

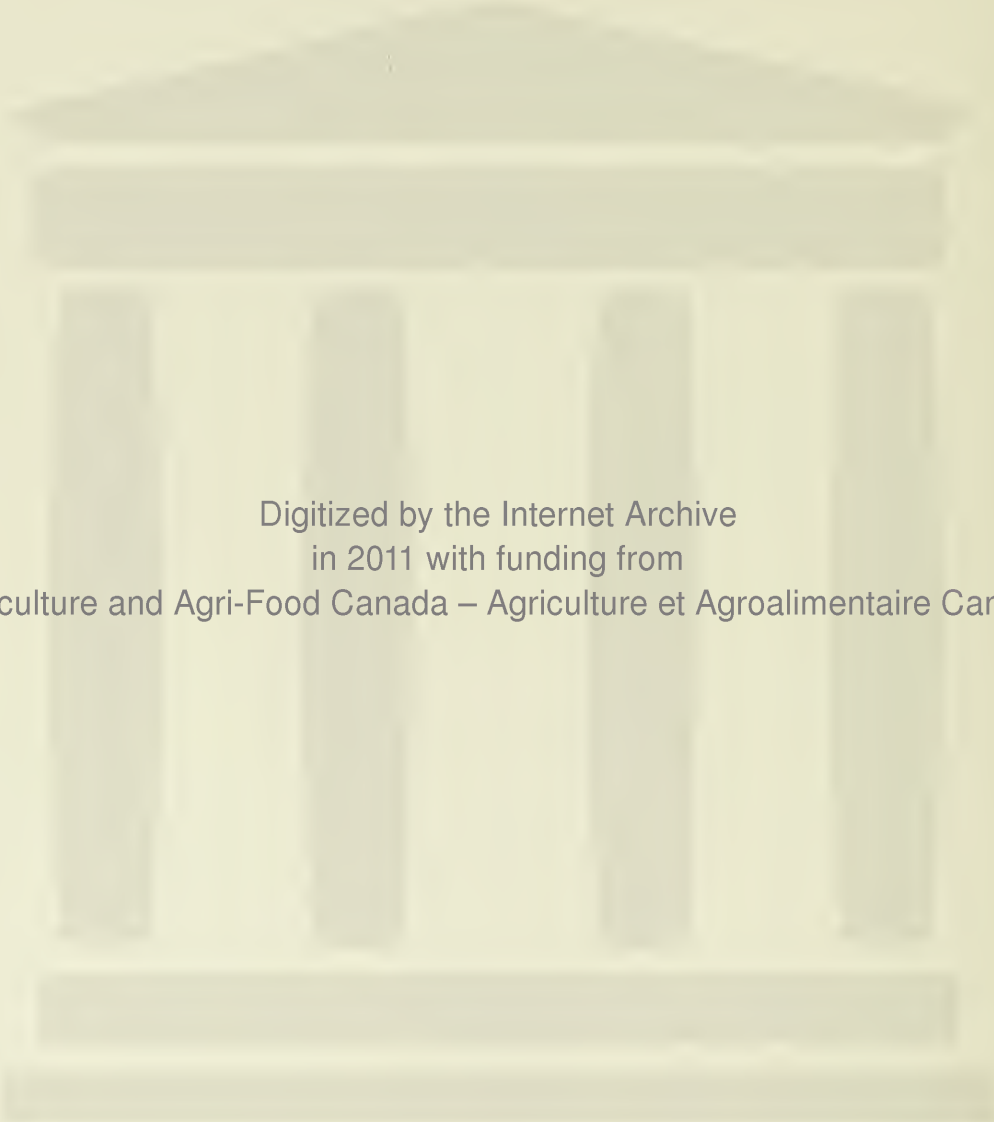


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ARCTIC ADAPTATIONS IN PLANTS

Monograph No.6

1972



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ARCTIC ADAPTATIONS IN PLANTS

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Monograph No.6

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Preface

This study had its genesis in 1958 when I became reinvolved in arctic biology after a lapse of several years. In the interval I had worked for three summers in British Columbia with J. A. Calder, and inevitably became interested in adaptations of plants to climates ranging from upper sonoran to high alpine, and also in problems of plant geography and the effective means of dispersal upon which geographic patterns depend.

Returning to the Arctic with broadened interests, I found that several widely accepted concepts were untenable, and was forced to reexamine the relationships of plants to their physical environment notably in terms of late pleistocene history. From my discussions with staff of the Entomology Research Institute it became clear that flowering plants, insects, and fungi had occasionally evolved analogous solutions to environmental problems. A book to deal with arctic adaptations in all organisms was then planned. After long delays and unforeseen problems the project had finally to be abandoned, and only now has it become possible to present the botanical parts.

Because of other research commitments it has not been feasible to incorporate fully the literature of the last four years. However, the loss is perhaps not very serious, for the study was originally planned as an expression of my personal ideas and observations, rather than as an encyclopedic (and surely tedious) review of the world literature on growth in cold climates. In any event the study asks nearly as many questions as it answers, and it will be long before a definitive work on arctic adaptations can be written. If the questions stimulate new research I shall be amply rewarded.

D. B. O. Savile
Ottawa
September 1971

Contents

	Page
I Introduction	7
A Scope	7
B Age and origins of the arctic flora	7
C Gradation in arctic climate	9
D Characteristics of arctic environment important to plants	11
II Flowering plants	14
A Introduction	14
B Winter survival	15
1 Winterhardiness	15
2 Snow abrasion and desiccation	15
C Summer survival	22
1 Frost resistance	22
2 Adaptations to low temperature	23
<i>a</i> Physical adaptations	23
<i>b</i> Physiological adaptations	26
3 Adaptations to short season	29
<i>a</i> Morphological adaptations	29
i Rapid initiation of growth in spring, 29. ii Vegetative reproduction, 30. iii The annual habit, 32. iv Periodic and aperiodic growth, 33.	
<i>b</i> Genetic adaptations	35
4 Genetic implications of breeding system modifications	38
5 Adaptations to conditions of illumination	40
6 Adaptation to low nitrogen supply	42
D Dispersal	44
III Cryptogamic plants except fungi	55
A Introduction	55
B Bryophytes	55
C Lichens	57
D Algae	58
E Vascular cryptogams	60
IV Fungi	61
A Introduction	61
B Adaptations to cold, short summer	62
1 Saprophytes and facultative parasites	62
<i>a</i> Simplification of life cycle and breeding system	62
<i>b</i> Gradual development of sporocarps	63
<i>c</i> Prolonged development of mycelium in soil	64
2 Obligate parasites	65
C Dispersal	74
V Conclusions	76
Acknowledgments	77
References	78

I Introduction

A Scope

Although the flora of the arctic regions is very attenuate, it includes representatives of all the major categories of plants: flowering plants, vascular cryptogams, mosses and liverworts, a variety of algae, lichens, typical fungi, down to the slime-molds and primitive aquatic organisms so simple that we cannot unequivocally assign them to kingdom. Even if we knew enough about the arctic representatives of all these groups to discuss their adaptations encyclopedically, the recital might overwhelm the reader with minor details and tedious repetitions. But our understanding of arctic plants is actually so uneven that a complete treatment is quite impossible.

We shall discuss the flowering plants in most detail, for this is the group that has received most, although not adequate, attention. Most of the cryptogams can be discussed only very briefly, for they have been subjected to almost no studies that bear upon our theme. However, the fungi can be considered in more detail, for, although the experimental approach has been neglected, we have a considerable mass of pertinent observations on their characteristics and behavior in the Arctic.

B Age and origins of the arctic flora

Stretching from southwestern Banks Island to Meighen Island, in the Canadian Arctic Archipelago, is a band of unconsolidated sand and gravel: the Beaufort formation. Preliminary palynological studies suggest that this formation dates from late Pliocene or the Pliocene-Pleistocene boundary (Craig and Fyles, 1960). On Banks Island it yields abundant pollen of spruce, pine, fir, and hemlock, and significant amounts of that of several temperate hardwoods and herbaceous plants. As far north as Meighen Island (80° N lat.) the Beaufort formation contains abundant well-preserved and unfossilized coniferous wood, apparently largely or wholly spruce (*Picea*). Most of the trunks have disintegrated, but numerous branches, although decorticated and superficially discolored, are hard and well-preserved. The abundance and condition of this wood suggests that the trees grew in situ and were killed by the climatic deterioration at the onset of the Pleistocene. This is the familiar situation when standing spruce trees are killed by various causes. Decay of the trunks spreads up from the roots, but the relatively small, dry branches persist in sound condition until the trunks disintegrate. The fact that the branches did not decay suggests that intense cold set in at about the time that the trees collapsed. The branches have since been almost continuously frozen except when beneath the sea during the interglacial intervals (Savile, 1961 *b*).

We thus have a picture of spruce trees growing until the onset of the Pleistocene on an island that today has proved flora of only 17 species of vascular plants, bears a small central ice cap, and has the severest climate of any sea-level land in the Arctic that is currently ice-free. (In contrast, some protected valley sites up to 200 km further north support about 100 species of

vascular plants.) It thus appears that, if Meighen Island supported spruce trees until approximately the onset of the Pleistocene, no truly arctic flora can have existed in North America except perhaps on high mountains.

The length of the Pleistocene was, until recently, widely accepted as about 1,000,000 years; but it now appears that this estimate must be substantially raised. For example, Bed 1 of Olduvai Gorge in Tanzania, accepted from faunal associations as lower Pleistocene, has been shown by two completely independent methods (potassium-argon and fission-track dating) to extend over nearly 2,000,000 years (Fleischer et al., 1965). It is accordingly believed that the Pleistocene may have lasted approximately 3,000,000 years.

The mountains of Ellesmere and Axel Heiberg islands apparently resulted from the Tertiary orogeny that gave rise to the North American Cordillera, the Alps, and other mountain systems. If the same general age holds for other arctic mountain systems, high-latitude alpine habitats gradually became available during the Tertiary. Probably much of the uplifting was not completed until late Tertiary. Thus no truly arctic habitats seem to have developed until well into the Tertiary and appreciable arctic plains and marshes have probably existed for little more than 3,000,000 years.

A period of, at most, perhaps 15,000,000 years, and for some species 3,000,000 years or less, is a short evolutionary span. The complete elaboration, within the Arctic, of complex morphological and physiological adaptations is scarcely to be expected in such a relatively brief time. This conclusion is supported by the constitution of the flora, for in any group of plants we find almost no arctic genera, a moderate number of well-defined arctic species (together with others that also occur outside the Arctic), and a large number of subspecies or nearly cryptic species. Some authors have postulated a much earlier origin of the arctic flora, but their conclusions have generally been based on apparent misconceptions of arctic dispersal mechanisms, as will be shown in Section II, D.

If we examine sample genera of flowering plants that are freely represented in the Arctic, we are forced to the conclusion that the region was populated by repeated invasion from various regions, and that only moderate radiation has occurred within the Arctic. Two important genera for which reasonably complete and acceptable taxonomic treatments are available are *Carex* and *Saxifraga*. *Carex* contains approximately 2000 species, of which some 66 occur in the Arctic. The arctic species belong to four of five subgenera (the other being essentially tropical) and are distributed through 33 sections or subsections, each represented by one to seven species. The sections and subsections are of diverse geographic origin. *Saxifraga* contains more than 300 species, of which some 25 are recorded in the Arctic (figures modified from Polunin, 1959). The arctic species belong to 15 sections or clearly defined subsections, each represented by one to four species. Some of the sections or subsections are primarily European-Alpine (e.g., *Porphyron*), Himalayan (e.g., *Hirculus*), Beringian (e.g., *Trachyphyllum*), or Cordilleran (e.g., *Nivali-virginienses*), but some of their arctic representatives have become nearly or completely holarctic. In a few groups the geographic spread can be followed in considerable detail. Thus, *Saxifraga* sect. *Hirculus*, with 11 subsections and about 90

species, is almost wholly confined to the Himalayan region. However, four species, in as many subsections, have reached the Arctic, and two of them have become circumpolar. In both *Carex* and *Saxifraga* the arctic species belong to both primitive and advanced sections.

From other genera that have a number of arctic representatives (e.g., *Eriophorum*, *Juncus*, *Salix*, *Draba*, *Potentilla*, *Pedicularis*, *Erigeron*, and *Taraxacum*) we receive the same impression: the arctic flora is a depauperate miscellany from various regions. Not only are arctic genera essentially unknown, but even sections and lesser species groups are scarce.

