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Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts

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Abstract

Timing of snowmelt is a crucial factor determining the phenological schedule of alpine plants. A long-term monitoring of snowmelt regimes in a Japanese alpine revealed that snowmelt season has been accelerated during last 17 years in early snowmelt places, but such a trend has not been detected in late snowmelt places. This indicates that the warming effect on snowmelt pattern may be site specific. Flowering phenology of fellfield plants in an exposed wind-blown habitat was consistent between unusually warm year (1998) and normal year (2001). In contrast, flowering occurrence of snowbed plants varied greatly between the years depending on the snowmelt time. The number of flowering species in a fellfield community was large in the middle to late June and the middle to late July. Flowering of an early-melt snowbed community showed a peak in the middle of flowering season, and that of a late-melt snowbed community showed a peak in early flowering season. These habitat-specific phenological patterns were consistent between 1998 and 2001. Effects of the variation in flowering timing on seed-set success were evaluated for an entomophilous snowbed herb, *Peucedanum multivittatum*, along the snowmelt gradient during five years. When flowering occurred prior to early August, mean temperature during the flowering season positively influenced the seed set. When flowering occurred later than early August, however, plants enjoyed high seed-set success irrespective of temperature conditions if frost damage was absent. This is probably because the availability of pollinators depends not only on ambient temperature but also on seasonal progress. These results suggest that the effects of climate change on biological interaction may vary depending on habitat in the alpine ecosystem in which diverse snowmelt patterns create complicated seasonality for plants within a local area.

Keywords Alpine plants, flowering phenology, global warming, seed production, snowmelt time

Introduction

There are some evidences that global warming has accelerated flowering time of plants because the timing of flowering is sensitive to temperature (Fitter and Fitter 2002). Global warming is expected to bring most serious impacts on arctic and alpine ecosystems (IPCC 2001), in which the length of growth season is seriously restricted. The timing of flowering event is an important determinant of reproductive success for alpine plants, because late flowering often results in fail to mature seeds due to too short season length and early flowering may causes pollen limitation due to low pollinator activity (Kudo 1991, 1993; Molau 1993). Therefore, changes in flowering schedule should affect reproductive success of arctic and alpine plants. Flowering phenology of alpine plants is mainly determined not only by ambient temperature but also by snowmelt time, because snow distribution in alpine regions is heterogeneous even within a local area. Such a heterogeneous snow distribution is a major factor creating diverse plant communities in alpine ecosystem (Billings and Bliss 1959; Kudo and Ito 1992). Although spatial pattern of snow dynamics is consistent among years, actual timing of snowmelt varies greatly from year to year reflecting inter-annual variation in climate conditions. Thus, long-term monitoring of snowmelt patterns and flowering phenology is important to detect the effects of global change on alpine ecosystems. So far, only a few long-term studies of flowering phenology have been conducted in subarctic tundra communities (Thórhalsdóttir 1998; Molau et al. 2005), and phenological studies in the middle-latitude alpine regions are reported only for some restricted species (e.g. Walker et al. 1995; Saavedra et al. 2003). Because alpine flora of middle-latitude mountains is isolated and scattered around the southernmost edges of their geographic distributions, the middle-latitude alpine ecosystem must be more sensitive to the warming effect than the high-latitude tundra ecosystem.

Seasonal transition of ambient air temperature in the middle-latitude alpine is generally steeper than that in the high-latitude tundra (Kudo and Suzuki 2002). A steep temperature gradient from the beginning to the middle of growth season in the middle-latitude alpine causes a clearer seasonal trend of pollinator activity than in the subarctic alpine, resulting

that pollination success of insect-pollinated plants obviously increases as season progress (Kudo and Suzuki 2002). Thus, the modification of flowering schedule by global climate change may cause serious impacts on pollination success of middle-latitude alpine plants if plants and pollinators respond to the warming differently. However, the effects of climate change on flowering phenology of alpine plants may not uniform even within a local area due to the heterogeneous snow distribution reflecting the undulating topographic features in mountain regions. Alpine ecosystem is composed of fellfield habitat and snowbed habitat. The fellfield habitat is situated on wind-blown ridges and plateaus where snow disappears in early season, and plants are exposed to cold weather during the winter and spring. In contrast, the snowbed habitat is covered with thick snow until middle of season and initiation of plant growth is determined by the time of snowmelt. As the snowmelt time is influenced not only by ambient temperature but also by irradiation, precipitation, and the amount of snowfall during the winter, the temperature effect on the phenological events of snowbed plants may be indirect. Thus, the impact of global warming on the flowering phenology may differ between the fellfield and snowbed habitats.

In this article, we compare inter-annual variations in the flowering patterns of fellfield and snowbed communities in the alpine region of northern Japan between an extreme warm and early-snowmelt year and a normal year. Based on the long-term monitoring of snowmelt pattern along a snowmelt gradient, we predict the habitat-specific warming effects on flowering phenology.

Then, we evaluate the effects of temporal variation in flowering season on reproductive success of an entomophilous snowbed herb, *Peucedanum multivittatum* Maxim. (Apiaceae), along a snowmelt gradient over five years. Global climate change may cause at least two major impacts on the reproductive situation of alpine plants, that is thermal conditions during the flowering season (as a direct warming effect) and the modification of flowering schedule caused by the temporal variation in snowmelt timing (as an indirect warming effect). An increase in ambient temperature often accelerates the activity of pollinator insects in arctic and alpine regions, resulting in higher pollination success (Inouye and Pyke 1988; Totland 1994; Bergman et al. 1996). Seasonal changes in flowering schedule may change

the availability of pollinators if phenological responses to global warming differ between plants and pollinators (Kudo et al. 2004; Inouye et al. 2000). *Peucedanum multivittatum* is an ideal plants to assess the relationship between flowering conditions and pollination success, because (1) this species is self-compatible but pollinator visitation is necessary for considerable seed set due to the well-organized dichogamous flowering within individuals (Kudo 1997), and (2) the distribution range is wide from early to late snowmelt places resulting that flowering season is highly variable along a snowmelt gradient (Kudo 1997). In this study, we focus on the discrimination of the direct warming effect and the effect of flowering timing on the reproductive success of alpine plants.

Final goal of this article is to figure out the heterogeneous responses of alpine plants to global climate change based on the unique structure of alpine ecosystem that the steep snowmelt gradient creates the diverse seasonality within a local area.

