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## Dormancy of alpine and subalpine perennial forbs

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**Abstract** Depth of dormancy of alpine and subalpine perennial forbs in autumn was investigated, which was judged by the number of days required for growth initiation at 24 °C. The depth of dormancy differed depending on Raunkiaer's life-form and shoot habits. Chamaephytes with perennial shoot-axes showed shallower dormancy than hemicryptophytes with annual shoot-axes, and geophytes with annual shoot-axes showed the deepest dormancy. The results strongly suggest that the dormancy is more endogenously controlled in forbs less hardy to freezing stress. Potential growth ability of alpine herbaceous chamaephytes in autumn is an adaptive advantage, since they utilize the short vegetative period as long as possible. All of the species with annual shoot-axes had winter buds covered with scales. In plants with perennial shoot-axes, percentage of winter buds covered with scales increased with increasing depth of dormancy. The results indicate that the shoot apices are well protected by bud scales in forbs with a long endogeneous-dormant period.

**Keywords** Alpine plants · Bud scale · Frost hardiness · Raunkiaer's life-form · Shoot habit

### Introduction

Perennial plants cease growth more or less at the beginning of the unfavorable season. The growth cessation of perennial plants native to temperate regions is generally more endogenously controlled than that of plants native to tropical and subtropical regions (Larcher 1980). The deep dormancy of the temperate plants is adaptive, since

the photosynthetic carbon gain is limited and the carbon loss due to frost injuries increases at low temperatures if they grow in the unfavorable season.

From the viewpoint of the carbon budget, alpine perennial plants may be expected to have deeper dormancy than temperate plants because of severe low temperatures during the unfavorable season, unless snow cover protects the plant from freezing. However, it is known that some alpine perennial plants have the ability to tolerate extremely low temperatures in winter and also to resist moderate frost temperatures, even in summer (e.g., Pisek et al. 1967; Sakai and Otsuka 1970; Käinmüller 1975; Larcher 1977; Larcher and Wagner 1983; Sakai and Larcher 1987; Körner and Larcher 1988; Körner 1999). These alpine plants do not appear to have much of a need to develop deep dormancy during the unfavorable season because of low risk of frost injuries.

Depth of dormancy of alpine and arctic plants has been known to differ depending on the snow cover of the habitat. Alpine snow-patch plants lack an endogenous dormancy, or at any rate the period of dormancy has only a very short duration (Rübel 1925; Sørensen 1941). This appears to be related to low risk of frost injuries under the snow cover, and this condition enables the plants to start growth as soon as snow disappears. The dormancy of alpine plants living in windswept ridges is more endogenously controlled than alpine snowbed plants (Körner 1999). This property enables the plants to avoid careless growth during the unfavorable season at the habitat, where they experience winter sunshine and daytime canopy warming above 20 °C (Körner 1999). The percentage of arctic plants that have no endogenous dormancy in terms of the development of flower organs increased in late snow-free localities (Sørensen 1941). An adaptive significance of this lack of endogenous dormancy was considered to be an effective utilization of even a very short period with favorable temperatures for continued development (Sørensen 1941). On the other hand, little information is available on the relationship between the depth of dormancy and

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frost hardiness. This study focuses on this relationship in alpine and subalpine perennial forbs.

If the depth of dormancy of perennial forbs depends on the frost hardiness, it must be closely associated with traits associated with hardiness. Raunkiaer's life-forms (1934) indicate the frost hardiness of winter buds of temperate plants; chamaephytes are harder than hemicryptophytes, and geophytes are the least hardy (Till 1956). The same relationships were also found for the potential frost hardiness, as obtained by frost-hardening treatments (Yoshie and Sakai 1981). It has been demonstrated that, in temperate regions, geophytes show a deeper dormancy in autumn than hemicryptophytes (Yoshie and Yoshida 1989).

Shoot habits, or shoot life-spans, of perennial forbs indicate their hardiness. Annual shoot-axes that bear shoot apices die back in the unfavorable season. Shoot apices for the next growing season are newly formed in winter buds that are situated near the base of the old shoot-axes. The buds form and endogenously enter a dormant state during the current growing period. On the one hand, perennial shoot-axes that bear shoot apices survive for over one year. The shoot apices grow during the current growing season and survive during the unfavorable season, and the persistent shoot apices resume growth in the next growing season. Since annual shoot-axes do not have much of a need to develop a freezing tolerance, they are logically considered to be less hardy to freezing stress than perennial shoot-axes.