It appears probable that, as the arctic environment developed, the arctic regions were populated largely by alpine plants from nearby mountain ranges, by cool-temperate plants (especially those of bogs and marshes), and by plants from sea cliffs and beaches where exposure often induces a pseudo-alpine vegetation. This reconstruction visualizes the initial population of the Arctic, and its partial repopulation with each glacial retreat, by plants that were preadapted in varying degrees to an arctic existence, the initial adaptations later being modified within the Arctic.

Plants that penetrate the Arctic may be initially adapted in several ways. (1) They may be so largely preadapted, through evolution in alpine regions, as *Saxifraga oppositifolia* evolved in the Alps, that they quickly become fully and widely established when they reach the Arctic. (2) Plants that are phenotypically plastic may become conditioned (phenotypically adapted) on exposure to arctic conditions. Morphological conditioning is commonplace, and we shall see (Section II, C, 2, *b*) that physiological conditioning is also possible. (3) Following either of the preceding alternatives, plants become ecotypically (genetically) adapted. This process is probably often rapid. Characters that have been carried in the genotype without expression may be expressed, and subject to selection, under novel conditions. In addition to individual selection there may now be recombination with reinforcing genes until the character is expressed under any environment. This process, which Mayr (1963) has termed threshold selection, may be important in stimulating some of the comparatively abrupt adaptations that many plants seem to have made in penetrating the Arctic from a fluctuating subarctic environment. This phase of arctic botanical study is in its infancy, but one apparent example of this process will be discussed in Section II, C, 5.

C Gradation in arctic climate

The limits of the Arctic have been defined in various ways (see, e.g., Kimble and Good, 1955; Polunin, 1959), but for botanical purposes it is most convenient to regard the arctic tree line as the boundary between arctic and subarctic, for the sharpest biological discontinuity occurs at this point. The only conspicuously discordant region resulting from this definition is extreme southwest Greenland, where spruce thrives when planted and is naturally absent only because of the lack of seed, and where various boreal forest plants grow in the shade of tall willows and alders.

Although the Arctic may be conveniently zoned in several ways, we

inevitably have a continuous gradation of terrestrial climate from tree line to the limit of land, determined by latitude, altitude, topographic relief, cloud cover, precipitation, wind speed and direction, and marine circulation. Climatic delineation is accordingly complex, and we should use categories such as high and low arctic with discretion in any discussion of arctic adaptations, for in terms of plant development a high-arctic site may be far south of some low-arctic sites. A few examples will emphasize this point.

Great Whale River, on the southeast coast of Hudson Bay at 55° 17' N, is technically a forested site but the settlement is within a narrow coastal strip of tundra. In 1949 only five adventive plants could be found at the settlement, although one resident had kept, somewhat unsuccessfully, a vegetable garden for many years, and others had periodically tried to raise flowers or vegetables. All these adventives, aggressive weeds in the south, were very scarce and all but one were confined to the fenced garden areas. In a brief visit 10 years later no weeds were seen, which does not prove that they had been eliminated but indicates that they had not become aggressive. By contrast Hadač (1941) listed 52 species of adventive plants in Spitzbergen, some 23° of latitude further north. Admittedly the traffic into Spitzbergen has been much greater and has extended over a longer period than that into Great Whale River. However, it is still remarkable that so many weeds and cultivated plants have been able to establish themselves at such a latitude. The contrast seems due mainly to Spitzbergen being enveloped by the Gulf Stream, which ensures relatively mild winters and a long, if cool, summer, whereas Great Whale River lies immediately to the lee of Hudson Bay, where pack ice keeps the temperature low in spring and where killing frosts occur periodically in summer.

Provided that an arctic site possesses most of the important potential habitats, its flora of vascular plants correlates quite closely with its mean July temperature. Thus, if we have from a site either reasonably complete plant collections or several years' temperature records, we can compare its growth potential meaningfully with that of other stations, although barriers to dispersal may necessitate adjustment for some sites (Savile, 1964 *b*; Section II, D).

From latitude alone we can tell little about the flora of a locality. Table I compares the summer climate of three localities in Greenland and Ellesmere Island (Ella Ø, Central Peary Land, Hazen Camp), subject to warming by foehn winds descending from mountains and ice fields, with three localities in regions of low relief where winds sweep off cold water or pack ice with little modification. The latter three sites have been chosen in the knowledge that numbers of species have been eliminated from their regions since the end of the postglacial hypsithermal. Thus the totals approximately represent the potential for the present climate, and cannot be explained on the basis of there having been inadequate time for many plants to reach any locality.

Although the summer temperatures are not precise, owing to short records, the figures convincingly indicate the significance of summer as opposed to annual temperature regimes (Hazen Camp is exceptionally cold in winter) in governing the flora, and also show the importance of factors other than

TABLE I. Effect of summer temperature on size of flora

Locality	N latitude	July mean 0 C	No. of species of vascular plants
Ella Ø	72° 50'	ca. 9.0 ^a	184
Coral Harbour	64° 12'	7.8	169
Central Peary Land	82° 20'	ca. 6.4 ^b	106
Hazen Camp	81° 49'	ca. 6.0 ^c	105 ^d
Resolute	74° 41'	4.3	70
Isachsen	79° 47'	3.6 ^e	48

^a9.6 C in single, apparently warm season (Sorensen, 1941).

^bBased on 2 years records (Holmen, 1957).

^cBased on 7 years records.

^dProbably about 115 species in whole valley of L. Hazen.

^eBased on 13 years records to 1960; cold summers in 1963, 1964, and 1965 have reduced the mean nearly to 3.0 C.

latitude in governing climate. The rapid attenuation of the flora with increasing altitude in the high arctic, even when water supply is not limiting (Savile, 1959, p. 972), further emphasizes the importance of summer temperature.

In this paper the terms high and low arctic will be used without any great precision to distinguish regions of very severe climate, devoid of shrubs and with much unoccupied ground, from those of more benign climate, often but not always close to the tree line, in which shrubs are frequent and ground cover is usually nearly complete except on ridges of rock or gravel.

D Characteristics of arctic environment important to plants

It may be helpful to review briefly the physical factors of the environment that clearly affect terrestrial flowering plants. Most factors affect other plants to some degree. We are far from an adequate understanding of the ways in which plants adapt to these factors, and often cannot completely separate the effects of two of them. If a device operates against two factors, it may be difficult to tell which originally stimulated the adaptation or even which factor is currently the more important.

1 Low winter temperature

In general, all parts of terrestrial plants must freeze with impunity. See Section II, B.

2 Low summer temperature

Direct effects are depression of metabolic rate and intermittent freezing of tissues (Sections II, C, 1 and 2). Indirect effects include reduced activity by pollinating insects. Related to low summer temperature is the shallow active soil layer, which limits the effective depth of roots. In partial compensation, the frozen layer reduces water loss.

3 Short summer

Coupled with the low metabolic rate imposed by low temperature, the short growing period imposes a critical problem for most flowering plants, which must complete flowering and fruiting in a single season. See Section II, C, 3.

4 Strong wind

Wind causes direct damage through flailing, sand abrasion, and especially desiccation and snow abrasion in winter (Section II, B, 2). Indirectly it reduces the activity of pollinating insects. On the credit side, wind greatly assists dispersal (Section II, D).

5 Long photoperiod

Arctic plants must be adapted to a long photoperiod or be insensitive to day length. See Section II, C, 5.

6 Low light intensity

The long photoperiod is partly offset by low light intensity, but generally the intensity must be substantially higher than that on a forest floor. It is probably seldom critical except for submerged aquatic plants. See Section III, D.

7 Low nitrogen supply

Most arctic soils have very low nitrogen contents, but nitrogen is not always a limiting factor in growth. See Sections II, C, 6 and III, D.

8 Low precipitation

Summer rainfall is low in much of the Arctic and often limits plant growth. If winter snowfall is also low, growth may be largely confined to areas of runoff from snowdrifts or the active layer on mountain slopes. In sheltered fiords and deep valleys summer aridity may be extremely severe.

9 Simple population structure and low density

Although not a part of the physical environment, these characteristics result from it and may profoundly affect many plants. The low density of birds and mammals makes some temperate dispersal devices ineffective. The weakly filled habitats, with few species and much unoccupied ground, increase the likelihood of introduced seeds establishing the species, and thus promote rapid spread. These points will be discussed further in Sections II, C, 4 and II, D.

II Flowering Plants

A Introduction

Flowering plants are especially notable for their great phenotypic plasticity, and this characteristic is strongly developed in many arctic species. Although most flowering plants are strongly mobile as species, the individuals are stationary. Because they cannot retreat from environmental vicissitudes, plasticity in both structure and physiology are of obvious value to plants in a severe and variable climate. Unfortunately, our awareness of such pronounced phenotypic variation may cause us to overlook very similar genetic variation. The latter may not be recognized unless the plants are grown in a controlled environment. We now realize that genetic dwarfing is not uncommon in high-arctic populations, but our knowledge is still fragmentary in this field.

The exact causes of most phenotypic changes are obscure and may prove to be complex. Indeed the complexity may prevent us from recognizing them as being nongenetic, and thus lead us into taxonomic difficulties. Fisher (1965) has shown that in the temperate grass, *Poa pratensis*, there are three distinct stages of development in the rhizomes, during which they have quite different physiological responses. It is possible that some such behavior may partly explain the puzzling local variations that we often see in the widely ranging arctic species *Poa arctica*. Until many more of these plants are grown under controlled conditions, we cannot completely understand either their adaptations or their taxonomy.

In the following sections it has been necessary to discuss observations under whatever environmental element appears most appropriate but it must be realized that there may be a substantial overlap. Thus low summer temperature aggravates the main problem that is discussed under short season: the completion of fruiting before the onset of winter. We cannot fully separate the effects of snow abrasion and desiccation in winter, for the former must aggravate the latter, and in practice we must treat them as a single phenomenon. Similarly a pulvinate habit both protects from abrasion and influences the microclimate.

A substantial literature has accumulated on the physiology of arctic and alpine plants, which has been reviewed by Bliss (1962) and Larsen (1964). Some of these observations are discussed in succeeding sections. Much of the work, however, does not directly bear upon arctic adaptations and, inevitably, most of the experimental work has been done in alpine situations, which are generally more accessible than arctic ones. One of the most pressing needs in arctic biology is for broadly based studies in plant physiology, relating growth and morphology to light, temperature, water, and nitrogen supply, and investigating the basis of summer coldhardiness.

B Winter survival

1 Winterhardiness

It might be thought that winterhardiness is the most important of all arctic adaptations in plants, but it is very doubtful whether arctic plants differ significantly from alpine or temperate continental species in this respect. A detailed consideration of winterhardiness in plants is thus beyond the scope of this paper. For a general review of the field the reader is referred to Levitt (1956). Numerous modifications in the physiology of the cell help to increase hardiness, but no complete picture of the process is yet available. It has been suggested that only extracellular freezing can be tolerated, but it appears both that extracellular freezing can be accompanied by injury and that in some tissues internal freezing can be tolerated. The actual mechanism of protoplasmic injury is not yet settled. Levitt (1962) has proposed that frost injury is due to denaturation of the structural proteins of protoplasm through an unfolding process caused by local stresses at the time of freezing, and that the stresses are applied through the formation of disulfide bonds between proteins as water is removed. It is suggested that hardiness results from prevention of the formation of new disulfide bonds both by physical means (undercooling, increased permeability, increased osmotic concentration, reduced moisture content before freezing) and by biochemical means through one or more of several possible mechanisms. Siminovitch et al. (1967) present strong evidence that a marked increase in the protoplasmic content of the cell is involved in the mechanism of freezing resistance. Siminovitch et al. (1969) have further shown that an increase in membrane phospholipids accompanies hardening, and it is believed to contribute materially to total coldhardiness.

