Overwinter Phenology of Plants in a Polar Semi-desert

Arctic and temperate-latitude tundra plants must make efficient use of the growing season, because it is very short. A variety of leaf-development strategies permit growth in the cool summers[1,2]. Among these is the "wintergreen" growth pattern described by Sørensen[3]. Wintergreen leaves begin to develop and partially expand during one summer, mature in the following summer and die at its end. Evergreen leaves are active for longer than two summers. Presumably, these phenological strategies represent an adaptation to a short, cold growing season in that plants are ready to begin photosynthesis in the spring, with minimal time spent in leaf expansion. By contrast, the leaves of summergreen plants develop, and complete their lives, during a single summer. About one-third of the tundra species examined in Greenland by Sørensen[3] and in Colorado by Bell[4] exhibit wintergreen phenology.

Since wintergreen leaves appear beneficial for plants of the more hospitable tundra areas, they might also be expected in plants of Polar Deserts and Polar Semi-deserts. To determine the phenological strategies of plants living in these very severe habitats, observations were made in the northeastern part of King Christian Island, N.W.T. (in the vicinity of 77°45'N, 101°10'W). King Christian Island affords a variety of Polar-Desert and Polar Semi-desert habitats, from moist meadows dominated by mosses and *Luzula* spp. to well-drained flat ridges. The summers there are brief and cold, and soils remain thawed for about seven to ten weeks annually. July and August air temperatures at 25 cm above the ground averaged 2.4°C in 1973 and 2.6°C in 1974[5]. King Christian Island is among the coldest areas in the Arctic, with an average of 162 degree-days above 0°C in 1973 and 1974, compared with averages in 1971-73 of 162 at Isachsen, N.W.T. (78°50'N, 106°00'W); 304 on the Truelove Lowland of Devon Island, N.W.T. (75°50'N, 84°40'W); 321 at Barrow, Alaska (71°16'N, 156°50'W); and 637 at Ella Ø in northeastern Greenland (72°50'N, 25°30'W)[6].

Winter phenology was observed under field conditions for 27 of 33 angiosperm species found on King Christian Island. The remaining six species were not common, and were difficult to find under the snow in spring. Between 15 and 200 plants of each species were examined at the time of fall freeze-up in 1973 and 1974 and about two weeks prior to spring thaw in 1974. Leaf phenology was the same at freeze-up and before thaw, and the conditions of leaves observed at these times was assumed to be that maintained over the entire winter. The number of leaves produced annually on each stem or tiller was noted. Leaves that had overwintered invariably had brown or red edges, even in early summer; new leaves were entirely green. Leaf longevity was estimated using observations of both annual leaf production and the number of leaves which had survived the winter. For example, if a tiller produced two new leaves annually and had only two leaves with brown tips shortly after spring thaw, those leaves were assumed to be wintergreen. A stem producing two new leaves annually and having five or six brown-edged leaves in early summer, was considered to have evergreen leaves. There were very slight differences in average annual production of leaves between 1973 and 1974[7]. In all cases, estimates of leaf longevity were based upon the greater number of new leaves.

Of the 27 species examined, six had at least some evergreen leaves. Of the remaining species, all except *Oxyria digyna* followed the wintergreen pattern of development (Table 1). *Oxyria* leaves occasionally survived into the early part of the second summer, but most developed from a dormant bud and died within a single growing season. In wintergreen species, development of all leaves began in mid- to late summer. The extent of leaf expansion in the first summer varied among species and between individual shoots. The leaf blades of *Ranunculus* spp. and *Saxifraga cernua* expanded little, but their petioles were fully developed and greatly swollen by the presence of starch grains (identified by iodine staining). The more common pattern was for new leaves to be about 25-50% expanded at the time of fall freeze-up. Rhizomes of the monocots appeared to function as starch storage organs. This tendency was especially pronounced in *Luzula* spp.