The winter buds of alpine forbs are classified into two types: buds with scales and buds without scales; some alpine forbs form compact winter buds covered with scales while others form buds without any scales, where the shoot apices are protected by living or withered leaves and petioles (Yoshie 1998). Since bud scales protect shoot apices from physiological stresses, mechanical damage, and biological attack during the dormant period, protection of shoot apices by scales is expected to be more predominant in forbs with longer dormant periods. The duration of the dormant period depends on the shoot habit and the depth of the dormancy.

The objective of this study is to clarify (1) whether the depth of dormancy in autumn differs depending on the life form and the shoot habit, and (2) whether the bud type differs depending on the shoot habit and the depth of dormancy in alpine and subalpine perennial forbs.

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## Materials and methods

Experiments were done in three temperate high-mountain regions of Japan to avoid reducing natural populations of alpine forbs and to increase the diversity of the species tested. They were: Mt. Senjogadake (2,600–3,010 m elevation, 35°43'N, 138°11'E), Japanese Southern Alps, central Honshu; Mt. Okudainitidake (2,400–2,550 m elevation, 36°36'N, 137°35'E), Japanese Northern Alps, central Honshu; and Mt. Kurodake

(1,750–1,900 m elevation, 43°42'N, 142°55'E), Taisetu Mountains, Hokkaido, northern Japan. Seventy-seven species and varieties found abundantly in these regions were selected as experimental materials.

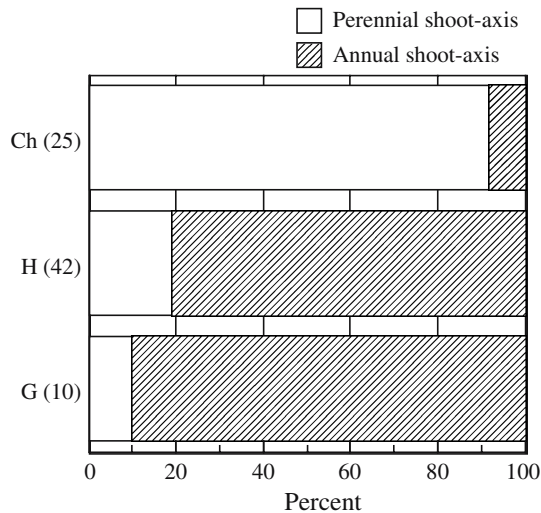
Experimental sampling on each mountain was performed close to the time of the first snowfall, in order to make sure that the phenological stages of tested plants were uniform. Sexually mature individuals were observed and collected at Mt. Senjogadake and Mt. Okudainitidake in late October of 1991 and 1992, and collected at Mt. Kurodake in late September of 1992. The materials were dug carefully from the ground in order to avoid damaging subterranean organs and so that was little or no effect on the survival. Exceptionally, a part of rhizomes below ca. 25 cm depth from the ground surface were cut away in *Polygonum weyrichii*.

At each sampling time, the positions of winter buds and the survival of shoot-axes and leaves were observed for every species. The survival of shoot-axes and leaves was also observed in the growing season of 1991–1993. Shoot-axes and leaves were regarded as perennial and wintergreen, respectively, if all or large parts them had little or no sign of frost damage at the sampling time and during the next summer. Classification of Raunkiaer's life-forms of the materials was performed at the sampling site, but a few species (*Pedicularis resupinata* and *Tilingia ajanensis*) were classified according to Shimizu (1982).

Immediately after the sampling, the materials were transferred to the laboratory. Over seven individuals per species, as a rule, were used for the dormancy experiment. They were potted with uniform soils adjusted for horticultural herbs on the market, and were cultivated in temperature-controlled room at 24 °C. The potted forbs were irradiated with fluorescent light (ca. 190  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  at the pot surface) under a long-day regime (16 h day). Initiation of growth was monitored at intervals of one or two days for the 250-day duration of the experiment. The initiation of flowering and the elongation of stems or flower stalks was also recorded. The nutrients of Hyponex solution were supplied adequately during the experimental period.