Materials and Methods

Study site

This study was conducted in the central part of the Taisetsu Mountains of Hokkaido in northern Japan (43º33'N, 142º52'E). On a southeast-facing slope near the Lake Hisago, we established five 20 x 20 m plots (named plot A to E) in 1988 (Fig. 1). These five plots were arranged by snowmelt order along a snowmelt gradient (1790–1900 m altitude). All plots were located within 700 m distance. Snowbed vegetation composed of dwarf shrubs and forbs develops in these plots (see Kudo and Ito 1992 for species composition). We have monitored snowmelt pattern of these plots since 1988. One fellfield plot named plot O (about 50 x 50 m) was established on a plateau at 1910 m altitude (Fig. 1), where snow-cover is thin during the winter due to strong wind blowing away the snow and soil surface is usually exposed from snow-cover by early to mid-May. Ericaceous dwarf shrubs and lichens are common component in the fellfield (Kudo and Suzuki 2002).

The Taisetsu Mountains are characterized by cold, snowy winter and mild, wet summer. Mean air temperature measured at a 40 cm above the ground

near the Lake Hisago (1700 m altitude; Fig. 1) was 4.1ºC in May, 9.0ºC in June, 13.2ºC in July, 12.9ºC in August, and 7.6ºC in September (Table 1). Mean precipitation during the summer (June-August) was 767 mm, ranging 494 mm to 1010 mm (seven years record by G. Kudo). During a decade, summer in 1998 and 2000 were very warm, and summer in 1995 and 2002 were cool.

Phenological survey

Flowering sequences of major entomophilous plant species were recorded throughout the growth season in plot O, plot B and plot D in 1998 and 2001. The growth season in 1998 was warmest during a decade and the snowmelt in this year occurred earliest during the last 17 years (see Results). Whereas, the temperature condition in 2001 was normal. Flowering stage of individual species was classified by visual observation as follows: rank A: <25% of flower buds have opened, B: 25-50% of flower buds have opened, C: 50-75% of flower buds have opened, D: 75-100% of flower buds have opened, E: no flower buds are remained and about 50% of flowering has been finished, and F: no flower buds are remained and about 75% of flowering has been finished. Rank A and F are scored "1", rank B and E are scored "2", rank C is scored "3", and rank D is scored "4" for a quantification of flowering sequence in this study. Observation intervals were 3-10 days. The number of species observed was 14 in plot O, 19 in plot B, and 12 in plot D.

Seed-set success

Peucedanum multivittatum is a Japanese endemic alpine herb that commonly grows in snowbed habitat. This species is andromonoecious that terminal umbel contains both hermaphrodite and male flowers and lateral umbels usually have only male flowers. Each hermaphrodite flower has two pistils, which contain one ovule in each. Flowering of lateral umbels occurs after anthesis of the terminal umbel (Kudo 1997). Major pollinating insects are syrphid and other flies, and sometimes bumblebees. Flowering season and seed-set success of *P. multivittatum* were monitored in plot A, C, D and E in 1995, 1997, 1998, 2000 and 2001 (but monitoring in plot E was performed only in 1995, 1997 and 1998). At the beginning of the flowering season, 40–100 individuals having flower buds were randomly selected in

each plot, and the number of hermaphrodite flowers was measured. At the fruiting season, mature fruits were harvested, the number of developed seeds was counted, and the seed-set percentage was calculated. Peak flowering season in individual plots was measured as mentioned above. Mean daily temperature during the major flowering season in each plot was calculated using an hourly air-temperature record measured at the 40 cm above the soil surface at 1700 m altitude (Fig. 1). We did not compensate elevation difference in temperature for individual plots because altitudinal difference among plots was small.

To evaluate the effects of temporal variation in flowering timing and ambient temperature of flowering season on seed-set success, a generalized linear mixed model of a penalized quasi-likelihood method (PQL) (Venables and Ripley 2002) was applied using a glmmPQL function in the "MASS" library of an open source system, R ver.2.0.1 (http://www.r-project.org/). In this analysis, "plot (P)", "peak flowering season (S)" and "mean temperature during the flowering season (T)" were considered as fixed factors, and "year" as a random factor. The peak flowering season of each plot was expressed as the sequence at 5-day intervals from July 1, i.e. July 1–5 = 1, July 6–10 = 2, and so on. Data of 1995, 1997 and 1998 were used for this analysis because data from plot E were lacking for 2000 and 2001. The logistic regression model used in this analysis is as follows:

$$\log_e (p/(1-p)) = \beta_0 + \beta_P P + \beta_S S + \beta_T T + \beta_{ST} ST + \varepsilon,$$

where p is the probability of ovules set seeds in individual plants, β_0, β_P, β_S, β_T and β_{ST} are regression coefficients, and ε is an error term of the random factor (year).

Results

Snowmelt conditions

The time of snowmelt varied greatly among years within each snowbed plot, but snowmelt progressed from plot A to E every year (Fig. 2). In average, snowmelt occurred in early June in plot A, late June in plot B, early July in

plot C, late July in plot D, and early August in plot E. There were about two month differences in the time of snowmelt in every plot between the earliest (1998) and latest years (1993).

The time of snowmelt has become earlier during the 17 years in early snowmelt plots A and B (r = –0.52, P = 0.042 and r = –0.52, P = 0.043, respectively, Spearman's rank correlation test), but no significant trends have been detected in other plots (P > 0.1).

In the fellfield, snow usually disappeared prior to mid-May although occasional spring snow remained on the ground during short period in the middle to late May. In 1998, snow disappeared in late April.

Flowering phenology

At community level, the number of flowering species in the fellfield (plot O) was large in the middle to late June and the middle to late July (Fig. 3). The later peak was larger than the earlier peak. The length of whole flowering season in plot O was 85 days in 1998 and 80 days in 2001. In the early-snowmelt snowbed, plot B, peak flowering occurred in the middle of whole flowering season, it was late June in 1998 and mid-July in 2001 (Fig. 3). The length of whole flowering season in plot B was 85 days in 1998 and 75 days in 2001. In the late-snowmelt snowbed, plot D, peak flowering occurred in the early flowering season within the plot, it was mid-July in 1998 and mid-August in 2001 (Fig. 3). The length of whole flowering season in plot D was 55 days in both years.