From our standpoint, the important consideration is that essentially all cells of hardy temperate plants exposed to the extreme minimum temperatures of a continental winter, approximately -30°C to -35°C , are frozen, with little or no liquid water remaining. It thus appears that subjection to the even greater extremes of cold in the Arctic (-45°C to -50°C or occasionally even lower) can have little or no effect on such plants. In fact Siminovitch et al. (1967) have demonstrated that phloem tissues of black locust, *Robinia pseudo-acacia*, in the hardened state withstand the temperature of liquid nitrogen, -192°C . We accordingly cannot class winterhardiness as a distinctive attribute of arctic plants. If there is any distinction it is perhaps that in many arctic plants the shallow root system with negligible snow cover is subjected to approximately the same temperature as the aerial organs, whereas in many temperate plants the roots are so protected by snow or litter that they scarcely go below 0°C .

2 Snow abrasion and desiccation

The most serious form of winter injury to arctic plants is unquestionably that due to abrasion by wind-driven snow particles. This seems to be a combination of mechanical injury and desiccation; and desiccation may be doubly important in winter because lost water cannot be replaced until the ground starts to thaw. The two types of injury are seldom separable and will

be considered jointly. Some wind damage occurs in summer through flailing or sand abrasion, but it is generally very minor.

It is essential that we understand the mechanics of abrasion by wind-blown snow, for this inadequately appreciated process plays a substantial part in controlling the location of the arctic tree line in much of North America at least (Savile, 1963*b*) and in governing the abundance and distribution of many plants within the Arctic. The first snowfalls of autumn may consist of large, soft flakes such as are familiar in temperate regions. This snow may become compacted into a protective layer, but often it is inadequate to cover more than scattered depressions. In oceanic regions, such as southwest Greenland and southeast Baffin Island, which are close to permanently open water, much snow of this type may fall later in the winter and form a good protective blanket. In more continental regions, however, and here we must include most of the Canadian Arctic Archipelago whose islands are surrounded by essentially unbroken ice for 9 months in the year, the cold is so intense and the moisture content of the air so low that much of the snow consists of small, hard and sharp crystals, probably often mere hexagonal needles or plates (Fig. 1). These crystals, driven on winter gales, are severely abrasive. If we examine

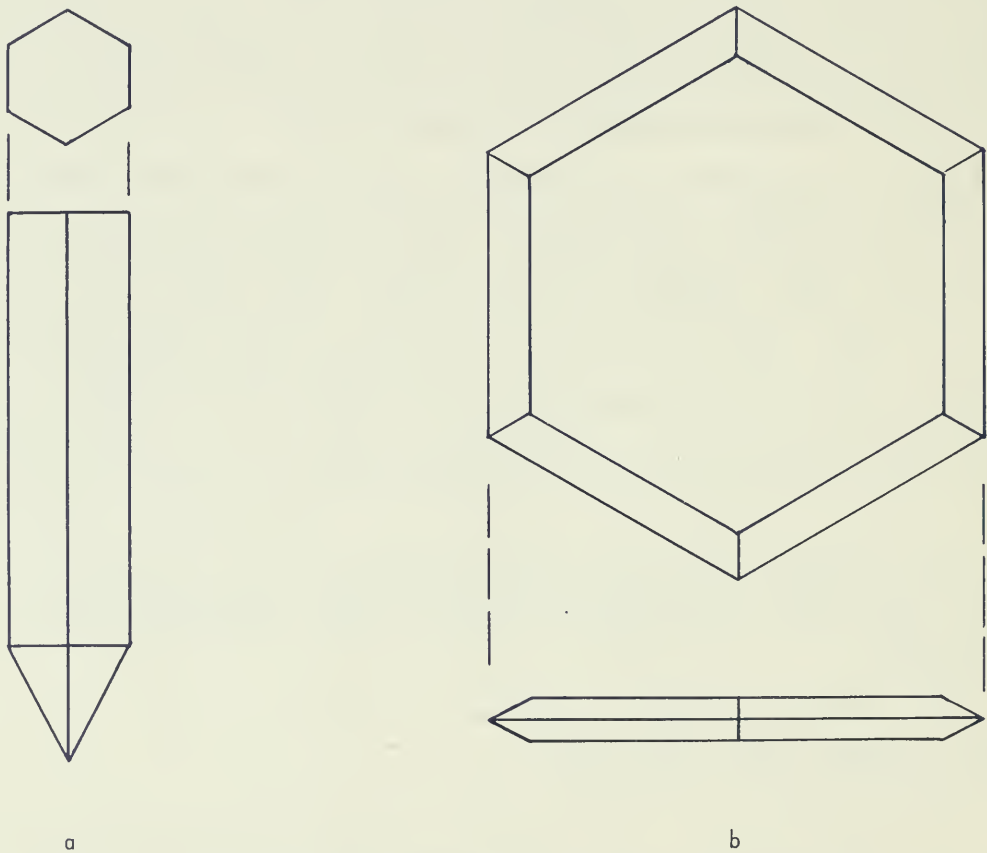


Fig. 1. Simple abrasive ice crystals formed at very low temperatures: (*a*) Hexagonal needle, such as produces parhelia, halos, and other refractive phenomena; (*b*) Hexagonal plate, such as produces sun pillars.

isolated spruce trees, *Picea glauca* or *P. mariana*, at the tree line in regions of strong winds, such as the coasts of Hudson Bay, we find that the branches within 30 cm or so of the ground are well developed. Above this height we see either no growth or an essentially bare trunk for 1–2 m. If the tree survives beyond this height, it then throws out increasing numbers of normal branches. The lowest branches are protected by the soft early snow. For the next meter or more abrasion kills most or all of the lateral buds, but the terminal bud, surrounded by a whorl of laterals and needles, receives some protection and may survive (Fig. 2, *a*). Finally, above the level at which much snow is carried by the wind, lateral branches begin to persist. Once a few laterals survive, they cause sufficient eddying to provide mutual protection, growth becomes relatively unimpeded and we get the mop-head effect familiar at all windswept tree-line sites (Fig. 2, *b*). This type of development clearly shows that the injury is caused by snow and wind in combination, for the wind velocity is greater above the drift than in it.

At the tree line, and in isolated areas beyond it in the shelter of ridges or stream banks, spruce trees persist by layering and sending up a group of secondary trunks. Bryson et al. (1965) have shown that on the Keewatin barrens such isolated trees set no seed but have persisted since the retreat of the forest, in some instances since the end of the Hypsithermal Interval. Each of the trunks plays its part in reducing abrasion by causing eddies, which strongly reduce wind velocity. At tree line the resultant mutual protection

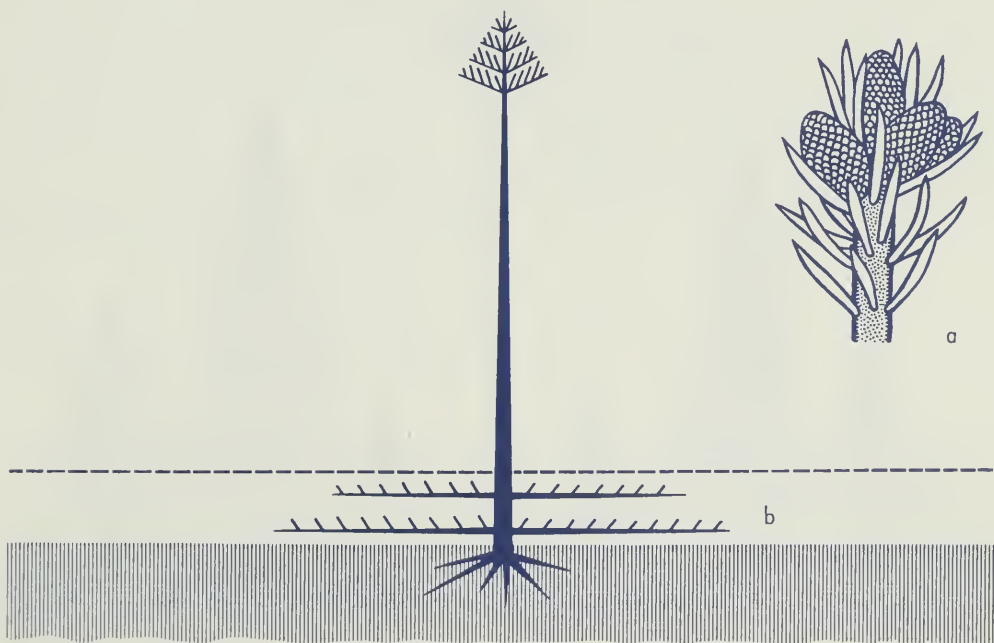


Fig. 2. (*a*) Growing point of spruce, showing how whorled lateral buds protect terminal bud. (*b*) Form of spruce commonly seen at wind-swept sites. Lowest branches are protected by soft snow of early winter. Above this level, lateral buds are killed by snow abrasion until the limit of severe drifting is reached, where survival of some branches causes eddying, which reduces wind speed.

may be sufficient to allow the development of sturdy and compact clonal colonies (Fig. 3).

This abrasion mechanism helps to explain the abruptness of the arctic tree line in some regions where it may be the most important of the many factors that limit the advance of spruce (Savile, 1963*b*). Where abrasion is a serious factor, the degree of abrasion is closely correlated with the density of growth. If the density falls below a critical figure, killing through abrasion may be inevitable. But we must remember that other factors, such as early defoliation of small spruce trees growing up through a carpet of *Ledum* or *Empetrum*, which are alternate hosts of spruce needle rusts, *Chrysomyxa* spp., may initially control the density.

We may say that the principal adaptation of spruce to snow abrasion lies in its layering ability, upon which compound growth is dependent, but this device is insufficient to allow its development, as opposed to mere persistence, within the Arctic.

In our context we are more concerned with snow abrasion north of the tree line than at it. We must accordingly consider its effect on arctic shrubs and herbs, which is generally more difficult to analyze than the effect on spruce. Observations made many years ago at Chesterfield, and presented in part by Savile and Calder (1952), throw some light upon the effect on shrubs. Chesterfield, despite its relatively low latitude ($63^{\circ} 21' N$), is nearly 500 km beyond the tree line and has the severest January wind-chill figure for any

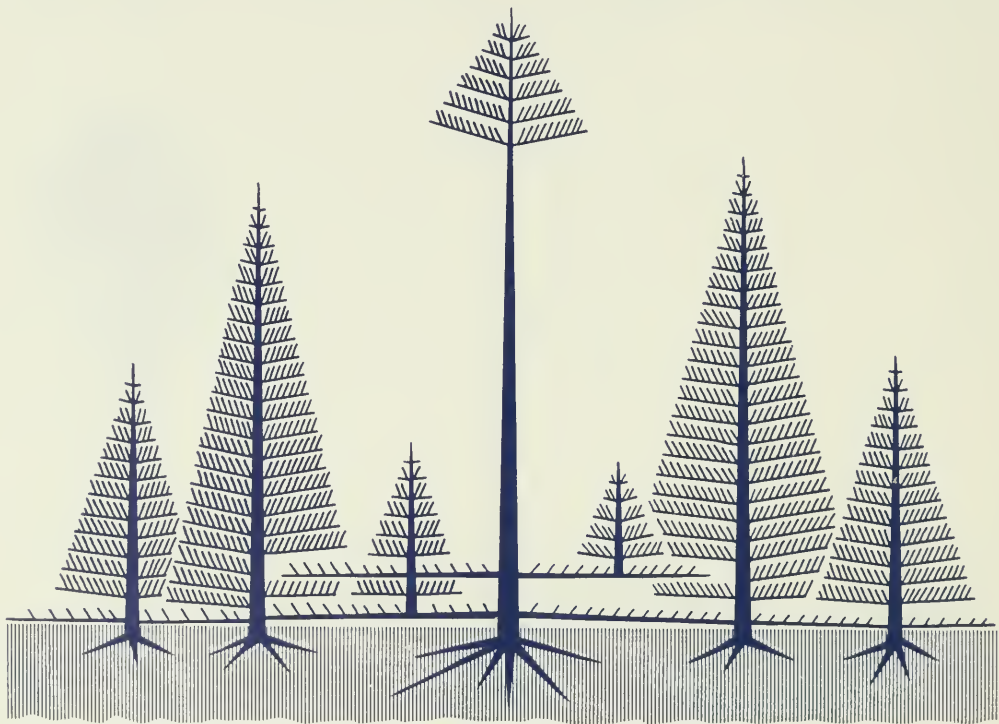


Fig. 3. Clonal spruce grove resulting from layering of basal branches. Grouped trunks afford mutual protection from snow abrasion by reducing wind velocity through eddying.