The depth of dormancy was evaluated via the mean number of days required for growth initiation. Growth initiation was indicated by (1) an elongation of young foliage leaves (group 1: species belonged to chamaephytes and hemicryptophytes without bud scales), (2) an emergence of new foliage leaves out of scales (group 2: chamaephytes and hemicryptophytes with bud scales), and (3) an emergence of young shoots above the soil surface (group 3: geophytes). In all cases, the plants exhibited normal green leaves during a two-month observation period following the initiation of growth. Some forbs did not initiate growth within the 250 days, but browning of the organs was not detected, and they were all alive at the end of the experiment.

The numbers of days required for growth initiation were compared among plant groups, based on Raunkiaer's life forms and shoot habits. Growth initiation was



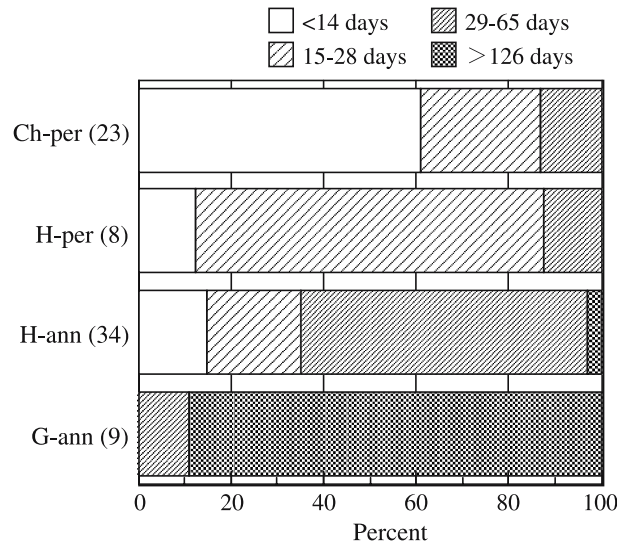
**Fig. 1** Relationship between shoot habits and Raunkiaer's life forms. *Ch* chamaephytes, *H* hemicryptophytes, *G* geophytes. Numbers of species are shown in parentheses

investigated in exactly the same way for nine species, and only minor differences were observed in the number of the days required for growth initiation between years or between sites for a particular species (see the Appendix). Mean values were used for the analysis of these species. To clarify whether the bud scales differentiate, the buds of three individuals per species were carefully dissected into their components under a microscope in the laboratory. The data for the bud structures of 63 species were obtained from Yoshie (1998).

## Results

Shoot habit was different among Raunkiaer's life-forms ( $\chi^2$ -test,  $P < 0.001$ ). Almost all of the chamaephytes had perennial shoot-axes (Fig. 1), for which the leaves were wintergreen or summergreen. In contrast, except for one species, geophytes had annual shoot-axes. Most of the hemicryptophytes had annual shoot-axes which usually elongated upward and were classified into protohemicryptophytes and partial rosette plants. The remaining hemicryptophytes had perennial shoot-axes with summergreen leaves, which usually produced rosettes or large radical leaves and were classified into rosette plants or partial rosette plants.

The number of days required for growth initiation in the autumn was compared among four numerically predominant plant groups (Fig. 2). The number of days differed depending on the plant groups ( $\chi^2$ -test,  $P < 0.001$ ). More than half of the chamaephytes with perennial shoot-axes initiated growth within two weeks. These forbs exhibited potential growth ability at warm temperatures in autumn, although their growth was reduced in their native habitats. The initiation of growth of chamaephytes with perennial shoot-axes (mean  $\pm$  SD,  $18.7 \pm 15.6$  days) and of hemicryptophytes with



**Fig. 2** Percent distribution of the number of days required for growth initiation in four plant groups classified by Raunkiaer's life-forms and shoot habits. *Ch-per* chamaephytes with perennial shoot-axes, *H-per* hemicryptophytes with perennial shoot-axes, *H-ann* hemicryptophytes with annual shoot-axes, *G-ann* geophytes with annual shoot-axes. Numbers of species are shown in parentheses

**Table 1** Bud type in relation to shoot habit and days to growth initiation

Shoot habit (number of days required for growth initiation)	Bud type	
	Buds without scales	Buds with scales
Perennial shoot-axes (< 14 days)	15	0
(> 15 days)	8	9
Annual shoot-axes	0	45

perennial shoot-axes ( $19.8 \pm 6.0$  days) occurred much earlier than in hemicryptophytes with annual shoot-axes ( $35.0 \pm 16.4$  days in 33 species; one species did not initiate growth within 250 days). The results indicated that chamaephytes and hemicryptophytes with perennial shoot-axes showed a much shallower dormancy in autumn than hemicryptophytes with annual shoot-axes. In nine species of geophytes with annual shoot-axes, seven species did not initiate growth within 250 days. They never sprout leaves and stems in autumn in native habitats. These results indicate that geophytes have the most endogenously controlled dormancy of all the plant groups.