At the fellfeild plot, flowering time and duration of individual species were similar between 1998 and 2001, irrespective of great difference in temperature conditions (Fig. 4). Mean flowering period of individual species was 18.2 days (ranging 15-30 days) in 1998 and 19.6 days (ranging 15-30 days) in 2001. Peak flowering season of *Arctous alpinus* was 10 days earlier in 1998 than in 2001, but almost similar between the years for other species. Many flower bud of *Diapensia lapponica* did not open in 1998 because of frost damage, resulting in low floral density in the peak season.

As a representative of the snowbed plots, flowering sequences of 12 species in plot D were shown in Figure 5. In contrast with the patterns in the fellfield, flowering timing of snowbed plants was strongly influenced by the snowmelt time, and flowering in 2001 occurred 15-30 days later than that in

1998. However, flowering durations of individual species were similar between the years. Mean flowering period was 17.1 days (ranging 10-25 days) in 1998 and 17.5 days (ranging 10-30 days) in 2001.

Variation in seed-set success

Variations in seed-set percentages of *Peucedanum multivittatum* over five years (three years for plot E) are shown in Figure 6. Mean seed-set values throughout the plots and years was 30.8%. The seed-set success tended to be lower in the early-melt plots and higher in the late-melt plots although there were large variations among years within plots. In plot A, the seed-set percentage in a warm year (1997, when mean temperature during the flowering season was 19.4°C) was higher than that in other years (Fig. 7). In plot C, the seed-set success positively depended on the temperature of flowering season. When daily mean air temperature was lower than 15ºC, seed set was smaller than 25% in these plots. In plot D and E, however, seed set was large even under cool conditions (11–13ºC) in which flowering usually occurred later than early August. Only in 1997, plants growing in plot D showed relatively small seed set (23%, indicating as a gray square in Fig. 7), because many flowers were damaged by frost in late August.

Results of the logistic regression indicated that flowering season significantly influenced the seed-set success (Table 2). Effect of temperature during flowering season was not significant but the interaction between flowering season and temperature was significant (Table 2). This means that temperature effect on pollination success may vary as seasonal progress. When flowering occurred in early season, seed-set success was influenced by the temperature of flowering season, in which warmer conditions resulted in higher seed set. In contrast, when flowering occurred in late season, temperature had little effect on seed-set success if frost damage was absent.

Discussion

Phenological variation

Responses of flowering phenology to the extremely warm year were completely different between the fellfield and snowbed communities.

Because snow usually disappears prior to the initiation of growth in the fellfield, variation in snowmelt time may have little effects on phenological events. In contrast, the timing of snowmelt strongly influences the initiation of growth in the snowbed, because ambient temperature has been usually enough warm for plant growth at the time of snowmelt (Holway and Ward 1965; Kudo 1991; Kudo and Suzuki 1999). There was a 23-day difference in the time of snowmelt between 1998 and 2001 in both plot B and D, but the phenological difference between the years was smaller in plot B than in plot D (Fig. 3). This means that the variation in snowmelt time may not always correspond to the variation in flowering time exactly even in snowbed plants when snowmelt occurs in very early season (e.g. mid-May 1998 in plot B).

Surprisingly, flowering phenology of the fellfield community was not accelerated in 1998 despite the daily mean temperature in May and June was 2.7ºC and 2.5ºC warmer, respectively, in 1998 than in 2001. In contrast to the daily mean temperature, daily minimum temperature in June 1998 (0.9ºC) was lower than that in 2001 (3.4ºC), and the number of days that minimum temperature decreased below 0ºC was 14 days in 1998 and 7 days in 2001. Thus, low nighttime temperature might decelerate the development of floral buds despite of warm daytime temperature in 1998. In the warming experiment using open-top-chamber (OTC) in the fellfield of the Taisetsu Mountains, flowering phenology of dwarf shrub, *Vaccinium uliginosum*, did not change by the warming treatment in which daily mean temperature was 2.5-2.9ºC higher but daily minimum temperature was 0.3ºC lower than control (Suzuki and Kudo 2000). Similar result was reported in alpine Norway that flower development of *Ranunculus glacialis* was conservative in the warming treatment by the OTC (Totland and Alatalo 2002). These results indicate the importance of minimum temperature for onset of flowering.

Flowering phenology of plants is a temperature-dependent phenomenon in many cases (Rathcke and Lacey 1985) and the cumulative temperature above a certain threshold value from a certain starting date (i.e. effective cumulative temperature) has been often used as an indicator of flowering traits (Rathcke and Lacey 1985; Diekman 1996; Molau et al. 2005). Flowering pattern of a local community is determined by the interaction between seasonal transition of temperature and the thermal-demand for

onset of flowering of individual species (Kudo and Suzuki 1999). When a community is exposed from snow cover in early season, the effective cumulative temperature will increase gradually at first, but the increase rate will be accelerated after that as seasonal progress because air temperature increases rapidly from mid-June to mid-July. In such a case, realized flowering will be distorted toward later within the flowering season (negative skewness). When a community is exposed from snow cover in mid-summer when ambient temperature attains at maximum level, the effective cumulative temperature will increase constantly at first, but the increase rate decelerates later due to the decrease in air temperature toward autumn. In such a case, realized flowering will be distorted toward earlier within the flowering season (positive skewness). The previous study (Kudo and Suzuki 1999) revealed that the distribution of temperature-demand for flowering of fellfield species is bimodal with wide range, while that of snowbed species is unimodal with narrow range that results in simultaneous flowering. Therefore, the flowering pattern of individual communities is potentially habitat-specific and conservative against inter-annual climatic variations if changes in temperature regime are not drastic.