Canadian station. The combination of severe cold (with its effect on snow structure) and strong winds ensures abundant abrasion, which is reflected in the stature of the shrubs. Dwarf birch, *Betula glandulosa*, is seldom more than 15 cm high. Some of the shrubby species of willow, *Salix*, attain a height of 1 m or more when they grow among large moraine boulders, but such sites are rare in this region of low relief and most plants of these species are less than 15 cm high. In fact the more exposed plants of some technically shrubby willows are completely prostrate and their habit so closely simulates that of the genetically prostrate species, such as *S. arctica*, except for their failure to form adventitious roots, that it considerably puzzled a taxonomist to whom some specimens were referred. This phenotypic reaction, itself a minor adaptation, clearly indicates the incomplete adaptation of such shrubs to severe arctic conditions. Indeed the weak development or virtual absence of a shrub tundra from northeast Mackenzie District across Keewatin to northernmost Quebec seems to be primarily due to snow abrasion in this zone of strong winds (Savile, 1968). This region contrasts markedly with much of Alaska, Yukon, western Mackenzie, and the Siberian arctic, in which shrub tundra is widely and strongly developed. The reaction to abrasion seems to be due to selective killing of the more exposed winter buds and young twigs, and is of interest in view of the buds of willows being rather elaborately covered by a single firm scale formed from two coalescent prefolia. Crowded twigs of deciduous shrubs must provide appreciable mutual protection, but probably much less than that for equally crowded spruce branches, whose needles normally persist for 2 years or more. The mutual protection allows the strong development of shrub tundra in regions of moderate wind or deep, soft snow, but it is clearly inadequate in regions of strong wind and abrasive snow.

The genetically prostrate willows, of which *Salix arctica* is the most successful representative, reaching the northern limit of land and being almost circumpolar, are the woody plants best adapted to severe arctic conditions, but it must be noted that they avoid abrasion rather than withstand it. Indeed, the appearance of *S. arctica* on very severe sites emphasizes the appropriateness of a poet's description:

“. . . crawling under rocks
grovelling among the lichens
bending and curling to escape”*

Although injury from snow abrasion is less spectacular to herbs and subshrubs in the Arctic than that to erect shrubs, the potential injury is as great or greater, for the growing points are frequently unprotected by hard bud scales. Those parts of the high arctic with a continental climate and without mountainous terrain are frequently subjected to severe abrasion because the snow cover is often very light. Published wind data for arctic stations may be very misleading, for prolonged calms, during anticyclones with marked ground-level inversions, alternate with gales. It is not unusual for

*From *Trees at the Arctic Circle* by Al Purdy, quoted by courtesy of the author.

a gale with an average wind speed of 18 m/sec (40 mph) to last for more than 24 hr (Section II, D and Table III). The snow tends to fill depressions and to smooth contours. Consequently turbulence at ground level is less than over terrain impeded by trees or high ground relief, and wind velocity close to the ground is only slightly reduced.

Some plants of the high arctic avoid damage by being confined to depressions that are quickly filled by drifted snow in early winter. Various marsh plants fall in this category. Among mesophytes the evergreen subshrub *Cassiope tetragona* is an excellent example. In oceanic low-arctic situations it may occur quite widely, but in dry, high-arctic locations it is strictly confined to concave slopes to leeward of the prevailing winter wind, or at least of the wind that brings most snow. Within such sites it flourishes at very high latitudes, but shoots that project beyond the snow cover are generally killed promptly. The shoots of *C. tetragona* produce very few leaves per annum, for the leaves normally function for four to five seasons. A single exposure to abrasion will therefore reduce the vigor of a plant for several years, which may prove fatal.

Plants of other habitats must generally withstand abrasion. Rocky ridges and beach crests serve as venturis when packed snow has smoothed their contours (Fig. 5, *a*), and the wind velocity across them may be considerably enhanced. Consequently they may be virtually bare of snow all winter. A col between two rounded hills also serves as the throat of a venturi when the wind direction is normal to it, and the wind passing through it may remove soil and gravel from its surface. But even a level plain may be swept bare of snow and suffer some soil erosion. We might expect the winter buds of arctic plants to be particularly well protected by hard scales, but this is not generally true. In fact Sørensen (1941) showed clearly that active bud protection (the possession of true bud scales, fused young leaves or fully protective ochreae) is negatively correlated with frequency of occurrence in the high arctic. High-arctic species (in the ecological sense; Section I, C) generally have passive protection, such as old leaves, or are unprotected, but the species with unprotected buds are predominantly plants of late snow patches, which are thoroughly protected by snow throughout the winter. Heavy bud scales are actually a hindrance to rapid spring development and thus are generally inadapative in the very short season of the high arctic (Section II, C, 3, *a*). The negative correlation between bud protection and latitude may even be seen within a family. Of arctic Caryophyllaceae, only *Arenaria* (*Honckenya*) *peploides* has fully developed bud scales and it is predominantly low-arctic and subarctic. The species of *Arenaria*, *Cerastium*, and *Stellaria* that are frequent in the high arctic have no definite winter buds, the shoot apex looking much the same throughout the year. Clearly desiccation of uninjured tissues is not a critical problem for these plants. They do, however, require protection from abrasion. The plants grow in dense, prostrate mats (e.g., *Saxifraga oppositifolia*, *Stellaria* spp.), or in rosettes (*Draba*, *Potentilla*, *Saxifraga*) or cushions (*Silene acaulis*), with no living parts projecting above the general surface. Much of this general surface is made up of old leaves, surrounding the growing points in successive whorls of various ages, the outermost ones generally several years old and often reduced to

cartilaginous petioles and midribs or mere vascular strands. All these parts not only directly shield the growing points from abrasion but are mutually protective, causing, on a small scale, eddies that sharply reduce wind velocity at the surface of the rosette, and allowing some of the snow particles to be deposited gently in a protective layer rather than blasting past as lethal agents. In addition, the dead fruiting stems of several years' duration often project above the general surface of the plant and cause further eddying. Sometimes, as in the nearctic *Saxifraga tricuspidata*, a pronounced xerophyte that is often found on rocky ridges or beach crests, the leaves are evergreen. In this species the leaves function for about 3 years, but they are also strongly cartilaginous and are tipped by three rigid spines. The dead leaves remain in place for several additional years, their tips giving additional protection to the winter buds (Fig. 4). This effective protection, in which most of the abrasion operates upon dead leaves or the hard apical spines (which serve also to discourage grazing animals), allows *S. tricuspidata* to survive on exposed rock and gravel ridges provided that these sites receive some rainfall in summer. The closely related *S. bronchialis* of Siberia occupies similar habitats.

The monocotyledons of exposed sites (Gramineae, Cyperaceae, and Junceae) generally form dense tussocks, in which leaves and fruiting stalks persist for several years and effectively protect the sheathed growing points. In a few arctic grasses we occasionally see a bleached wedge in the panicle, indicating premature emergence from the protecting leaves. These were at first thought to be due to frost injury in early summer, but examination proves death to have occurred at a very early stage of development, and it is evidently a sign of excessive development in autumn in species that are somewhat aperiodic (Section II, C, 3, *a*). The part of the panicle that is not

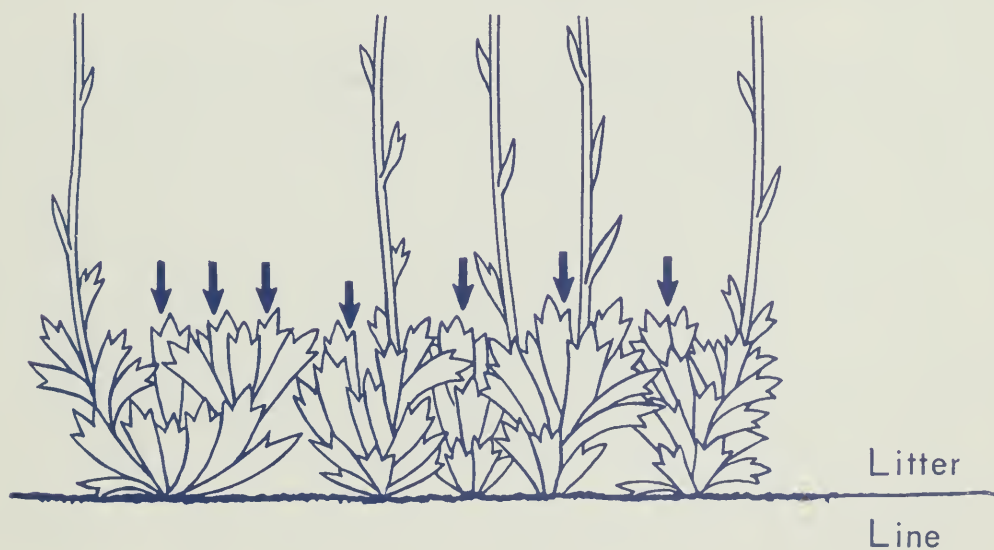


Fig. 4. Part of clump of *Saxifraga tricuspidata*, showing how growing points, marked by arrows, are protected by old leaves and stems. For clarity several stems and many leaves have been omitted.

fully protected by leaves and leaf sheaths during the winter is evidently killed by abrasion, for the leaf covering could have little effect in protecting against the sustained cold of winter. It should be noted, however, that some grasses of dry and generally exposed habitats, such as *Festuca brachyphylla*, *Agropyron violaceum*, and *Poa hartzii*, were shown by Sørensen (1941) to be strictly periodic and to winter in a very early stage of development, which minimizes the risk of the culm elongating enough to be abraded.

The persistence of chaffy or cartilaginous leaves, sheaths, or stems for several years is possible in the Arctic because of the slow and often negligible activity of bacteria, which would cause rapid collapse of these organs in temperate regions.

C Summer survival

1 Frost resistance

If flowering or vegetative shoots of arctic plants were seriously injured by summer frosts, which often occur repeatedly in every month, the plants would seldom mature seeds. Temperate species that sparingly invade the Arctic often lack the ability to withstand freezing in summer. I have seen *Lathyrus japonicus*, and to a lesser degree other plants, killed back nearly to the ground by frosts in late July at the tree line, but I have never seen such damage to true arctic plants even under substantially more severe conditions. It is a commonplace that many arctic plants may be brittle with frost, sheathed in ice or buried in snow, even during the period of most rapid growth, and yet resume growth without injury as soon as the weather permits. In many such plants it is obvious that the tissues freeze with impunity, but in plants with woody stems and coriaceous leaves we cannot tell by inspection whether the tissues freeze or resist freezing.

Arctic plants must therefore be at least substantially cold resistant all summer, but they must be able to metabolize normally in the hardy state, to avoid delay in resuming growth. This process seems to be distinct from that seen in hardy temperate plants, which must gradually attain the hardy state at the end of summer through a series of metabolic changes, and which, as a safeguard against injury after a winter thaw, emerge from dormancy very slowly. The arctic plants seem to bear more resemblance in this respect to alpine plants in which diel temperature fluctuations become greater with lessening latitude until, at the equator, we find "summer every day and winter every night" (Hedberg, 1964). In the Arctic the diel fluctuations are generally small, but the total growing time is so limited that delay in breaking dormancy would often be fatal.

The mechanism of summer coldhardiness is still unknown. It appears to be a fruitful field for investigation, and it may even throw light on the precise mechanism of temperate winterhardiness, which has received considerably more attention.

Elaborate morphological adaptations have been developed in some large Afroalpine plants to provide insulation of conducting tissues that might

otherwise remain frozen after the leaves resume activity at sunrise (Hedberg, 1964). We see no such parallel in the Arctic, where the diel temperature range is much less and the plants are so small that leaves and stems must freeze and thaw almost simultaneously.

2 Adaptations to low temperature

a Physical adaptations. On sunny days the temperature at and very close to the ground is usually far above the air temperature as measured in the standard thermometer screen. The majority of arctic plants form basal rosettes or cushions or are low-spreading to prostrate in habit. By such means most of their metabolic activity is carried on in the most favorable temperature zone.