Bud types of perennial forbs differed depending on the shoot habit ( $\chi^2$ -test,  $P < 0.001$ ). All of the species with annual shoot-axes had winter buds covered with scales (Table 1). Bud types of perennial forbs with perennial shoot-axes differed depending on the depth of dormancy ( $\chi^2$ -test,  $P < 0.01$ ). All of the species that initiated growth within two weeks had winter buds

without any scales, while more than half of the species that required over 15 days for growth initiation had buds covered with scales. These results indicate that the shoot apices are well protected by bud scales in the forbs with long endogeneous-dormant periods.

## Discussion

This study revealed that the depth of dormancy of alpine and subalpine perennial forbs in autumn differed among plant groups classified by Raunkiaer's life-forms and shoot habits; chamaephytes with perennial shoot-axes showed shallower dormancy than hemicryptophytes with annual shoot-axes, and geophytes with annual shoot-axes showed the deepest dormancy. The results strongly suggest that the dormancy is more endogenously controlled in forbs less hardy to freezing stress.

The percentage of herbaceous chamaephytes (such as cushion plants and passive chamaephytes) for which the shoots were persistent increased at high altitude (Raunkiaer 1934). The results suggest that the percentage of forbs with shallow dormancy increases at high altitude. Potential growth ability of alpine herbaceous chamaephytes in autumn is an adaptive advantage, since they can then utilize as much of the short vegetative period as possible. Chamaephytes tended to flower and elongate stems or flower-stalks normally during the experimental period, suggesting a shallow dormancy (see the Appendix).

Protohemicryptophytes avoid autumnal growth of annual shoot-axes, which are probably frost-sensitive, by exhibiting much deeper dormancy than chamaephytes. Winter buds of geophytes were the least hardy to freezing stress (Till 1956; Yoshie and Sakai 1981). In general, active plant organs are less resistant to freezing stress than inactive dormant organs. Although the buds

of geophytes are protected from severe low temperatures below the ground, breaking the dormancy and activating the buds in autumn would lead to serious frost damage. Geophytes avoid the activation of buds by exhibiting the deepest dormancy.

The percentage of chamaephytes was also high for arctic tundra (Raunkiaer 1934). Sørensen (1941) studied the developmental morphology and phenology of Greenland plants. When we analyzed his data for perennial forbs (99 species), we observed comparatively high percentages of chamaephytes (40.4%), species with wintergreen leaves (46.4%), and species without any bud scales (83.8%). These traits are characteristic of alpine forbs that have shallow dormancy. Arctic plants are phylogenically related to alpine plants. These results suggest that the percentage of forbs with shallow dormancy also increases at high latitudes.

Almost all of the chamaephytes in this study had perennial shoot-axes. Photosynthetic carbon gain of alpine plants is constrained by low temperatures, short vegetative period, and low soil fertility (Scott and Billings 1964; Bliss 1971; Friend and Woodward 1990; Körner 1999). In these less-productive habitats, a prolonged life-span of the shoot axis increases the efficiency of use of carbon and nutrients, and is potentially an adaptive advantage for photosynthetic carbon gain, as has been indicated before for plant leaves (Chapin 1980; Chabot and Hicks 1982; Kudo 1992). The location of the winter buds on perennial shoot-axes above the ground surface leads to a herbaceous chamaephyte morphology.

