (*Sieversia pentapetala)* became longer (Fig.5). In evergreen shrubs, whereas, fruiting periods were rather stable independently of their flowering times.

Relationship between effective cumulative temperatures for flowering and fruit maturation in each species are shown in Figure 6. Summed value of the effective cumulative temperatures of pre-flowering and fruiting periods indicates the potential adaptability for seed maturation under the condition of short snow-free period. Required effective cumulative temperature for fruit maturation was minimum in *Potentilla matsumurae* (270°C•day) and maximum in *Solidago virgaurea* var. *leiocarpa* (510°C•day). Possibility of successful seed maturation in later exposed places was higher in *Potentilla matsumurae* and *Primula cuneifolia,* and lower in *Solidago virgaurea* var. *leiocarpa, Rhododendron aureum, Phyllodoce aleutica* and *Phyllodoce caerulea.*

Discussion

Phenology or seasonal growth cycle of plants is determined by interaction of environmental conditions and phylogenetic constraints (KOCHMER and HANDEL, 1986). If plants can adjust their phenological events, it is expected that pre-flowering and/or fruiting periods should decrease in later exposed places where growth season is highly restricted. However, there was no evidence about the ability of phenological adjustment for successful seed set against the shortened growing season. As a reson for absence of phenological adjustment, physiological limitation is considered. Decrease in fruiting period means the reduction of carbon or mineral investment to seeds due to shortened assimilation period (BLISS, 1971; CALLAGHAN, 1974), and it deteriorates the quality of seeds which directly affects seedling survivals (GALEN and STANTON, 1991). Under such limitation, it may be more important for plants to produce high quality seeds in occasional long and warm years without decreasing the fruiting periods, because snow condition is highly variable from year to year even in same place.

In this study, it was proved that pre-flowering and fruiting periods of alpine plants were firstly regulated by ambient temperature as denoted by

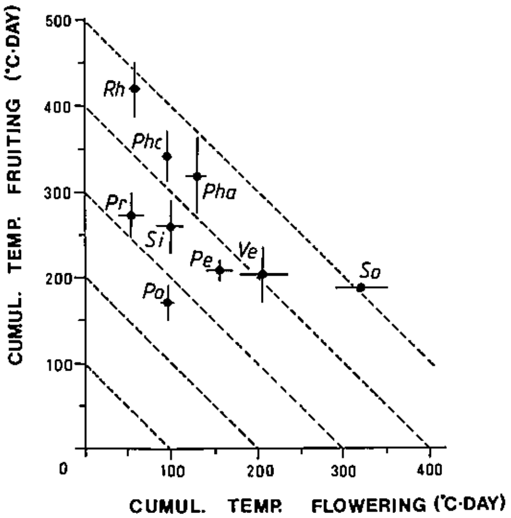

Fig. 6. Relationship between the effective cumulative temperatures (5°C in threshold temperature) during pre-flowering and fruiting periods. Vertical and horizontal lines denote S. D. No S.D. data for fruiting in *Solidago virgaurea* var. *leiocarpa* because of only two data. Broken lines show the isothermal lines of cumulative temperature for seed maturation from snow disappearance. Pe: *Peucedanum multivittatum*, Pr: *Primula cuneifolia*, Ve: *Veronica stelleri* var. longistyla, So: *Solidago virgaurea* var. *leiocarpa*, Po: *Potentilla mutsumurae*, Si: *Sieversia pentapetala*, Rh: *Rhododendron aureum*, Phc: *Phyllodoce caerulea*, Pha: *Phyllodoce aleutica*.

BILLINGS (1974), and WIELGOLASKI and KARENLAMPI (1975). Time of snow disappearance was secondly factor which affects the starting point of cumulative temperature. MIZUNO (1987) mentioned that flowering times of *Primula cuneifolia* and *Potentilla matsumurae* were determined by the period from exposure rather than by cumulative temperature. However, this is because he used the cumulative temperature of the daily mean above 0°C. The cumulative temperature above 5°C is more substantial for determination of phenological events in alpine plants than merely the period from exposure.