The formation of dense mats, rosettes, and cushions reduces wind movement among the leaves, as noted in Section II, B. On sunny days warm air is thus trapped in the interstices of such plants. The degree of warming depends largely on the color of the plant parts. If abundant red anthocyanin is superimposed upon green, leaves and shoots become a deep purple approaching black. When deep pigmentation is combined with dense growth, as in *Silene acaulis* or *Saxifraga caespitosa*, the rise in temperature of the organs and trapped air may be spectacular. Porsild (1951) cited Wulff as recording 3.5 C in a saxifrage clump in northern Greenland when the air temperature was -12 C. At the same time the temperature in a very dark clump of mosses was 10 C. The effect of pigmentation on flower temperatures was studied by Tikhomirov et al. (1960), who found that when the temperature inside white flowers was 0.7 C to 2.0 C higher than the adjacent air, it was 3.4 C to 4.2 C higher in blue flowers. Bliss (1962) summarizes other observations in this field. It is notable that many species with white or yellow petals, adaptive to pollination by Diptera (Section II, C, 3, *b*), such as *Saxifraga cernua* and *S. flagellaris*, possess abundant anthocyanin in their leaves, stems, and sepals. Thus their metabolic tissues are usually substantially above air temperature.

Deeply pigmented plants may absorb enough light to commence growth under the snow in spring. Such heating seems to be important when the snow is deep enough to allow considerable thawing and freezing into a macrocrystalline form, which transmits a high percentage of light but, through the greenhouse effect, traps almost all the outgoing infrared radiation. It is worth noting that Shamurin (1966) considered the greenhouse effect sufficiently important at Tiksi Bay, where snow cover is generally ample, to justify recognition of a "greenhouse-spring" subseason of about 15 days duration.

The amount of pigment, or perhaps its occurrence in colored rather than leuco form, may be genetically controlled, as in *Oxyria digyna*, in which color is generally rather constant within a single clonal colony, but often varies sharply between adjacent or even overlapping colonies. At stations with very cold summers, such as Isachsen, all *Oxyria* plants may be deeply pigmented, but it is not known whether the effect is partly phenotypic or entirely due to genetic selection. In many species, however, the control seems to be largely environmental. *Saxifraga caespitosa* may be light green throughout in a warm, sheltered site, but in the same colony progressively increasing pigmentation is

seen as one passes to more exposed sites. Under extreme conditions, the flowering stems and calyces are almost black, the change being correlated with decrease in size. Heavy pigmentation is presumably less advantageous in alpine regions, where radiational losses at night are significant, than in the Arctic.

Phenotypic dwarfing may be largely the result of snow abrasion, as in the shrubby willows, but in herbs it commonly results from low summer temperature and occasionally lack of water or nitrogen. Phenotypic dwarfing must often be strongly adaptive as a prompt reaction to low temperature, for it enables a small quantity of seed to be matured with certainty in almost every year, even on severely exposed sites where warming of the lowest stratum of air is only moderate. Tall flowering stems on such sites would use up a large amount of carbohydrate and often fail to produce any seed. *Saxifraga caespitosa* in the Canadian Arctic Archipelago provides a good example of this type of adaptation. On a benign, sheltered site it grows often to 12 and occasionally 18 cm in height with one to three flowers per stem and the flowers 8 to 10 mm long. On exposed sites a few meters away the plants may be less than 8 cm high with solitary flowers 5 to 8 mm long, and, as noted above, deep pigmentation. These phenotypic changes may not be equally marked in all populations of this variable species. Such phenotypic plasticity clearly adapts a species both to a range of environments and to highly irregular summer climates. The occurrence of *S. cernua* over a range of 35° of latitude in North America, with apparently little genetic variation, must be partly due to its marked phenotypic plasticity, but it may also contain local races whose existence is masked by its plasticity.

A related phenomenon, which is at least largely phenotypic, is seen in various rosette-forming herbs, including *Papaver radicum*,* *Draba* spp., and *Potentilla hyperbatica*, at places with severe summer climates, such as Isachsen. On exposed sites at such places the flower buds often open while still touching the basal rosette. The scapes later elongate to varying degrees during the summer, while the seeds are developing. The delayed elongation, however, allows more rapid development up to anthesis than would otherwise be possible (as well as encouraging cross-pollination under conditions that limit insect activity) by holding the flowers within the warmest stratum of air.

Genetic dwarfing at the species level is quite common, especially in species confined to the high arctic (Section I, C). These plants change little in stature when grown under temperate conditions, even when more water and nitrogen are available than they receive in the Arctic. It might be argued that such plants became genetically dwarfed prior to invading the Arctic, being merely preadapted, although distribution data and taxonomic relationships often strongly suggest the contrary. However, there are various recorded cases of genetically dwarfed alpine or coastal races of erect species of plants, which preserve their prostrate habit in sheltered situations. Clausen (1965) has

*The arctic poppies are a complex involving several chromosome numbers. Throughout this paper, *Papaver radicum* is used in an inclusive sense because many of the plants on which observations are based cannot be delimited precisely.

recently reviewed this topic and gives several examples among willows and conifers. Although alpine rather than arctic, his examples show how such races evolve under selective pressure. Observations at the arctic tree line on the coast of Hudson Bay do not suggest appreciable genetic changes in the form of any trees or shrubs. Probably there is less opportunity for extensive accumulation of appropriate genes in this region, for climatic fluctuations have periodically wiped out populations over great areas, eliminating potentially incipient races. The situation could conceivably be different in Alaska and Yukon, where populations have survived in intermontane refugia, but several colleagues who have worked in the region report no indication of prostrate forms such as Clausen records from farther south.

A good example of a genetically dwarfed race of a wide-ranging herb is seen in *Cardamine bellidifolia*. Although most specimens from predominantly alpine situations in Alaska, Yukon, and British Columbia are barely distinguishable from specimens collected in Ellesmere and Axel Heiberg islands, G. A. Mulligan (unpublished data) has shown that, when plants from seed collected in the two areas are grown to maturity in temperate conditions, the distinctions are pronounced. The alpine plants are tall and have large, irregular leaves, but those from high-arctic seed remain as small as plants on the more desirable sites at 80° to 82° N, and have small, regular leaves. Thus the alpine plants retain the potentiality for great growth and increased seed production that may be realized in warm summers or on favorable sites such as open talus slopes below the general tree line. The arctic plants are genetically dwarfed, ensuring that no flowers are produced so far from the ground that reduced temperature is likely to prevent the production of seed. *Cardamine bellidifolia* is an instructive example because the northern population probably segregated, in or near Peary Land, during or immediately before the last glaciation. Presumably the two populations were amply connected during the preceding interglacial.

Although genetic dwarfing limits potential seed production and may reduce seed dispersal, the compensating advantage of practically guaranteed seed maturation seems to be adaptive on balance in the high arctic, where premature killing of tall flowering stems drains food reserves and prevents seed formation. In the low arctic such dwarfing is less advantageous, and may be deleterious on warm sites where air temperature near the ground may sometimes rise above the optimum for growth. Near the arctic tree line, where habitats are often fully occupied and competition between species becomes important, greater genetic plasticity in stature than is possessed by many high-arctic plants must be strongly adaptive. It is apparent that genetic dwarfing must be added to the factors that Russell (1940) cites as keeping growth below the limits of carbon assimilation (Section II, C, 2, *b*).

Dense pubescence is a common characteristic of mid-latitude alpine plants and, as Hedberg (1964) has pointed out, it is very pronounced in the Afroalpine flora on peaks at or close to the equator. Its principal function on surfaces exposed to the sun seems to be protection from intense insolation at high altitudes. Hedberg noted that densely pubescent plants are commoner on the drier eastern peaks than on Ruwenzori where cloud cover is frequent.

However, as Hedberg and others have suggested, heavy pubescence must also serve to trap outgoing radiation of long wavelengths, and it is thus doubly important at low latitudes where heat loss at night is critical. I suspect that most of the arctic plants that are densely pubescent throughout, such as *Antennaria* spp., have been derived relatively recently and with little genetic change from alpine regions. Probably a dense tomentum is not appreciably important in the Arctic as a device for temperature control. The lanate leaves of a rosette of *Potentilla* may be secondarily adaptive in protecting winter buds from abrasion. When heavy pubescence is largely confined to the lower leaf surface, as in *Dryas*, it probably functions principally in limiting water loss by reducing air circulation close to the stomata.

It may be significant that *Potentilla hyparctica*, the only species of its genus found on Ellef Ringnes and adjacent islands, bears only long, straight "guard" hairs, and lacks the dense tomentum of several other arctic species. In this region water loss is seldom a problem and the prevailing low temperatures make a shield against incoming radiation decidedly inadapative. *P. hyparctica* prefers mesic habitats and is scarce or absent in arid areas, but flowers and fruits at temperatures that are low even by arctic standards. Its pubescence is of the type seen on catkins of *Salix arctica* and some other willows. The hairs do not appear white by reflected light but are essentially transparent. It is probable that they exercise a pronounced greenhouse effect, passing most incoming light but trapping the outgoing infrared radiation. Such a device to speed leaf and catkin development of *Salix arctica* and other species of high latitudes, early in the season while the air temperature is still very low, seems to be clearly adaptive. Krog (1955) found that normal willow catkins with transparent hairs reached higher temperatures in the sun than even clipped and blackened ones, indicating that the greenhouse effect may be very important. But we must remember that, below the hairs, the catkin elements generally are deeply pigmented with anthocyanin, which assists in heat absorption.

Hocking and Sharplin (1965) have demonstrated that within some parabolic-shaped flowers that turn to face the sun, notably *Papaver* and *Dryas*, the temperature may be raised by several degrees, owing to concentration of the sun's rays at the focus, and that insects bask in these flowers. These solar heaters, which combine controlled shape and a sun-tracking mechanism, may have become perfected through attracting potential pollinators or through speeding up maturation of the gynoecium, which lies approximately at the focus. It is probable that both functions are performed to some degree. It should be noted that the petals of *Dryas*, *Papaver*, *Ranunculus*, and *Potentilla*, among others, generally persist several days beyond anthesis in the Arctic, but perhaps only because of low temperature rather than through genetic modifications.

b Physiological adaptations. We have little definite information on actual growth rates in the Arctic and on the metabolic efficiency of arctic plants at low temperatures. Rodin and Bazilevich (1964) have shown that productivity in the Arctic, whether measured by biomass, quantity of litter, or other means, is much less than in any other vegetation zone not extremely deficient in

water. This very low productivity is partly due to low temperature, but short growing season, limited nitrogen supply, and other factors may contribute to it. All arctic plants must obviously have some ability to metabolize effectively at low temperatures. Their ability may be actual adaptation to cold (with peak productivity at an unusually low temperature) or may be simply cold tolerance (with nearly optimum growth over a wide temperature range). Cold adaptation is not necessarily wholly genetic, but is partly conditioned in alpine and montane plants, and the same may be true in the Arctic. Mooney et al. (1964) tested plants from high and low elevations in a uniform environment and found that those from high elevations were generally adapted to maximum photosynthesis at lower temperatures than those from low elevations. The alpine plants had the lowest photosynthesis-to-respiration ratios, which accords with the belief that a high respiration rate is adaptive to a cold climate. However, Mooney and West (1964) subjected plants from various warmer vegetation zones to subalpine conditions for a few weeks. All became acclimated to lower than normal temperatures, as indicated by a shift in peak photosynthesis. This finding indicates how cautious we must be in assuming genetic adaptations to arctic conditions from inadequately controlled tests. The findings of Mooney and West are doubly interesting because they suggest a way in which temperate plants may have established arctic bridgeheads. A plant possessing the property of conditioning its peak metabolic rate to low temperatures may well spread a short distance into the Arctic and maintain itself until genes adaptive to the new conditions begin to accumulate; or, probably more often, genes unexpressed in the original conditions may now be expressed and become subject to selection. The latter alternative would be a case of threshold selection (Mayr, 1963).

Warren Wilson (1964) compared radial growth of stems of *Salix arctica* at Resolute (ca. 75° N, July mean 4.3 C) with the same species in east Greenland (ca. 74° N, July mean probably ca. 8 C). (The temperatures given are those of the standard thermometer screen, and exact correlation with temperature in the growth zone would demand identical sunshine and wind conditions.) Growth in east Greenland was three times that at Resolute, where, it may be noted, growth of this species is luxuriant in comparison with that at Isachsen (see Table I) where it is rare and apparently at its climatic limit. Warren Wilson showed that other woody plants at low-arctic and subarctic sites have radial growth 6 to 15 times, and temperate plants approximately 30 times, that of the Resolute plants. Even this prostrate willow, which is extremely widespread in the Arctic and is probably better adapted to the whole range of arctic conditions than any other woody plant, is far from completely adapted to high-arctic temperatures in its metabolism.