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## Appendix

**Table 2** Days to initiation of growth and flowering (mean  $\pm$  SD), elongation of stem, shoot habit, differentiation of bud scales, and Raunkiaer's life forms of high-mountain forbs, and altitude, site, and year of collection

Species	Days to growth initiation	Elongation of stem	Days to flowering initiation	Shoot habit	Differentiation of bud scale	Life form	Altitude (m)	Site	Year
<i>Hypericum kamtschaticum</i> var. <i>senanense</i>	3.5 $\pm$ 1.5 <sup>a</sup>	+	33.0 $\pm$ 4.3	pe(w)	ud	Ch	2,400	Ok	1991
<i>Barbarea orthoceras</i>	4.7 $\pm$ 0.5 <sup>a</sup>	–	nf	pe(w)	ud	Ch	2,400	Ok	1992
<i>Barbarea orthoceras</i>	6.3 $\pm$ 1.7 <sup>a</sup>	–	28.5 $\pm$ 3.5	pe(w)	ud <sup>f</sup>	Ch	2,400	Ok	1991
<i>Arabis serrata</i> var. <i>glauca</i>	7.4 $\pm$ 0.9 <sup>a</sup>	+	73.0 $\pm$ 9.4	pe(w)	ud	Ch	1,890	Ku	1992
<i>Stellaria nipponica</i>	7.7 $\pm$ 2.1 <sup>a</sup>	+	49.4 $\pm$ 6.8	pe(w)	ud <sup>f</sup>	Ch	3,010	Se	1992
<i>Stellaria nipponica</i>	8.1 $\pm$ 2.3 <sup>a</sup>	+	32.0 $\pm$ 4.9	pe(w)	ud	Ch	3,000	Se	1991
<i>Hypericum kamtschaticum</i>	8.2 $\pm$ 1.4 <sup>a</sup>	+	36.8 $\pm$ 5.7	pe(w)	ud <sup>f</sup>	Ch	1,750	Ku	1992
<i>Cirsium gratiosum</i>	8.6 $\pm$ 2.4 <sup>a</sup>	–	nf	an	d <sup>f</sup>	H	2,700	Se	1991
<i>Taraxacum Yatsugatakense</i>	8.7 $\pm$ 0.8 <sup>a</sup>	–	nf	pe(s)	ud <sup>f</sup>	H	2,700	Se	1991
<i>Geranium eriostemon</i> var. <i>reinii</i>	8.7 $\pm$ 0.5 <sup>a</sup>	–	nf	an	d	H	2,650	Se	1991

Table 2 (Contd.)