Some herbs and deciduous shrubs prolonged their fruiting periods when they bloomed in later season. It obviously seemed to be disadvantageous for successful seed maturation. Since low air temperature reduces photosynthetic efficiency, the rate of carbon assimilation decreases in autumn (SCOTT and BILLINGS, 1964). Also, the decrease in soil terperature affects the water and nutrient absorptions from roots (BLISS, 1962; KRAMER, 1942). Thus, it is considered that the decrease in temperature from mid September brings about the extension of fruiting periods in herbs and deciduous shrubs as a result of slow carbon or mineral allocation to fruits.

Sincere thanks to Prof. K. ITO for his variable comments on this study, and to K. ONIMARU and N. WADA for their help in field work. Thanks also to Drs. YAMADA and Y. KODAMA for their useful information about air temperature. This study was supported in part by a Survey Project Grant from the Ministry of Education, Science and Culture Japan (No. 02954013).

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摘　要

北海道大雪山系の雪田植物群落で，高山植物9種類（ハクサンボウフウ・エゾコザクラ・エゾヒメクワガタ・コガネギク・ミヤマキンバイ・チングルマ・キバナシャクナゲ・エゾノツガザクラ・アオノツガザクラ）の開花•結実フェノロジーを融雪傾度に沿った5つの調査区で比較した。消雪から開花までに要する期間と，開花から結実までに要する期間はそれぞれの種類に特有の有効積算温度によって規定されており，消雪の遅い場所においても繁殖活動に要する期間を短縮させるような種内レベルのフェノロジーの調節は見られなかった。従って雪解けの遅い1989年は消雪の遅い調査区で，種子成熟期間不足のため結実できない種類が多かった。気温の低い6月下旬以前に消雪する場合，消雪が早いほど開花に要する期間は長くなった。一方，6月下旬以降に消雪する場合には，日平均気温は10°C以上に上昇しており，消雪後開花までに要する期間はどの種類でも安定していた。草本植物や落葉低木は，気温が急激に低下する9月中旬以降に結実する場合，結実までに要する期間は長くなっている。これに対して常緑低木では低温の影響を受けにくかった。高山植物にフェノロジーの調節能力が欠けていることは，消雪時期の年変動の激しさと関係していると考えられる。

(Received December 20, 1991)

○　白山総合学術書編集委員会編　白山一自然と文化一　橋本確文堂企画／北国新聞社発行・発売。1992年11月20日発行。A4判，グラビア12頁+本文514頁。定価　16000円。

今年は白山国立公園発足30周年記念の年である。30周年を記念していろんな行事が行われたが，この学術書の出版もその一つである。平成元年1月に金沢大学名誉教授絈野義夫氏を委員長とする上記委員会が発足し，これまで集積された各分野の研究成果を集約しまとめた学術書とする一方，白山をよりよく理解し貴重な文化遺産が将来にわたって守られていくことの手助けとなるよう，より平易に記された啓蒙書とすることをねらって，縦書き二段組のスタイルの本書ができ上った。これは，昭和45年に白山学術調査団による学術書「白山の自然」以来，22年ぶりの総合学術書である。

内容はグラビア・序文・序章・第一篇　白山のなりたち（地形・地質・古生物），第二篇　白山の生物，第三篇　白山の歴史と文化（信仰・生活），終章　白山地域の変貌と環境保全および地形・地質・火山地質の3種の付図から成る。植物関係の記事は，第二篇第一章「白山の植物」にすべて収められている。この章は第一節　植物相と植生，第二節　キノコ，第三節　岩間温泉の付着珪藻類および白山植物目録から成る。この企画は既存の資料を基に執筆し，新たな調査は行わないという条件で進められたため，決定版というにはほど遠い。たとえば「白山植物目録」は，シダ植物と種子植物をとりあげ，標本の裏づけのある種類に限るという原則で，暫定的に作成したもので現地調査で確認するという手数をふんでいないので，相当数の遺漏があるものと見込まれる。それにしても，この目録は今まで完成された目録がなかっただけに，新たな白山植物調査の礎石として貢献できるだろう。この目録の作成に関わった一人として今後，逐次，目録の完成に近づけていくつもりである。

（清水建美）