Seed-set success

Five-year census of the seed-set percentages in *P. multivittatum* along the snowmelt gradient demonstrates that the temperature effect on seed-set success varies as seasonal progress. Positive effect of ambient temperature of flowering season was obvious only in plot A and C, where flowering commonly occurred in July. Such a seasonal variation may be related to the seasonal changes in the activity and availability of pollinating insects. Flowers of *P. multivittatum* are commonly visited by dipteran insects (syrphid and other flies) throughout the season, but bumblebee workers sometimes visit the flowers in August to collect pollen (G. Kudo, personal observation). Because bumblebee workers usually appear in late July and they are most active in August in the Taisetsu Mountains, only late-flowering plants can use bumblebee workers as pollinators. Dipteran insects are most common pollinators in arctic and alpine regions, and their activity highly depends on ambient temperature (Hocking 1968; Kevan 1972; Levesque and Burger 1982; Inouye and Pyke 1988; Totland 1994). Thus, the

positive correlation between ambient temperature and seed set in early-melt plots may reflect the temperature-dependent activity of pollinators. As bumblebees are endothermic social insects, they are effective pollinators in arctic and alpine regions even under cool conditions (Fægri and van der Pijl 1979; Heinrich 1979; Bergman et al. 1996). This may cause high seed-set success independent of temperature conditions in the late-melt plots.

Increase in seed-set success as season progress has been reported in this site in the intraspecific (Kudo 1993 for *Rhododendron aureum*) and the interspecific comparisons (Kudo and Suzuki 2002). This is because of both seasonal increase in ambient temperature and the seasonality of pollinator availability. In contrast, several studies demonstrated that seed-set success was higher in early-flowering individuals of species in the Scandinavian Mountains (Stenström and Molau 1992; Totland 1994, 1997a, b) and in the Rocky Mountains in USA (Galen and Stanton 1991). Thus, seasonal trend of seed-set pattern may be region-specific phenomena (Kudo and Suzuki 2002).

On the other hand, too late flowering sometimes results in failure of seed maturation of *P. multivittatum* due to the lack of seed-developing period by the onset of winter or frost damage in late summer (Kudo 1997 and result of this study). *Peucedanum multivittatum* is a relatively late-flowering species among snowbed plants, and sensitive to harsh weather conditions in late summer. In 2002, for example, most plants in the late-melt plots failed to set seeds due to the physical damage by snowfall in late August (AS Hirao, personal observation). It is predicted that late-flowering species will bloom earlier, reproduce more, and grow larger under global warming (Totland 1997b; Molau et al. 2005). However, this prediction is possible only when both flowering phenology and insect seasonality sift to earlier together. The extent of phenological synchronization between flowering season and pollinator activity is a crucial issue for the prediction of climate change impacts on alpine ecosystem (Inouye et al. 2000).

Implications for climate change

There are many predictions and reports that ongoing climate change may reduce the snow-pack and accelerate the time of snowmelt in arctic and alpine regions (e.g. CSIRO 1994; Whetton et al. 1996; IPCC 2001). However, the average date of snowmelt in the Colorado Rocky Mountains has not

changed during past 25 years despite a trend for warmer spring temperature, probably due to the increase in winter snowfall (Inouye et al. 2000). In the Taisetsu Mountains, acceleration of snowmelt time was detected only in the early-melt places during last 17 years. Therefore, warming effects on snow regimes seem to vary between regions and between sites within a region. In the Taisetsu Mountains, topographic features may determine the maximum snow depth around the bottom of snowbed because wind-blown snow accumulates on depression places. Whereas, the snow depth around the marginal snowbed may depend on the snowfall, and the timing of snowmelt may be sensitive to the spring weather condition due to relatively shallow snow accumulation. Thus, the plants growing in the early-melt habitat may respond to the climate change more sensitive than in the late-melt habitat.

Acceleration of snowmelt time often decrease the survival, growth and reproductive activity of alpine plants in the early-melt habitat when early exposure from the protection by snow-cover enhances the risk of frost damage and water stress for plants (Walker et al. 1995; Inouye et al. 2002; Saavedra et al. 2003). It is reported that an evergreen cushion plant *Diapensia lapponica* abruptly decreased the biomass by 22% and the flower production by 55% due to frost damage caused by the extremely early snowmelt during the last three years in the early-melt habitat, while plants in the late-melt habitat had little or no damage in the subarctic alpine of northern Sweden (Molau 1996). Also in our study, floral buds of *D. lapponica* were damaged by frost in the extremely warm year (1998). Although the phenological responses of fellfield plants to the warm condition were small, early exposure from snow-cover may enhance the risk of frost damage because reproductive organs of arctic and alpine plants are sensitive to freezing temperature (Billings 1974). Thus, the loss of snow insulation in early season may cause a serious frost impact on the survival and reproduction of plants in the fellfield and the early-melt snowbed habitats under global warming (Inouye 2000).

Existence of snowmelt gradient is a crucial factor maintaining biodiversity of alpine ecosystem that creates various habitat types and seasonally diverse phenological features within a local area. Our recent study revealed the existence of genetic structure among neighboring populations having different snowmelt conditions, probably because segregated flowering season

isolates the gene flow via pollination process (Hirao and Kudo 2004). Modification of flowering phenology along the snowmelt gradient may change the spatial genetic structure among local populations if climate change increases the flowering overlap among populations.

Acknowledgements

References

Bergman P, Molau U, Holmgren B (1996) Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. Arc Alp Res 28:196-202

Billings WD (1974) Adaptations and origins of alpine plants. Arc Alp Res 6:129-142.

Billings WD, Bliss LC (1959) An alpine snowbank environment and its effect on vegetation, plant development, and productivity. Ecology 40:388-397

CSIRO (1994) Climate Change and Snow Cover Duration in the Victorian Alps. Report to the Environmental Protection Authority. CSIRO Division of Atmospheric Research, Publication 403, Australia

Diekmann M (1996) Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. Can J Bot 74:528-537

Fægri K, van der Pijl L (1979) The Principles of Pollination Ecology. 3rd ed. Pergamon Press, Oxford, UK

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. Science 296:1689-1691

Galen C Stanton ML (1991) Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). Am J Bot 78:978-988

Heinrich B (1979) Bumblebee Economics. Harvard University Press,

Cambridge and London

Hirao AS, Kudo G (2004) Landscape genetics of alpine-snowbed plants: comparisons along geographic and snowmelt gradients. Heredity 93:290-298

Hocking B (1968) Insect-flower associations in the high Arctic with special reference to nectar. Oikos 19:359-387

Holway JG, Ward RT (1965) Phenology of alpine plants in northern Colorado. Ecology 46:73-83

Inouye DW (2000) The ecological and evolutionary significance of frost in the context of climate change. Ecol Letters 3:457-463

Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. PNAS 97:1630-1633

Inouye DW, Morales MA, Dodge GJ (2002) Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. Oecologia 130:543-550