Species	Days to growth initiation	Elongation of stem	Days to flowering initiation	Shoot habit	Differentiation of bud scale	Life form	Altitude (m)	Site	Year
<i>Cerastium shizopetalum</i>	8.0 ± 1.4 <sup>a</sup>	+	28.9 ± 3.0	pe(w)	ud <sup>f</sup>	Ch	2,900	Se	1991
<i>Cerastium shizopetalum</i>	9.8 ± 1.5 <sup>a</sup>	+	29.7 ± 4.8	pe(w)	ud	Ch	2,900	Se	1992
<i>Rumex montanus</i>	9.0 ± 0.7 <sup>a</sup>	+	37.0 ± 6.6	an	d <sup>f</sup>	H	2,600	Se	1991
<i>Arabis lyrata</i> subsp. <i>kamchatica</i>	11.0 ± 1.8 <sup>a</sup>	+	37.0 ± 4.3	pe(w)	ud <sup>f</sup>	Ch	2,950	Se	1992
<i>Sedum japonicum</i> var. <i>senanense</i>	11.0 ± 2.7 <sup>a</sup>	—	nf	pe(w)	ud <sup>f</sup>	Ch	2,850	Se	1992
<i>Dianthus superbus</i> var. <i>speciosus</i>	11.6 ± 1.2 <sup>a</sup>	+	46.5 ± 7.1	pe(s)	ud <sup>f</sup>	Ch	2,950	Se	1991
<i>Cirsium kamtschaticum</i> subsp. <i>pectinellum</i>	11.7 ± 4.1 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	1,750	Ku	1992
<i>Hieracium japonicum</i>	13.1 ± 1.4 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,440	Ok	1991
<i>Saxifraga laciniata</i>	13.2 ± 2.1 <sup>a</sup>	+	42.1 ± 5.0	pe(w)	ud <sup>f</sup>	Ch	1,880	Ku	1992
<i>Saxifraga merkii</i>	13.5 ± 1.9 <sup>a</sup>	+	30.0 ± 4.2	pe(w)	ud <sup>f</sup>	Ch	1,890	Ku	1992
<i>Potentilla matsumurae</i>	11.6 ± 3.1 <sup>a</sup>	+	nf	pe(s)	ud <sup>f</sup>	Ch	2,750	Se	1991
<i>Potentilla matsumurae</i>	13.4 ± 3.8 <sup>a</sup>	+	15.7 ± 2.4	pe(s)	ud	Ch	2,560	Ok	1992
<i>Potentilla matsumurae</i>	15.5 ± 6.0 <sup>a</sup>	+	nf	pe(s)	ud	Ch	1,890	Ku	1992
<i>Saxifraga bronchialis</i> subsp. <i>funstonii</i>	14.0 ± 3.5 <sup>a</sup>	+	50.2 ± 6.4	pe(w)	ud <sup>f</sup>	Ch	3,000	Se	1992
<i>Campanula lasiocarpa</i>	14.0 ± 2.0 <sup>a</sup>	+	45.7 ± 5.0	pe(s)	ud <sup>f</sup>	Ch	2,850	Se	1991
<i>Primura cuneifolia</i>	15.1 ± 2.8 <sup>a</sup>	+	25.6 ± 3.7	pe(s)	ud <sup>f</sup>	H	1,900	Ku	1992
<i>Potentilla miyabei</i>	15.2 ± 2.9 <sup>a</sup>	+	nf	pe(s)	ud <sup>f</sup>	Ch	1,890	Ku	1992
<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	15.2 ± 3.2 <sup>a</sup>	—	nf	pe(s)	ud <sup>f</sup>	H	1,900	Ku	1992
<i>Cirsium babanum</i> var. <i>otayae</i>	15.3 ± 2.2 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,550	Ok	1992
<i>Saxifraga fusca</i> var. <i>kikubuki</i>	16.3 ± 2.6 <sup>a</sup>	+	64.0 ± 7.0	an	d <sup>f</sup>	Ch	2,640	Se	1992
<i>Saussurea nikoensis</i> var. <i>sessiliflora</i>	17.4 ± 3.0 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,730	Se	1992
<i>Stellaria pterosperma</i>	17.6 ± 0.8 <sup>a</sup>	+	nf	pe(w)	ud <sup>f</sup>	Ch	1,900	Ku	1992
<i>Artemisia pedunculosa</i>	18.8 ± 5.6 <sup>a</sup>	—	nf	pe(s)	d <sup>f</sup>	Ch	2,730	Se	1991
<i>Polygonum weyrichii</i> var. <i>alpinum</i>	20.9 ± 2.1 <sup>b</sup>	+	77.0	an	d <sup>f</sup>	H	2,550	Ok	1991
<i>Arabis tanakana</i>	21.4 ± 4.7 <sup>a</sup>	+	45.0 ± 4.1	pe(w)	ud	Ch	3,000	Se	1992
<i>Gentiana algida</i>	22.0 ± 1.0 <sup>a</sup>	—	nf	pe(s)	ud <sup>f</sup>	H	2,460	Ok	1991
<i>Anemone narcissiflora</i> var. <i>nipponica</i>	22.2 ± 2.9 <sup>a</sup>	+	59.2 ± 5.2	pe(s)	ud <sup>f</sup>	H	2,700	Se	1991
<i>Aquilegia flabellata</i> var. <i>pumila</i>	22.9 ± 2.5 <sup>a</sup>	+	87.5 ± 2.5	pe(s)	d <sup>f</sup>	H	2,950	Se	1992
<i>Saussurea triptera</i> var. <i>minor</i>	23.0 ± 7.9 <sup>d</sup>	—	nf	an	d <sup>f</sup>	H	2,730	Se	1991
<i>Ixeris dentata</i> var. <i>alpicola</i>	23.4 ± 6.9 <sup>a</sup>	—	nf	pe(s)	ud <sup>f</sup>	H	2,950	Se	1992
<i>Fauria crista-galli</i> subsp. <i>japonica</i>	24.3 ± 3.0 <sup>a</sup>	—	nf	pe(s)	d <sup>f</sup>	G	2,480	Ok	1992