Additional observations were made on eight species (indicated in Table 1) held under controlled conditions. Plants were held at a temperature of −5°C in darkness for six to nine months, then at constant temperatures of 1° or 5°±1° under constant light in relative humidity near 80% to simulate summer conditions. In all cases, the phenology of the dormant states was like that observed in the field. All eight species entered fall dormancy while being held under conditions of constant summer light and temperature.

The wintergreen and evergreen patterns of leaf development appear to be of much

TABLE 1. Overwinter conditions of plants on King Christian Island, N.W.T.

Species	Leaf phenology
**Alopecurus alpinus*	1 wintergreen leaf/tiller
**Phippsia algida*	1-2 wintergreen leaves/tiller
**Puccinellia vaginata*	1-2 wintergreen leaves/tiller
Festuca brachyphylla	2 wintergreen leaves/tiller
Juncus biglumis	1 wintergreen leaf/tiller
**Luzula nivalis*	1-2 wintergreen leaves/tiller, swollen rhizomes
**L. confusa*	1-3 wintergreen leaves/tiller, swollen rhizomes
Oxyria digyna	Dormant bud, occasional wintergreen leaves
Stellaria laeta	Wintergreen leaves
Cerastium alpinum	Wintergreen leaves
C. regelii	Wintergreen leaves
Arenaria peploides var. *diffusa*	Wintergreen leaves
A. rubella	Wintergreen leaves
Ranunculus sulphureus	Small wintergreen leaves with swollen petioles
**R. sabinei*	Small wintergreen leaves with swollen petioles
**Papaver radicatum*	Wintergreen leaves
Cochlearia officinalis	Evergreen leaves
Draba alpina	Wintergreen leaves
D. bellii	Wintergreen leaves
Saxifraga caespitosa	Evergreen and wintergreen leaves
**S. cernua*	Small wintergreen leaves with swollen petioles
S. flagellaris	Evergreen and wintergreen leaves
S. oppositifolia	Evergreen and wintergreen leaves
S. rivularis	Wintergreen leaves
S. tenuis	Evergreen leaves
Potentilla hyparctica	Wintergreen leaves

*These species were observed in controlled environments as well as under field conditions.

greater importance in the Polar Deserts and Polar Semi-deserts of King Christian Island than in other tundra environments with a short growing season where winter phenology is known. Twenty-five of the species described from King Christian Island have also been observed by Sørensen in northeastern Greenland[8]. The leaf types of these 25 species in these two locations are compared in Table 2.

In other areas with a short summer, the majority of tundra plants develop new leaves annually from dormant buds. Most of the exceptions are members of the Gramineae and Cyperaceae which often retain green leaf bases in winter[8,9]. On King Christian Island, wintergreen or evergreen leaves are present in almost all species, both monocots and dicots. In this High Arctic environment, cold during the growing season probably imposes a severe limit on the rate of leaf expansion. A leaf growing during a single season would have little time for maximum photosynthesis. The wintergreen or evergreen leaf growth strategy allows a more protracted use of leaves for photosynthesis. It is now quite well established that plants with evergreen or wintergreen leaves in the Arctic have slower growth rates and lower rates of net assimilation and transpiration; in general they are more conservative species[10-13]. Johnson and Tieszen[14] have shown that the longer life spans of leaves of plants at Meade River, Alaska (70°28′N, 157°26′W) compensate for their slow growth. A similar pattern appears to be necessitated by environmental limitations in the High Arctic.

TABLE 2. Wintering phenology of plants on King Christian Island and in northeastern Greenland.

Leaf type	Percentage of species: King Christian Island	Percentage of species: North-eastern Greenland
Summergreen	4	48
Wintergreen	72	52
Evergreen	24	0

Slow root growth may lend further importance to wintergreen and evergreen leaves. Plants on King Christian Island have small root systems, with ratios of live roots to live shoots generally between 0.2 and 0.6[7]. Very low soil temperatures appear to prevent extensive root development. Overwinter carbohydrate storage occurs, therefore, primarily in the shoots.