Inouye DW, Pyke GH (1988) Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorado, USA. Aust J Ecol 13:191-210

IPCC (2001) Climatic Change 2001: impacts, adaptations and vulnerability. Cambridge University Press, Cambridge, UK

Kevan PG (1972) Insect pollination of high arctic flowers. J Ecol 60:831-847

Kudo G (1991) Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. Arc Alp Res 23:436-443

Kudo G (1993) Relationship between flowering time and fruit set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. Am J Bot 80:1300-1304

Kudo G (1997) Sex expression and fruit set of an andromonoecious herb, *Peucedanum multivittatum* (Umbelliferae) along a snowmelt gradient. Opera Bot 132: 121-128

Kudo G, Ito K (1992) Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. Vegetatio 98:165-174

Kudo G, Nishikawa Y, Kasagi T, Kosuge S (2004) Does seed production of

spring ephemerals decrease when spring comes early? Eco Res 19:255-259

Kudo G, Suzuki S (1999) Flowering phenology of alpine plant communities along a gradient of snowmelt timing. Polar Biosci 12:100-113

Kudo G, Suzuki S (2002) Relationships between flowering phenology and fruit-set of dwarf shrubs in alpine fellfield in Northern Japan: a comparison with a subarctic heathland in northern Sweden. Arc Ant Alp Res 34:185-190

Levesque CM and Burger JF (1982) Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A., and their possible role as pollinators. Arc Alp Res 14:117-124

Molau U (1993) Relationships between flowering phenology and life history strategies in tundra plants. Arc Alp Res 25:391-402

Molau U (1996) Climatic impacts on flowering, growth, and vigour in an arctic-alpine cushion plant, *Diapensia lapponica*, under different snow cover regimes. Ecol Bull 45:210-219

Molau U, Nordenhäll U, Eriksen B (2005) Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. Am J Bot 92:422-431

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants Ann Rev Ecol Syst 16:179-214

Saavedra F, Inouye DW, Price MV, Harte J (2003) Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. Global Change Biol 9:885-894

Stenström M, Molau U (1992) Reproductive ecology of *Saxifraga oppositifolia*: phenology, mating system, and reproductive success. Arc Alp Res 24:337-343

Suzuki S, Kudo G (2000) Response of alpine shrubs to simulated environmental change during three years in the mid-latitude mountain, northern Japan. Ecography 23:553-564

Thórhalsdóttir TE (1998) Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia 114:43-49

Totland Ø (1994) Influence of climate, time of day and season, and flower

density on insect flower visitation in Alpine Norway. Arc Alp Res 26:66-71

Totland Ø (1997a) Limitations on reproduction in alpine *Ranunculus acris*. Can J Bot 75:137-144

Totland Ø (1997b) Effects of flowering time and temperature on growth and reproduction in *Leontodon autumnalis* var. *taraxaci*, a late-flowering alpine plant. Arc Alp Res 29:285-290

Totland Ø, Alatalo JM (2002) Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. Oecologia 133:168-175

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, Berlin Heidelberg New York

Walker MD, Ingersoll RC, Webber RC (1995) Effects of interannual climate variation on phenology and growth of two alpine forbs. Ecology 76:1067-1083

Whetton PH, Haylock MR, Galloway R (1996) Climate change and snow-cover duration in the Australian Alps. Climatic Change 32:447-479

Figure Caption

Fig. 1   Location of survey plots in the study site. Each snowbed plot (A to E) is about 20 x 20 m size, and the fellfeild plot (O) is about 50 x 50 m size. The fellfield plot is usually exposed from snow-cover by mid-May prior to the initiation of plant growth. Snowmelt of the snowbed plots progresses from A to E (see Fig. 2).

Fig. 2   Inter-annual variations in snowmelt time of individual plots during 1988-2004. Day number means calendar days from January 1. Snowmelt always progressed from plot A to E. The time of snowmelt has become earlier during the 17 years in plot A and B ($P<0.05$), but significant trends have not been detected for other plots.

Fig. 3   Flowering pattern at community level in the fellfield (plot O), early-melt snowbed (plot B) and late-melt snowbed (plot D) in 1998 and 2001. The number of species observed was 14 in plot O, 19 in plot B and 12 in plot D. Flowering duration in plot O was 85 days in 1998 and 80 days in 2001, that in plot B was 85 days and 75 days, and that in plot D was 55 days and 55 days, respectively.

Fig. 4   Flowering patterns of major fellfield species in plot O in the extremely warm year (1998 in gray lines) and normal year (2001 in broken lines). See text for flowering rank.

Fig. 5   Flowering patterns of major snowbed species in plot D in the extremely early-snowmelt year (1998 in gray lines) and normal year (2001 in broken lines). Snow disappeared on July1 in 1998 and July 23 in 2001. See text for flowering rank.

Fig. 6   Seed-set percentages of *Peucedanum multivittatum* under natural conditions in each plot (A, C, D and E) and year (1995, 1997, 1998, 2000 and 2001). Horizontal axis means the time of peak flowering in each year. The box plot represents the 75th, 50th and 25th percentile, the top whisker ranges from the 75th to the 90th percentile and the bottom

whisker from the 25th to the 10th percentile. Mean seed set throughout the plots and years was 30.8% (shown as broken lines).

Fig. 7   Relationship between the daily mean temperature during the flowering season and the mean value of seed set of *Peucedanum multivittatum* in each plot and year. In 1997, many plants in plot D were damaged by frost in late August, resulting in low seed set (shown as a filled square).

Table 1. Mean monthly temperature (ºC) at a 1700 m elevation near the
research site. Measurement was performed at one-hour intervals at the
height of 40 cm from the ground.

Year	May	June	July	August	September
1995	No data	8.2	12.8	11.8	6.1
1996	No data	10.1	13.4	12.6	7.5
1997	2.0	9.7	13.7	11.6	6.2
1998	7.4	10.4	14.9	13.5	9.9
1999	0.8	7.9	13.1	15.4	8.9
2000	6.0	9.1	14.0	15.0	9.0
2001	4.7	7.9	12.6	13.2	6.5
2002	3.5	7.0	13.4	11.9	7.3
2003	4.3	10.1	10.5	12.1	7.1
2004	No data	9.8	13.6	11.8	No data
Mean	4.1	9.0	13.2	12.9	7.6

Table 2. Results of logistic regression for seed-set success of *Peucedanum multivittatum*. Coefficients of intercept, plots, flowering season, mean temperature during flowering, and the interaction between flowering timing and temperature are shown with standard error (SE).