Mooney and Billings (1961) made detailed physiological and morphological comparisons of arctic and mid-latitude alpine populations of *Oxyria digyna*. It should be noted that, on morphological grounds, their material falls into two populations: one arctic, extending south to southern British Columbia, which is freely rhizomatous; and one alpine, in the Rocky Mountain states, which lacks rhizomes and has other minor morphological distinctions. It is not yet certain that these populations intergrade and their taxonomic status is in

question, but they seem to have been isolated from each other for a substantial period. Mooney and Billings found that the arctic plants have a higher photosynthetic rate and attain their maximum rate at lower temperatures than do the alpine plants. The arctic plants also have higher respiration rates at all temperatures and reach photosynthetic light saturation at lower light intensities than the alpine plants. Here we have a well-documented case of genetic physiological adaptation to arctic conditions, but we cannot say how long a period was needed for completion of the changes.

Mooney and Johnson (1965) compared the physiology of an alpine population of *Thalictrum alpinum* from 37° 31' N in California with that of an arctic population from 68° 06' N in Alaska and found the peak photosynthetic rate of the latter to be some 5 C lower than that of the former.

It would be impracticable to subject the majority of arctic and arctic alpine plants to such a detailed laboratory study as Mooney and Billings made of *Oxyria digyna*. However, it is clearly desirable that a few species, selected on the basis of field observations, should be studied thoroughly, including some that react markedly to temperature change and others that seem to be very insensitive to temperature. *Saxifraga cernua* and *S. caespitosa* react so markedly to temperature changes induced by differences in shelter that they probably have relatively high, and possibly sharply defined, optimal temperatures for growth. In marked contrast are *Alopecurus alpinus* and *Papaver radicum*, which seem to be markedly insensitive to a wide range of temperatures to judge from the heights of their flowering stems, which, given an adequate water supply, show no appreciable stunting with a mean July temperature of 3.5 C or less (Savile, 1959). It is still possible that low temperature markedly reduces the total biomass of these cold-tolerant species, and that the same plants would produce more leaves and flowering stems in a given time at high than at low temperature. When many plants from the high arctic, including various grasses and dicotyledons, were grown in temperate greenhouses at Ottawa the flowering stems were no longer than in the parent collections from northern Ellesmere Island. However, development was very rapid and the plants often flowered from seed in 6 to 7 months, or occasionally less, with a large clump or rosette of leaves that would have taken many years to develop in the Arctic. Thus the height is evidently genetically controlled and need not reflect indifference to temperature.

Russell (1940), working with *Oxyria digyna*, *Polygonum viviparum*, and *Ranunculus glacialis* on Jan Mayen Island, concluded that carbon assimilation was adequate to supply growth requirements and that the low growth rate of arctic plants is controlled by other factors such as low temperature and low nitrogen supply. It is not clear precisely how low temperature curbs growth if not through carbon assimilation. In addition, it seems probable that genetic stunting (Section II, C, 2, *a*), by which growth is halted early enough to ensure seed production, is one of the important factors in reducing the growth rate as judged on a seasonal basis.

The biochemical basis of effective growth at low temperature remains largely obscure, but it is interesting to note that Zenchenko (1964) has recorded that wheat grown in the Kola Peninsula had a markedly higher

cytochrome oxidase, and slightly higher peroxidase, content than the same varieties in the same stage of development at Moscow. He points out that cytochrome oxidase plays an important role in the respiration of embryos. It remains to be seen whether its content is genetically controlled at a high level in arctic plants.

3 Adaptations to short season

Conditions and adaptations to be discussed in this section cannot be wholly separated from those in the last section, for total growth is a product of the interaction of time and temperature. Nevertheless, the time element is so critical that its separate discussion is clearly justifiable. Most arctic plants must complete seed production in the short arctic summer, if not every year, at least with some regularity, for even in those species in which vegetative spread allows indefinite persistence, seed production is generally necessary for dispersal. It will be convenient to group the adaptations as morphological and genetic, the latter referring to the breeding system, but there is some overlapping.

a Morphological adaptations. Under this heading we must consider rapid initiation of growth in spring, vegetative reproduction, the annual habit, and periodic and aperiodic growth.

i Rapid initiation of growth in spring. In temperate deserts, where the growing period is limited by available moisture, we find that storage organs provide food reserves that allow the immediate resumption of growth when water is available, rather than that the plants gradually develop photosynthetic tissue. Fleshy roots or stems occur in several genera of arctic plants, notably *Oxyria*, *Polygonum*, *Erysimum*, *Pedicularis*, and *Taraxacum*. However, subterranean storage organs may not be particularly valuable in the Arctic where the soil often remains very cold almost to the surface and may remain largely frozen until well into summer. It may be significant that *Oxyria*, *Erysimum*, and *Taraxacum* tend to predominate on light, well-drained soils in which the permafrost recedes and the active layer warms promptly in spring.

Prompt spring growth in the Arctic requires the immediate availability of photosynthetic tissue. This important requirement may be met in several ways. True evergreens occur somewhat sparingly in the Arctic and most of them are abundant only in low-arctic regions with ample snowfall, where the leaves are protected from abrasion. Examples are *Empetrum hermaphroditum*, *Pyrola* spp., *Cassiope* spp., *Ledum palustre* including ssp. *decumbens*, *Loiseleuria procumbens*, *Phyllodoce coerulea*, *Rhododendron lapponicum*, *Vaccinium vitis-idaea*, *Saxifraga oppositifolia*, *S. bronchialis*, and *S. tricuspidata*. Of those that are abundant in the high arctic, *Cassiope tetragona* is confined to snow patches, but *Saxifraga bronchialis* and *S. tricuspidata* are equipped to withstand abrasion (Section II, B). *S. oppositifolia* withstands abrasion to some degree through its compact habit, but makes much better growth in sheltered places with good snow cover than on exposed sites. Evergreen leaves clearly are not the ideal system for rapid spring development.

A less conspicuous but more effective method of avoiding delay consists in the possession of winter-green (semievergreen) leaves. In numerous arctic dicotyledons the last leaves produced in one summer remain green and function at least in early spring of the next year. The rosette habit and the persistence of dead leaves allow such leaves to survive with minimal injury and photosynthesis may start in them as soon as they are exposed to light. This device is highly developed in *Saxifraga nivalis* and *S. tenuis*, in which the leaves may function for most of the second season. Other species of *Saxifraga* have the habit in varying degrees, as do most Caryophyllaceae and Cruciferae, *Papaver*, *Dryas*, *Armeria*, and individual species of other genera.

Among monocotyledons whole basal leaves may be winter-green as in *Tofieldia* and *Poa alpina* (Sørensen, 1941), and in *Pleuropogon sabinei* if snow cover is adequate. However, in almost all arctic monocotyledons except *Juncus* the basal parts of the later leaves often, if not always, persist. The exposed tips are killed, but the lower parts of the blades, covered by overlapping older leaves, are protected from abrasion. As soon as growth starts from the basal meristems, using stored food, these green blades are lifted free of their coverings and start photosynthesis substantially before the new leaves can do so. These green bases are readily seen in early summer both in specimens and in the field, but, as the leaves gradually fade later in the season, they may be difficult to detect unless a color band persists between the two zones. The distinction is very clear in *Eriophorum angustifolium* and *E. triste*, but the phenomenon may be fully as important in some other species in which it is less apparent. The culm leaves of *Eriophorum*, *Pleuropogon*, and perhaps some other grasses, are fully developed the year before flowering, and seem to winter without injury in protected sites. However, if snow is scanty, the unprotected tips of the blades may be killed. In *Pleuropogon* they survive regularly enough to allow a smut, *Ustilentyloma pleuropogonis*, to have a 2-year period of development (Section IV, B, 2). This mechanism, which is dependent on the basal meristems of the monocotyledons, is probably strongly adaptive in the high arctic, and may largely account for the proportionate increase of monocotyledons with increasing latitude.

The occurrence of semievergreen leaves must not be confused with a phenomenon often seen at cold and wet arctic sites where much of the vegetation remains green until the onset of winter. When the snow melts in spring this material is soft and green for a day or two, but it soon turns brown. These tissues play no part in spring photosynthesis, but the phenomenon indirectly benefits some plants through dispersal by geese (Section II, D).

As noted in Section II, B, winter buds protected by hard scales are exceptional in the high arctic. Generally the growing point is not markedly different in winter and in summer. This condition, especially when the cells contain anthocyanin, enables the plants to start photosynthesis and growth in spring approximately as soon as sunlight reaches them.

ii Vegetative reproduction. Vegetative growth through development of rhizomes or stolons, often with the eventual development of separate plants, permits a species to spread throughout an appropriate habitat, but has several limitations. It does not allow genetic recombination, it does not permit spread

to new areas of appropriate habitat, and it allows persistence on a site only so long as the habitat persists. If the habitat is destroyed by solifluction, flooding, or other means the colony is eliminated. In addition, an extensive solid stand of a plant is often more subject to heavy damage by insects or parasitic fungi than are small, scattered colonies. The production of bulbils, which may be scattered like seeds, permits a few arctic plants, including *Polygonum viviparum*, *Saxifraga cernua*, *S. foliolosa*, and viviparous strains of a few grasses, to combine successful dispersal with vegetative reproduction. *P. viviparum* and *S. foliolosa* produce seed frequently in the southern parts of their ranges. In *S. cernua*, sexual reproduction is uncommon even at subarctic sites, but we have specimens from Sugluk on Hudson Strait (nearly 500 km beyond the tree line) with several well-formed capsules, which would certainly have matured seed. It is probable that during periods of climatic amelioration even this species has produced some seed at much higher latitudes, and that some gene exchange has thus been intermittently possible. In some species of *Cerastium* and *Stellaria* abbreviated axillary shoots detach and supplement seed production. *Cardamine pratensis* seems never to set seed in the high arctic, where it is generally scarce although of wide range. It produces deciduous buds that seem to be dispersed mainly by water. Its general dispersal in the arctic may be partly achieved by seed being carried northward by waterfowl.

Vegetative reproduction tends to increase in amount and importance under adverse conditions in many plants and in various climates. Thus it seems to be critical for the survival of *Populus tremuloides* under marginal conditions in aspen parklands of western Canada. As noted in Section II, B, it contributes to the survival of spruce at the tree line, at least in windswept regions.

Although some rhizomatous grasses and sedges and, for example, *Oxyria digyna* seem capable of indefinite vegetative spread, provided that the appropriate habitat is unlimited, usually there seems to be a fairly definite age limit for the individual plant. *Salix arctica* roots at the nodes to some extent, but it does not generally form clearly defined clonal colonies, at least in the high arctic. The main stem produces a succession of branches, each of which may live for 30 years or more before dying and being replaced. Beschel and Webb (1963) indicate that when the main stem dies the whole plant dies, the adventitious roots being inadequate to sustain the branches. They suggest a maximum age of the order to 100 years for plants on Axel Heiberg Island. I have seen many plants of *S. arctica* that died apparently without intervention of disease or outside agency at substantially less than this age. Warren Wilson (1964), who studied this species at Resolute, found that the relative growth rate began to decrease after 10 to 20 years and approached zero after 50 years, which also suggests a well-defined maximum age.

Vegetative reproduction certainly allows some grasses and sedges to persist under marginal situations, where they rarely produce seed. On Somerset Island, *Carex misandra* and *C. membranacea*, which are widespread in marshes, generally produce only two to ten fruiting stalks per 100 m² in any year (Savile, 1959, 1963*a*). Clearly these species could not dominate the marshes in

this region without vigorous and indefinitely prolonged vegetative reproduction. In partial compensation for their limited seed production, these and other sedges on such marginal sites are apparently always free from infection by smut fungi (*Anthracoidea* spp.), which may seriously reduce seed production in more congenial situations (Section IV, B, 2).