Within the northwestern Queen Elizabeth Islands, woody subshrubs (e.g., *Vaccinium, Cassiope*, etc.) and evergreen-leaved cushion plants (e.g., *Dryas*) are a very minor component of the flora, if they occur at all. If the general growth form of evergreen leaves has adaptive value in these cold summer environments, it is not surprising that their place has been taken by herbaceous and rosette species that can maintain wintergreen or evergreen leaves.

The wintering condition of plant leaves does not have the same development pattern even throughout the High Arctic. The six evergreen species on King Christian are wintergreen in northeastern Greenland[3]. Of the 18 wintergreen species on King Christian, ten are summergreen in Greenland. The Scoresbysund, Greenland, area (70°30'N, 22°W) has a considerably milder climate (−15° January, 6.0° July monthly mean, −6.3° annual mean temperature, 395 mm annual precipitation, 3.5 months above 0°C) than does the King Christian — Isachsen, Ellef Ringnes Island area (78-79°N, 100-106°W) (−35.1° January, 3.3° July monthly mean, −19.1° annual mean temperature, 102 mm annual precipitation, 2.0 months above 0°C). This variability in behaviour could result from phenological plasticity or ecotypic differences. The consistency of plant behaviour under controlled environment tends to support the latter hypothesis. The full significance of overwintering leaf condition and the variability of this pattern within the High Arctic needs further investigation.

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REFERENCES

[1]Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics*, 2: 405-38.

[2]Billings, W. D. 1974. Arctic and alpine vegetation: plant adaptations to cold summer climates. In: Ives, J. D. and Barry, R. D. (eds.), *Arctic and Alpine Environments*. London: Methuen. pp. 403-43.

[3]Sørensen, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland*, 125(9).

[4]Bell, K. L. 1975. Root adaptations to a polar semi-desert. In: Bliss, L. C. (ed.), *Plant and Surface Responses to Environ-Mental Conditions in the Western High Arctic*. Ottawa: Department of Indian Affairs and Northern Development (Publication OS-8056-000-EE-A1). pp. 21-62.

[5]Addison, P. A. 1975. Plant and surface responses to environmental conditions in the western Canadian High Arctic. In: Bliss, L. C. (ed.), *Plant and Surface Responses to Environmental Conditions in the Western High Arctic*. Ottawa: Department of Indian Affairs and Northern Development (Publication OS-8056-000-EE-A1). pp. 3-20.

[6]Bliss, L. C. 1976. Truelove Lowland, a High Arctic ecosystem. In: Rosswall, T. and Heal, O. W. (eds.), *Structure and Function of Tundra Ecosystems*. Stockholm: National Science Research Council (Ecological Bulletin NFR 20). pp. 17-60.

[7]Bell, K. L. 1974. Autumn, winter and spring phenology of some Colorado alpine plants. *American Midland Naturalist*, 91: 460-4.

[8]Tieszen, L. L. 1972. The seasonal course of aboveground production and chlorophyll distribution in a wet arctic tundra at Barrow, Alaska. *Arctic and Alpine Research*, 4: 307-24.

[9]Muc, M. 1976. Ecology and primary production of the lowland sedge-moss meadow communities. In: Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. Edmonton: University of Alberta Press.

[10]Bliss, L. C. 1976. General summary, Truelove Lowland ecosystem. In: Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. Edmonton: University of Alberta Press.

[11]Svoboda, J. 1976. Ecology and primary production of raised beach communities, Truelove Lowland. In: Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. Edmonton: University of Alberta Press.

[12]Tieszen, L. L. and Wieland, N. K. 1975. Physiological ecology of arctic and alpine photosynthesis and respiration: In: Vernberg, F. J. (ed.), *Physiological Adaptations to the Environment*. New York: Intext Press. pp. 157-200.
[13]Courtin, G. M. and Mayo, J. M. 1975. Arctic and alpine plant water relations. In: Vernberg, F. J. (ed.), *Physiological Adaptations to the Environment*. New York: Intext Press. pp. 201-24.
[14]Johnson, D. A. and Tieszen, L. L. 1976. Aboveground biomass allocation, leaf growth and photosynthesis patterns in tundra plant forms of arctic Alaska. *Oecologia*, 24: 159-73.