<i>Heloniopsis orientalis</i>	24.3 ± 3.0 <sup>a</sup>	—	nf	pe(w)	d <sup>f</sup>	Ch	2,450	Ok	1992
<i>Leontopodium japonicum</i>	24.9 ± 9.0 <sup>a</sup>	+	nf	an	d <sup>f</sup>	H	2,750	Se	1992
	(17.0 ± 3.0 <sup>ad</sup> )								
<i>Arnica unalaschkensis</i> var. <i>tschonoskyi</i>	25.8 ± 7.7 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,850	Se	1991
<i>Pedicularis resupinata</i> var. <i>caespitosa</i>	26.0 ± 4.9 <sup>d</sup>	+	nf	an	d <sup>f</sup>	H <sup>g</sup>	2,800	Se	1991
<i>Geum calthaefolium</i> var. <i>nipponicum</i>	27.8 ± 5.7 <sup>a</sup>	—	nf	pe(s)	d <sup>f</sup>	Ch	2,500	Ok	1991
<i>Artemisia sinanensis</i>	29.0 ± 9.2 <sup>a</sup>	—	nf	pe(s)	d <sup>f</sup>	H	2,700	Se	1991
<i>Artemisia monophylla</i>	30.9 ± 14.2 <sup>a</sup>	+	nf	an	d <sup>f</sup>	H	2,450	Ok	1992
<i>Lilium medeoloides</i>	28.0 ± 8.0 <sup>a</sup>	—	41.0 ± 5.0	an	d	G	2,550	Ok	1991
<i>Lilium medeoloides</i>	34.0 ± 12.2 <sup>a</sup>	—	75.0	an	d <sup>f</sup>	G	2,550	Ok	1992
<i>Saussurea yanagisawae</i>	32.0 ± 6.0 <sup>c</sup>	—	nf	an	d <sup>f</sup>	H	1,880	Ku	1992
<i>Hedysarum vicioides</i>	33.4 ± 10.4 <sup>a</sup>	+	62.0	an	d <sup>f</sup>	Ch	2,950	Se	1991
<i>Conioselinum filicinum</i>	33.5 ± 6.6 <sup>b</sup>	—	109.0	an	d	H	2,800	Se	1991
<i>Solidago virga-aurea</i> subsp. <i>leiocarpa</i>	28.5 ± 7.5 <sup>c</sup>	—	nf	an	d <sup>f</sup>	H	2,500	Ok	1991
<i>Solidago virga-aurea</i> subsp. <i>leiocarpa</i>	39.3 ± 16.2 <sup>b</sup>	—	nf	an	d	H	2,500	Ok	1992
<i>Astragalus membranaceus</i> var. <i>obtusus</i>	34.4 ± 12.2 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,950	Se	1992
<i>Pedicularis chamissonis</i> var. <i>japonica</i>	35.3 ± 14.5 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,450	Ok	1991
<i>Schizocodon soldanelloides</i>	35.5 ± 8.0 <sup>a</sup>	—	nf	pe(w)	d <sup>f</sup>	Ch	2,500	Ok	1992
<i>Gentiana triflora</i> var. <i>montana</i>	38.6 ± 16.4 <sup>a</sup>	—	88.5 ± 15.5	an	d <sup>f</sup>	H	1,850	Ku	1992
<i>Patrinia sibirica</i>	38.7 ± 17.4 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	1,890	Ku	1992
<i>Pennelianthus frutescens</i>	38.8 ± 13.8 <sup>b</sup>	+	nf	an	d <sup>f</sup>	H	1,890	Ku	1992
<i>Aletris foliata</i>	40.3 ± 13.1 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,500	Ok	1992
<i>Tilingia ajanensis</i>	44.0 ± 10.7 <sup>d</sup>	+	nf	an	d	H <sup>g</sup>	2,450	Ok	1992
<i>Viola biflora</i>	46.0 ± 19.6 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	1,800	Ku	1992
<i>Artemisia arctica</i> var. <i>sachalinensis</i>	47.5 ± 21.0 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	1,880	Ku	1992
<i>Sanguisorba canadensis</i> subsp. <i>latifolia</i>	53.1 ± 28.4 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	1,870	Ku	1992
<i>Veronica stelleri</i> var. <i>longistyla</i>	54.5 ± 25.6 <sup>a</sup>	+	nf	an	d <sup>f</sup>	H	1,890	Ku	1992
	(10.0 ± 1.2 <sup>d</sup> )								
<i>Nepeta subsessilis</i>	54.8 ± 18.2 <sup>a</sup>	+	87.3 ± 62.5	an	d <sup>f</sup>	H	2,600	Se	1992
<i>Tilingia tachiroei</i>	57.0 ± 22.9 <sup>a</sup>	—	nf	an	d <sup>f</sup>	H	2,700	Se	1991
<i>Sedum rosea</i>	57.0 ± 26.0 <sup>a</sup>	—	27.3 ± 5.1	an	d <sup>f</sup>	H	2,980	Se	1991
<i>Sedum rosea</i>	58.0 ± 19.2 <sup>a</sup>	—	75.0	an	d <sup>f</sup>	H	2,980	Se	1992
<i>Trollius riederianus</i> var. <i>japonicus</i>	58.0 ± 11.4 <sup>c</sup>	—	nf	an	d <sup>f</sup>	H	2,690	Se	1991
<i>Trollius riederianus</i> var. <i>riederianus</i>	58.3 ± 17.5 <sup>c</sup>	—	nf	an	d <sup>f</sup>	H	1,750	Ku	1992