Parameter	Coefficient	SE	*t*-value	*P*-value
Intercept (Plot A)	−1.890	1.043	−1.811	0.070
Plot B	0.726	0.134	5.427	< 0.0001
Plot D	1.461	0.215	6.804	< 0.0001
Plot E	1.716	0.323	5.315	< 0.0001
Flowering season (*S*)	−0.472	0.157	−3.010	0.003
Mean temperature (*T*)	0.038	0.069	0.546	0.585
S x *T*	0.032	0.012	2.764	0.006

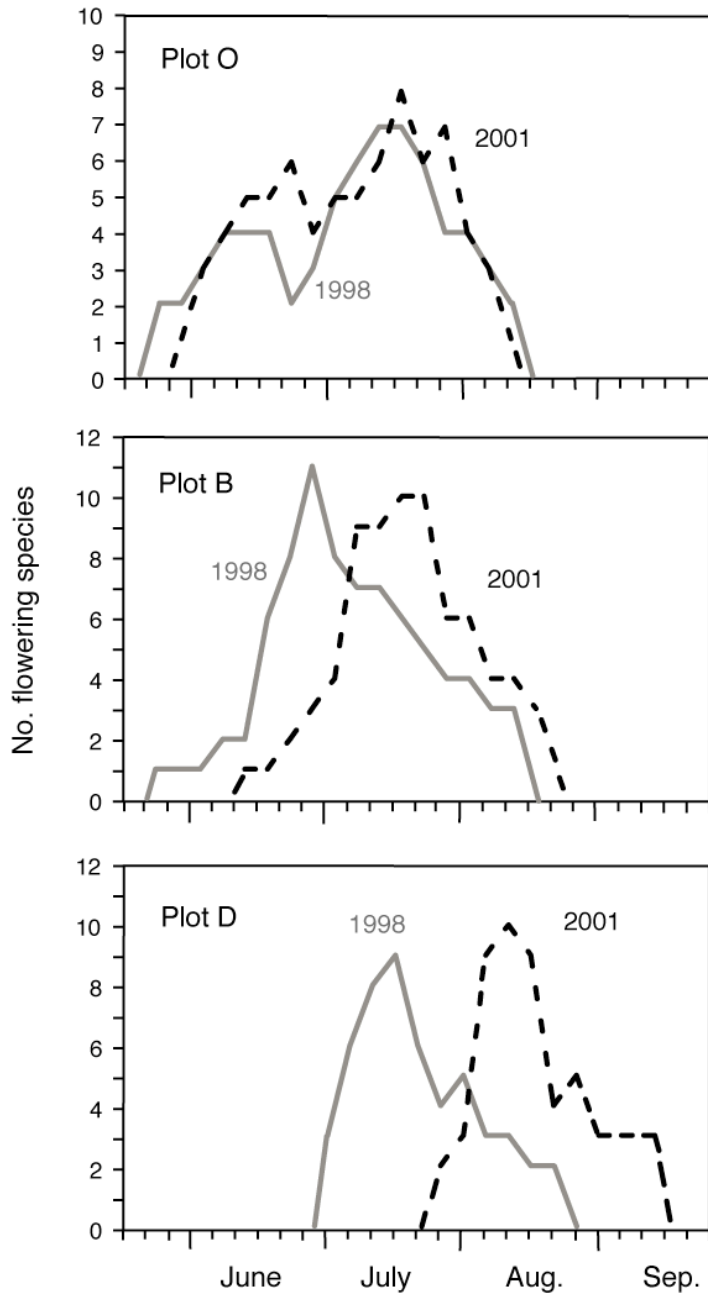Fig. 1 (Kudo & Hirao)
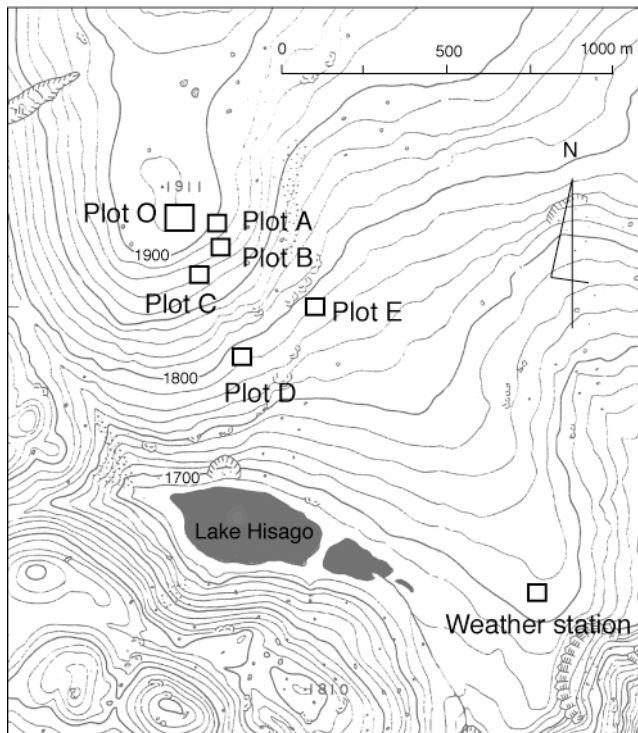
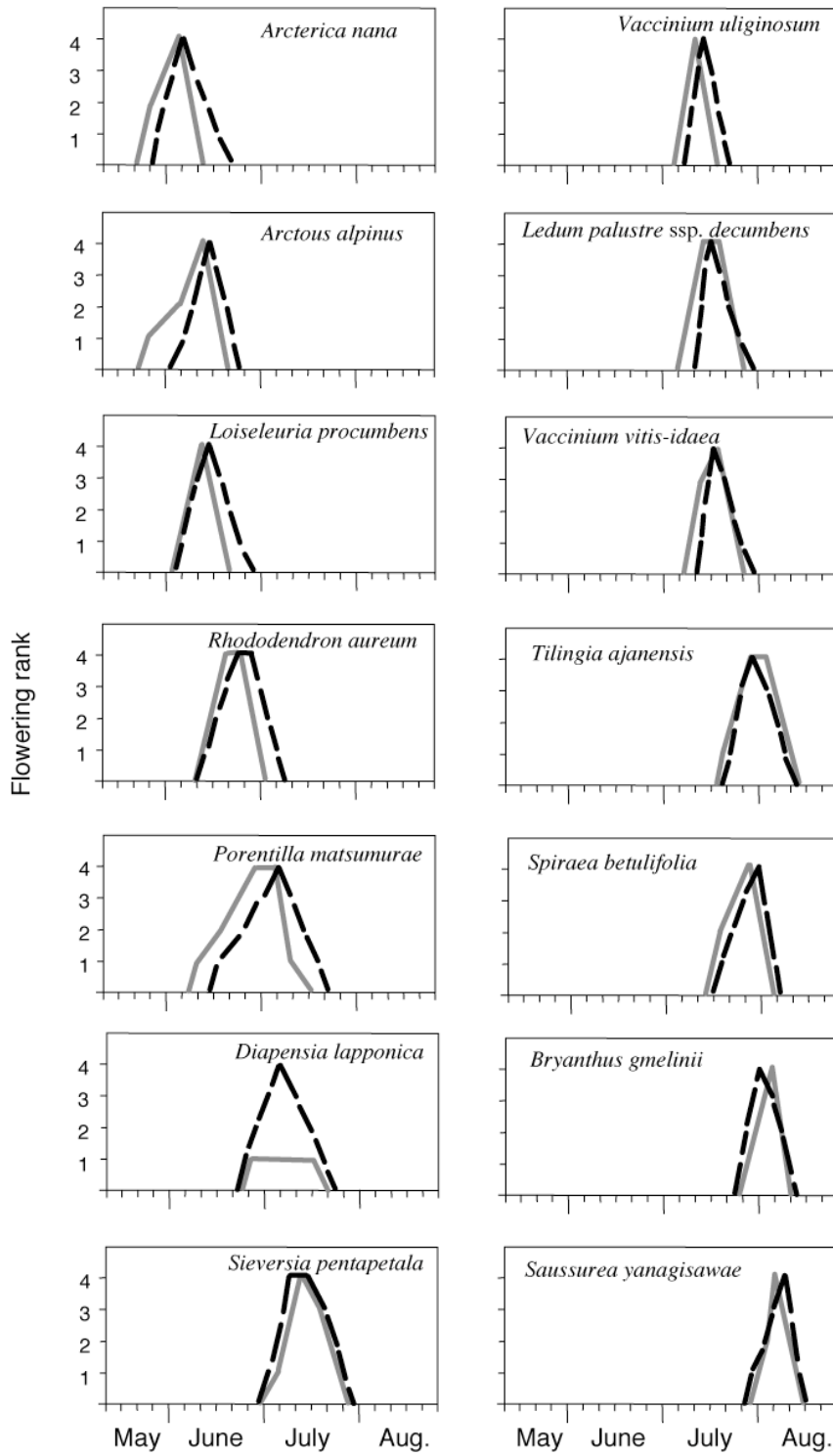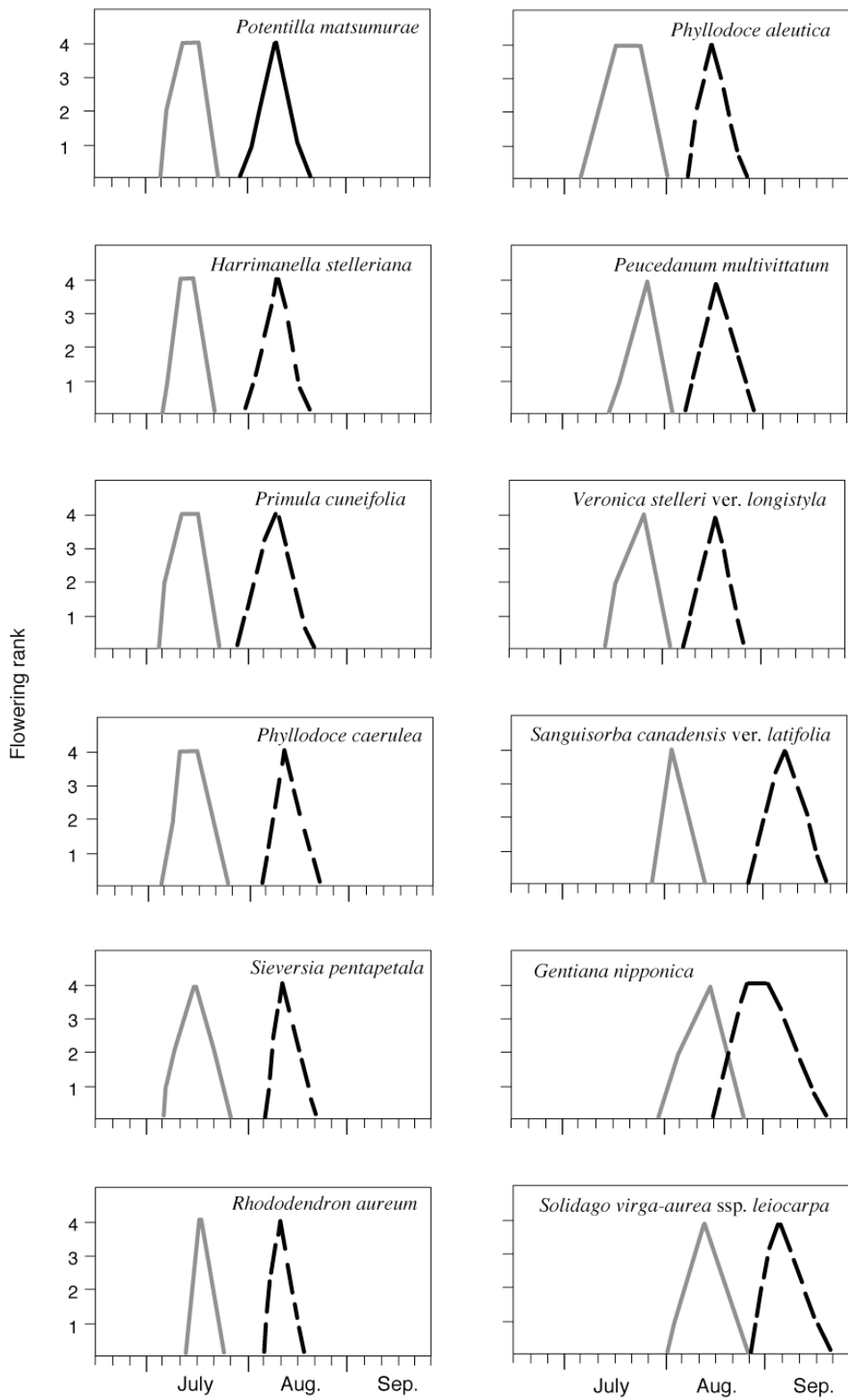Fig. 2 (Kudo & Hirao)
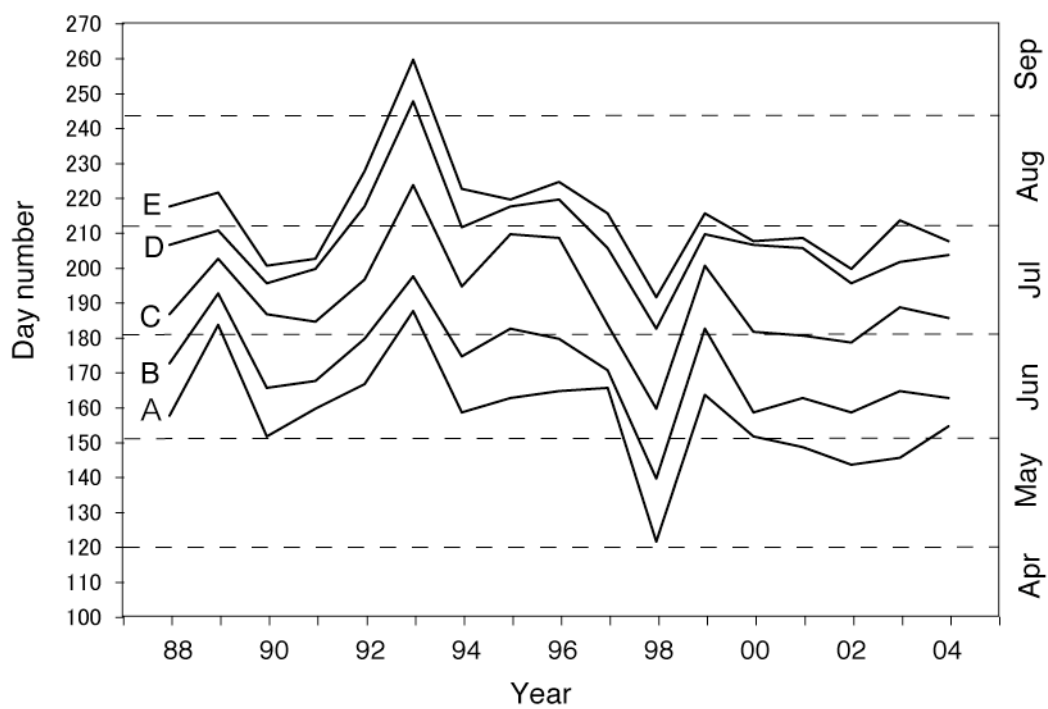
Fig. 3 (Kudo & Hirao)