In contrast to the sedges, some grasses regularly produce numerous inflorescences, but do not usually mature seed on marginal sites. At Isachsen (see Table I), *Arctagrostis latifolia*, *Deschampsia pumila*, *Poa arctica* ssp. *caespitans*, *Pleuropogon sabinei*, *Colpodium vahliianum*, and *Dupontia fisheri* failed to set seed in 1960, a typical summer, and most plants did not even reach anthesis (Savile, 1961 b). However, even the technically caespitose *Deschampsia pumila* and *Poa arctica* ssp. *caespitans* are generally short-rhizomatous at Isachsen and may form substantial mats. On solifluction slopes such mats tend to break up and disperse the grasses to a limited extent. Thus such species may occur quite widely in their principal habitats and may persist even if seed is produced only once in perhaps 50 years. A few viviparous grasses occur sporadically in the high arctic, and one is tempted to suppose either that the mutations controlling viviparity have occurred repeatedly or that the habit may be partly under environmental control, as true apomixis (agamosperry) seems often to be (Section II, C, 3, b).

Many arctic plants have little or no power of vegetative reproduction, and some rosette-forming dicotyledons have quite short life spans. Sørensen (1941) indicated that *Gentiana nivalis* and *Gentianella detonsa* live only 2 to 3 years and flower once, and that *Matricaria ambigua* lives only about 10 years, flowering two or three times. Although most rosette-forming species live substantially longer, probably none are very long-lived. In general we can say that vegetative reproduction is much less important in flowering plants than in the mosses and lichens.

iii The annual habit. The ultimate reduction in life span, with complete elimination of vegetative persistence, is seen in annual plants. As might be expected, annuals are scarce in the Arctic, where they lead a precarious existence. Even at low-arctic sites they may be seriously restricted in occurrence. At Chesterfield, only 63° 21' N but with very low relief and minimal protection from chilling winds, only three annuals occur: *Koenigia islandica*, *Limosella aquatica*, and *Montia lamprosperma*. All three species are confined to the sides or bottoms of shallow, temporary pools. On these sites the plants receive some protection from the wind and are thus in a pocket of warm still air on sunny days. They receive adequate water by seepage from higher ground, and, because the organic soil in these ponds is nearly black, they receive the maximum benefit from insolational heating. Nearly all plants of the three species mature at a height of less than 5 cm, reducing the growth period to a minimum and keeping all tissues close to the warm soil.

Most annuals penetrate only short distances into the Arctic, but *Koenigia islandica* occurs far to the north in areas where high relief both ensures dynamic warming of the air and allows stratification of the air close to the soil surface. It reaches Devon Island in the Canadian Archipelago, is widespread on both coasts of Greenland, and occurs sparingly in Peary Land. It might be

supposed that it sometimes behaves as a biennial, but Holmen (1957) found it to be strictly annual in Peary Land. If, as now seems unlikely, it ever does grow as a biennial, it must do so in areas of deep snow where it is thoroughly protected in winter. Sørensen found that all germinable seeds sprout promptly in their first spring. Partial delay of germination beyond the first year would be an effective safeguard against disastrous summers. However, unless it were confined to spring, it would presumably cause serious wastage through plants failing to mature before winter, for such plants are probably not winter-hardy in such a strictly annual species, in which selection has been predominantly for seed survival.

Raven (1964) notes that annuals are well adapted to temperate deserts where ability to pass the dry season as seeds is strongly adaptive. But the annual habit requires a reasonably regular coincidence of moisture and warmth, and this combination is frequently lacking in the Arctic, where summer warmth may be inadequate except on sites too arid to allow maturation of the plants.

iv Periodic and aperiodic growth. Sørensen (1941) categorized the plants of northeast Greenland, according to the phenology of their shoot development, into periodic (those whose development is halted at a particular stage of development even when abundant opportunity for further growth remains) and aperiodic (those that develop until halted by deteriorating weather). Periodic species may be subdivided into several categories, according to the stage at which development is halted. Despite a few species being unstable or intermediate in development, most arctic plants fit clearly into one of these categories. Each type of development has potential advantages. Aperiodic growth allows full utilization of the growth potential in each summer, but if development goes too far and the flowering stems elongate appreciably there is risk of their being killed. Strictly periodic growth provides insurance against winter injury, but sacrifices the opportunity for extensive growth in a favorable season.

When he grouped the Greenland plants by their latitudinal range, Sørensen found that, with increasingly high latitude, periodic species with advanced flower buds and aperiodic species each increased in percentage, but not in actual numbers, and that periodic species wintering in early stages dropped out more or less completely. Thus both tendencies have been developed, although periodic species are in a substantial majority even in the high arctic. When we analyze them by habitat we find that the aperiodic plants are predominantly species of snow beds, in which the habit is doubly adaptive. Firstly, spring comes very late to such sites, making the opportunistic aperiodic habit particularly suited to the exceptionally short growing season; and secondly, because of sustained snow cover, the risk of winter injury to advanced shoots is minimal.

Various grasses are aperiodic or not rigidly periodic. If the panicles partly emerge from the sheath, the exposed parts are killed and appear as bleached sectors during the succeeding summer (Section II, B). Most other monocotyledons are periodic. Among dicotyledons, according to Sørensen (1941), aperiodicity occurs scatteringly in several families: Caryophyllaceae (*Arenaria rossii*,

Stellaria humifusa); Cruciferae (*Braya humilis*, *B. thorild-wulffii*, *Draba crassifolia*, *Cochlearia officinalis*?); Papaveraceae (*Papaver radicum*?); Polygonaceae (*Oxyria digyna*); Rosaceae (*Potentilla hyperctica*, *P. rubella*); Saxifragaceae (*Saxifraga nathorstii*); Compositae (*Erigeron compositus*); Plumbaginaceae (*Armeria sibirica*); Polemoniaceae (*Polemonium boreale*).

Papaver radicum seems to be variable in its reaction, partly at least through environmental influences. At cool, wet sites I have seen it produce a succession of bloom to the end of summer, but at warmer and drier sites it appears to be periodic.

Some Cruciferae are of particular interest. In theory the ideal solution for arctic development is for the flowering stems to halt with impunity at any stage of development, including full flowering, and resume development in the following season. There have been various claims for such an ability, but the only adequately documented one is for *Braya humilis*, which Sørensen found able, in northeast Greenland, to overwinter its inflorescences at any stage and resume growth without injury. I saw no sign of this behavior at Hazen Camp, where aridity tends to check growth in late summer and where snow cover is often inadequate to protect elongating inflorescences. I suspect that both aperiodic behavior and survival depend largely upon environmental conditions, but it is conceivable that the difference in behavior has a genetic basis. The first claim for such overwintering of inflorescences was that of Kjellman (1883) for *Cochlearia*, but it has never been validated. However, collections of *C. officinalis* made by T. Mosquin on Melville Island in 1965 illuminate the behavior of this species. The summer of 1964 was disastrous in this region, with snow covering most of the ground until early August and many plants making almost no growth. On several plants of *C. officinalis* in 1964 some inflorescences had elongated slightly and a few buds had approximately reached anthesis. These buds were all killed but the growing points of some stems survived, presumably because they were promptly covered by snow at the onset of winter, and flowered freely in 1965. G. A. Mulligan (personal communication) states that some overwintering of partly developed flowering stems of *Capsella bursa-pastoris* is seen occasionally in temperate regions if snow cover is adequate. Thus the tendency for overwintering of inflorescences may be widespread among aperiodic species of Cruciferae, although it is probably never functional except in very mild winters or with continuous snow cover. No such tendency seems to have been reliably observed in any other family.

It is significant that *Potentilla hyperctica*, unlike most of its genus, is aperiodic. It is the only species that grows at Isachsen, where its open buds and slightly elongated flowering stems are generally well covered by snow and permit rapid development in spring. The species is much rarer at some warmer sites where snowfall is light.

An apparent exception to the general rule concerning overwintering flowers is noted by Sørensen in the staminate catkins of *Betula nana*. However, the flowers are fully protected by the bracteoles and bracts, the latter with a resinous covering, so that the whole catkin is sealed against desiccation and appears capable of withstanding considerable abrasion. It is also probable that the catkins are generally covered by drifted snow.

Although flowering stems of aperiodic species are frequently killed, the loss may not be quite as high as might appear. Sørensen supplied evidence that if shoots of *Papaver radicum* or *Erigeron compositus* develop beyond a critical point in late summer their food substances are translocated down into the crown of the plant, dooming the shoots to winter-killing but salvaging almost everything from them but the cellulose skeletons. It is possible that some other aperiodic species share this ability.

In an exceptionally severe season it is probable that no plants set seed. Most of the western half of the Canadian Arctic Archipelago remained essentially snow-covered in 1964 until early August. Examination of plants collected on Melville Island in 1965 by T. Mosquin suggests that inflorescences of most species were killed at or before anthesis. In a number of species, including *Poa arctica*, *P. glauca*, *Saxifraga hirculus*, *S. nivalis*, *S. tricuspidata*, *Polygonum viviparum*, *Stellaria monantha*, *Cerastium alpinum*, *Potentilla pulchella*, *Cassiope tetragona*, *Papaver radicum*, and several Cruciferae, there are no traces of 1964 inflorescences and it is probable that the shoots made almost no growth but overwintered to flower in 1965.

b Genetic adaptations. Because every day's delay in seed formation may be critical, we find in the Arctic various devices that eliminate the delays caused by cross-pollination. Some of these devices are potentially deleterious and would tend to be eliminated in favorable environments, but are presumably adaptive on balance in the Arctic.

As far as is known, no wholly arctic flowering plant possesses an incompatibility system, the most frequent and generally most stringent means of promoting outcrossing. Heterostyly (the possession of two flower types, one with short styles and long stamens and the other with the reverse) is often associated with self-incompatibility. Although it is known in some genera, such as *Armeria* and *Primula*, that reach the Arctic, apparently no arctic population is heterostylous (Baker, 1959).

Dichogamy (the differential timing of stigma receptiveness and anther maturity) apparently occurs only in partial form. Thus in *Saxifraga oppositifolia* the stigma matures first, allowing pollination from a more advanced flower if bees are available. But by about 2 days later, under cold conditions, the anthers have matured and the filaments have lengthened and curved inward until pollen is brought approximately in contact with the stigma and the first gust of wind ensures pollination. However, Kevan (1970 and in preparation) found markedly reduced seed set in selfed flowers of *S. oppositifolia* at Lake Hazen.

Dioecious plants are not uncommon in the low arctic, *Salix* being the principal such genus. They are scarce in the most severe high-arctic sites, only *S. arctica* reaching the limit of land. This species is very rich in nectar and is visited by many insects. The staminate and pistillate plants often grow in contact; the prostrate habit facilitates pollination even in weather that limits flight elevation to a few centimeters, and the set of seed is generally good. None of the arctic willows are specifically wind-pollinated, but possibly some casual pollination by wind may occur. Wind pollination is most important in the Arctic in Gramineae, Cyperaceae, and Juncaceae. Probably selfing is the

rule, and it is notable that the few dioecious species of *Carex* do not penetrate far into the Arctic. Nevertheless, occasional hybrids among grasses show us that cross-pollination does occur.

A substantial number of arctic plants are apomictic to varying degrees, normal seeds being formed without pollination. Apomixis in the strict sense (agamospermy) is presumably even more efficient than self-pollination in promoting seed set, but it is genetically equivalent to bulbil formation (Section II, C, 3, *a*), which some authors include in apomixis, and deprives the species of the opportunity for genetic recombination. Complete agamospermy is probably rare or absent except in some species of *Antennaria* in which staminate plants apparently do not occur. Knox and Heslop-Harrison (1963) demonstrated that in a grass, *Dicanthium aristatum*, the ratio of apomictic to sexually produced seed was controlled by alterations in day length. It is highly probable that the breeding system is modified by light, temperature, or possibly other factors in a number of species that are recorded as apomictic. Billings and Mooney (1968) quote Clebsch as finding that viviparity could be induced in *Trisetum spicatum* by environmental manipulation, but it should be noted that, even in the high arctic, sexual reproduction remains the rule in flowering plants. Certainly we must be cautious not to accept reports of apomixis uncritically. For example, *Poa glauca* has appeared in lists of apomictic species. However, this grass is notorious for forming hybrid swarms with other species of *Poa*, and at almost 82° N I collected a graduated series of specimens ranging from typical *P. glauca* to typical *P. hartzii*. It is accordingly highly improbable that it never sets seed from its own pollen. Hedberg (1962) showed that the sterile arctic triploid "*Puccinellia vacillans*" is a hybrid between *Phippsia algida* and *Colpodium vahliianum*.