Table 2 (Contd.)

Species	Days to growth initiation	Elongation of stem	Days to flowering initiation	Shoot habit	Differentiation of bud scale	Life form	Altitude (m)	Site	Year
<i>Coptis trifolia</i>	63.4 ± 22.7 <sup>a</sup>	+	45.5 ± 12.5	pe(w)	d <sup>f</sup>	Ch	2,500	Ok	1992
<i>Schizopcodon ilicifolius</i>	64.0 ± 26.9 <sup>a</sup>	–	nf	pe(w)	d	Ch	2,500	Ok	1991
<i>Gentiana makinoi</i>	57.5 ± 25.5 <sup>a</sup>	–	58.0	an	d <sup>f</sup>	H	2,460	Ok	1992
<i>Gentiana makinoi</i>	71.5 ± 18.1 <sup>a</sup>	–	nf	an	d	H	2,700	Se	1991
<i>Veratrum stamineum</i>	126.5 ± 28.5 <sup>b</sup>	–	nf	an	d <sup>f</sup>	G	2,690	Se	1991
<i>Maianthemum dilatatum</i>	250 <sup>e</sup>	–	nf	an	d	G	2,450	Ok	1992
<i>Dicentra peregrina</i>	250 <sup>e</sup>	–	nf	an	d <sup>f</sup>	G	1,880	Ku	1992
<i>Streptopus amplexifolius</i> var. <i>papillatus</i>	250 <sup>e</sup>	–	nf	an	d <sup>f</sup>	G	2,690	Se	1992
<i>Saussurea riederi</i> var. <i>yezoensis</i>	250 <sup>e</sup>	–	nf	an	d <sup>f</sup>	H	1,750	Ku	1992
<i>Smilacina yezoensis</i>	250 <sup>e</sup>	–	nf	an	d <sup>f</sup>	G	2,690	Se	1991
<i>Smilacina yezoensis</i>	250 <sup>e</sup>	–	nf	an	d	G	2,450	Ok	1992
<i>Diphylleia grayi</i>	250 <sup>e</sup>	–	nf	an	d <sup>f</sup>	G	2,690	Se	1991
<i>Aconitum senanense</i>	250 <sup>e</sup>	–	nf	an	d <sup>f</sup>	G	2,710	Se	1991
<i>Streptopus streptopides</i>	250 <sup>e</sup>	–	nf	an	d	G	2,450	Ok	1992

+ Stem elongated, – no stem elongated or some stems elongated but lengths were less than one sixth of the minimum length recorded in the natural habitats (Shimizu 1982, 1983)

nf No flowering, pe(w) Perennial shoot-axis with wintergreen leaves, pe(s) perennial shoot-axis with summergreen leaves, an annual shoot-axis, ud bud without any differentiated scale, d bud with differentiated scales, Ch chamaephytes, H hemicryptophytes, G geophytes, Ok Mt. Okudainichidake, Ku Mt. Kurodake, Se Mt. Senjogadake

<sup>a</sup> Over 81% of buds initiated growth

<sup>b</sup> 61–80% of buds initiated growth

<sup>c</sup> 41–60% of buds initiated growth

<sup>d</sup> 21–40% of buds initiated growth

<sup>e</sup> No buds initiated growth within 250 days; numbers in parenthesis, growth initiation from current annual-shoot axes

<sup>f</sup> Data are taken from Yoshie (1998)

<sup>g</sup> Data are taken from Shimizu (1982). Nomenclature follows Shimizu (1982, 1983)

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