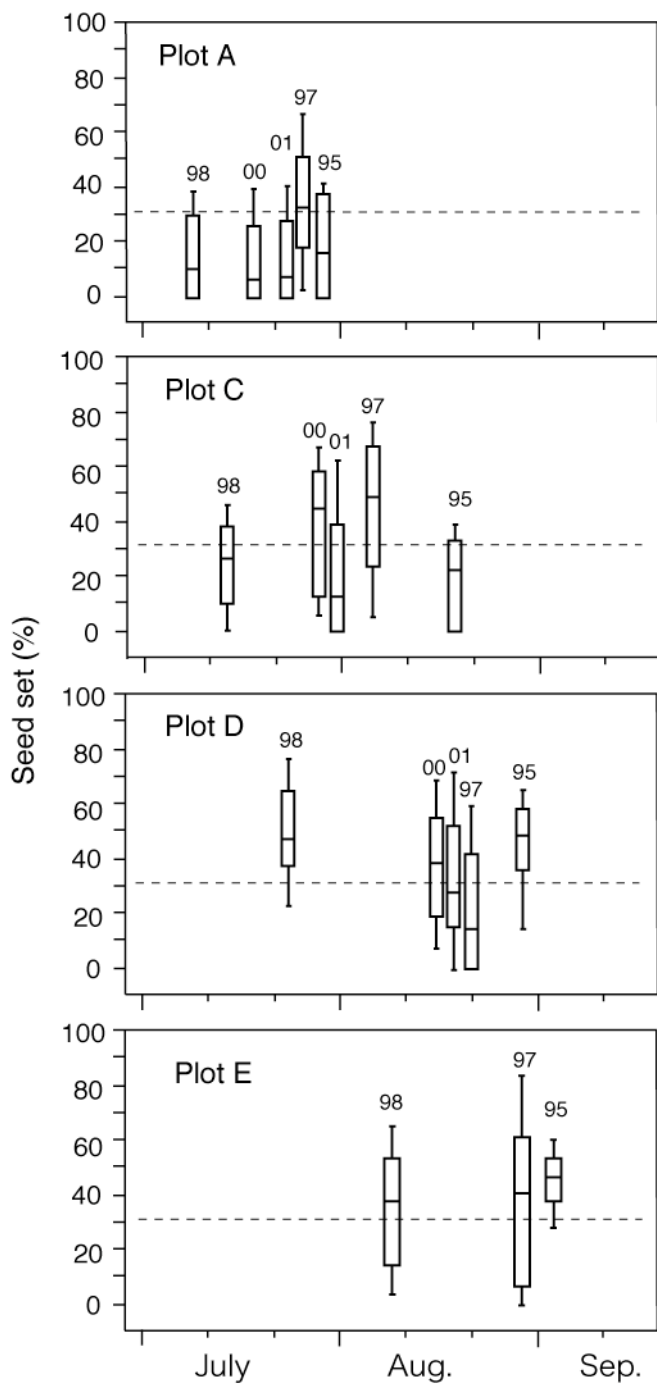Fig. 4 (Kudo & Hirao)

Fig. 5 (Kudo & Hirao)

Fig. 6 (Kudo & Hirao)

Fig. 7 (Kudo & Hirao)