There is a frequently expressed tendency to belittle the role of cross-pollination in the arctic and to assume that full apomixis or automatic selfing completely dominate almost all species. This view may have arisen partly through the work of Hagerup (1951) in the Faeroes, where insects are extremely few, and where cross-pollination must be extremely rare except in wind-pollinated Gramineae, Cyperaceae, Juncaceae, and a few other plants, and in a few rain-pollinated species (Hagerup, 1950). But in most arctic regions, where rain and wind are not so excessive in summer as in the Faeroes, the insect population is large, although much less varied than in temperate regions, with Diptera strongly predominant. It must be emphasized that bumblebees, Lepidoptera, and many Diptera do visit flowers freely in the Arctic, picking up many pollen grains, and unquestionably achieving some pollination. At Tiksi Bay, southeast of the Lena River delta (nearly 72° N but only slightly north of the Verkhoyansk Mountains and the limit of trees, and probably closely resembling the Yukon coast near the Mackenzie River delta), Shamurin (1966) recorded insects visiting 88 species of flowering plants (nearly all the potentially entomophilous plants in the region), and some legumes appeared to be self-sterile.

As we go progressively higher into the Arctic we find an increasing predominance of white or yellow flowers, generally shallow in form, often strongly radiate in pattern, and not infrequently with dark petal spots or deep

purple anthers that serve as honey guides. These are fly-flowers, which have evolved specifically to attract Diptera. It should be noted that even at Isachsen, with very low summer temperatures, Diptera do visit small white flowers (*Stellaria*, *Saxifraga*, Cruciferae) on which Mosquin and Martin (1967) did not record them.

Although it may be argued that some of the species with such flowers evolved them before entering the Arctic and simply have not dropped a now functionless character (see Mosquin, 1966), this is far from being generally true. Cross-pollination is often difficult to prove in the Arctic, but it is shown to occur when we find hybrids, as we do between fly-pollinated species of *Stellaria*. Occasionally we do find evidence of cross-pollination within a species. At Isachsen, where there are no bumblebees, two color forms of *Saxifraga oppositifolia* occur, with no intermediates. At Hazen Camp, where two species of bumblebees are available to visit this typical bee-flower, it was virtually impossible to find two clones of *S. oppositifolia* that agreed precisely in petal size, shape, attitude, and color. Although selfing doubtless occurs at Hazen Camp, it seems clear that enough cross-pollination occurs to give nearly complete reassortment of the genes visibly affecting the petals, which probably originate from two or at most three geographic populations. Kevan (1970 and in preparation) has recently confirmed this deduction in his studies at Lake Hazen (ca. 82° N). He found no seed set without insect pollination in *Pedicularis capitata** and the dioecious *Salix arctica* and greatly reduced set in *Dryas integrifolia*, *Pedicularis arctica*, and *Saxifraga oppositifolia*. The clear implication is that substantial cross-pollination must occur in many other species that do self-pollinate freely.

The various species or races of high-arctic plants restricted to northern Greenland, Ellesmere Island, and occasionally Axel Heiberg Island argue strongly in favor of an appreciable degree of cross-pollination, for it is difficult to imagine such distinct, yet coherent, populations developing without it in the span of the Wisconsin glaciation.

It is probably true that some species retain a pattern attractive to insects after becoming apomictic or fully selfing. The high-arctic race of *Erysimum pallasii* is as showy as the plant of Alaska and Yukon, but it is triploid and probably apomictic (Mosquin, 1966). Mosquin also noted that on Melville Island *Astragalus alpinus* is very fragrant and attracts bumblebees freely (as, indeed, it does elsewhere), but that *Oxytropis arctica*, with even showier flowers, had no detectable scent and was apparently never visited.† Sprague (1962) showed that, in California, *Pedicularis* is strongly self-sterile and includes remarkable examples of specialized pollinator relationships. However, some high-arctic species produce abundant seed even when conditions for pollination are extremely poor (Savile, 1959) and may be partly self-fertile.

*Kevan did not manually self-pollinate *P. capitata*, and we do not know whether it is self-sterile.

†Shamurin (1966) reported that all six species of Leguminosae observed at Tiksi Bay, much closer to the tree line than Melville Island, were freely visited by bumblebees.

In general the arctic plants seem to have reached a successful compromise. Through strong self-fertility they assure a good set of seed in almost every year, but the majority seem to attain enough outcrossing to maintain relatively homogeneous populations and to assure the incorporation of adaptive mutations into the gene pool. Regular outcrossing in every generation may be unnecessary in most plants. As Ernst Mayr (personal communication) points out, mate selection and habitat selection tend to reduce the degree of outbreeding in most animals, but the lack of these behavior patterns in plants reduces the need for regular cross-fertilization. Excessive outbreeding may swamp out ecotypes (genotypes adapted to local conditions within the main range of the species). It is thus possible that the rate of gene exchange within many arctic species approaches the optimum.

4 Genetic implications of breeding system modifications

Mosquin (1966) has thoroughly discussed the genetic implications of the modifications of breeding systems that are adopted in the Arctic, and the reader is referred to his paper for further details. He shows that essentially all the genetic devices in flowering plants that promote uniformity are frequent in the arctic flora, and that essentially all those promoting variability are relatively uncommon. He suggests that genetic uniformity, by preserving fitness, may actually be adaptive in arctic conditions. We have fortunately been able to discuss this problem with Dr. Ernst Mayr. He points out that near the middle of the range of a species even the extreme genotypes are well adapted and free gene exchange is tolerable or even desirable. However, at the edge of the range conditions are ecologically marginal and the preponderant genotype (ecotype) is one specially adapted to these conditions. Reduction of recombination in this peripheral genotype helps to protect it against swamping by undesirable genes from the middle of the range. This process clarifies the situation especially for temperate and subarctic species that penetrate the Arctic to a limited extent. It is clearly desirable that newly acquired characters adaptive to the new environment be protected, and anything that reduces recombination will help to protect them. What, however, is the situation in fully or predominantly arctic species? In these species the body of the range is subjected to the same pressure against gene exchange as the periphery. It is possible that some of these species arose from peripheral populations in which the trend to uniformity was too strongly developed to be reversed. But, when we recollect that the arctic flora is extremely heterogeneous in its origins, it is almost impossible to believe that all arctic immigrants reacted so uniformly. It is much more probable that we are dealing here with several phenomena, and it is desirable that we should examine alternative explanations.

Mosquin's thesis receives some support from the occurrence in some arctic plants, notably *Carex*, of very small chromosomes, which tend to reduce crossing over and strengthen linkage. The high percentage of polyploids in the Arctic may also support his thesis. It has been suggested by several authors (Hagerup, 1932; Melchers, 1946; Löve and Löve, 1949; Löve, 1964) that polyploidy is adaptive in the Arctic by virtue of its endowing plants with

greater variability than is possessed by the corresponding diploid populations. Mosquin questions this conclusion, pointing out that the majority of polyploids are genetically buffered against expressing variability. Almost no arctic polyploids have been analyzed as to derivation, and we cannot make a conclusive statement on their genetic behavior. If uniformity is actually adaptive in the Arctic, the high percentage of polyploids may be partly explained by this means. However, apart from peripheral populations, there seems to be no clear reason why uniformity should be desirable in the Arctic. The climatic variation during the growing season is relatively small, but it cannot be interpreted as conferring stability to the climate. The summer temperatures are so close to the limits for plant growth that a very small variation, such as would be negligible in warmer regions, is disastrous in its effects. The arctic environment must actually be rated as extremely unstable, both edaphically and climatically.

Individual cases of polyploidy may have other explanations. The induction of polyploidy is sometimes accompanied by the change from self-sterility to self-fertility, a change that is clearly adaptive through elimination of dangerous delays in pollination. Johnson and Packer (1965) have indicated that polyploidy in arctic Alaska is correlated with edaphic factors, but the relationship is not necessarily directly causal. The cold, wet, unstable soils on which they found polyploids to be most frequent are those with the shortest and coldest growing season, because snow accumulation delays the start of growth and high evaporation depresses summer temperature near the surface.

We should note the warning by Bell (1964) that polyploidy is not necessarily a reaction to latitude or altitude. He demonstrated in the genus *Eryngium* that polyploidy is correlated with sharp ecological gradients, predominating in regions subject to great climatic change. The chief stimulus in *Eryngium* may have been aridity, which demands rapid maturation.

Mooney and Johnson (1965) found that under identical arctic conditions triploid plants of *Thalictrum alpinum* produced 50% more leaves, each with substantially more leaflets, than normal diploids from the same site in Alaska. The peak photosynthetic rate of the triploids was 50% higher than that of the diploids, and reflectance of radiant energy was significantly lower in the 500 to 650 μ range. Here is a possible explanation for the adaptiveness of some arctic polyploids: enhanced growth rate under marginal conditions. The rarity of diploid and polyploid races of a species occurring naturally within the Arctic makes adequate direct testing of this phenomenon impossible, for comparison of arctic polyploids with temperate diploids gives no assurance that recorded differences are due to the level of ploidy rather than to normal selection.

I suspect that genetic uniformity in the Arctic is often an inevitable consequence of the devices that have been adopted to speed up seed production. In conditions of strong biological competition, such as we find in benign habitats, so great a degree of genetic uniformity would generally be intolerable. In vast areas of the Arctic, however, the ground cover is far from complete. Indeed, in the regions of most severe climate, plants commonly occupy between 1% and 10% of the ground surface. Only in the marshes is the

cover nearly complete, and here we find the cover to be mainly of bryophytes, which seem to form an essentially inert substrate upon which the flowering plants are scattered. Under such severe conditions competitive exclusion can seldom be of significance (Savile, 1960). Pronounced genetic uniformity may be tolerable when dynamic biological competition is much less of a challenge to a plant than the passive physical environment, for the physical environment does not automatically change when a plant has evolved to meet it, as do competing plant species. Thus genetic uniformity may often be a tolerable price for successful seed production, and be adaptive on balance in conditions that make rapid seed set essential. It may be partly for this reason that the tendency for genetic uniformity is common among weeds, which must also mature rapidly while a disturbed and essentially open habitat is available.

It is probable that all these potential explanations of genetic uniformity in the Arctic operate in some degree, and it would be dangerous to assume overwhelming superiority in any one of them.

5 Adaptations to conditions of illumination

The growing season in the Arctic is characterized by continuous daylight or, at most, short periods of darkness at relatively low latitudes and in late summer. Spring growth seldom starts before early June, only a week or two short of the summer solstice. Offsetting the essentially continuous daylight are low solar elevation and frequently heavy cloud cover, which greatly reduce light intensity. Total effective insolation may thus be approximately equal to that in mid latitudes. This is suggested by Russell (1940), who found a net assimilation rate for *Oxyria digyna* on Jan Meyen Island in late summer of 0.3 g/dm² per week and believed that in early summer it must approach the rate of 0.55 g recorded as the average for several temperate species.

A failure to adapt from moderate to very long days has probably restricted the northward movement of some species that might otherwise have penetrated the Arctic, but it is not necessarily a serious obstacle and the process need not be interminably slow. Although I have no documented case of rapid photoperiodic adaption in an arctic plant, the work of Cumming (1961, 1963) on *Chenopodium rubrum* provides an instructive example of how rapid the adaptation to continuous daylight may be in a temperate species. *C. rubrum* occurs in saline mud across North America and Eurasia. In Canada it grows on appropriate sites from Manitoba to Alberta, and also disjunctly in southern Yukon from far outside the unglaciated area to near the boundary between the glaciated and unglaciated regions. It is absent from the large unglaciated region of western Yukon and the interior of Alaska. It clearly reached Yukon from Alberta during the postglacial hypsithermal interval, when a prairie corridor existed through the lowlands of northeastern British Columbia, allowing various prairie elements to reach southern Yukon. This corridor was closed by coniferous forest at the end of the hypsithermal interval, some 3000 years ago, and the forest barrier is now almost continuous for roughly 800 km.

Cumming carried out numerous tests of *Chenopodium rubrum* at various day

lengths and various pretreatments and temperatures. Because he was primarily concerned in studying the phytochrome system in his plants, Cumming's most detailed studies incorporated, at the end of the photoperiod, terminal 30-min treatments with differing red to far red ratios. The detailed tests consequently included only photoperiods of 2 to 22 hr at 2-hr intervals, but some further tests included continuous light exposure. Allowing for differences imposed by other variables, we may summarize the tests by stating that at 15 C plants from Pelly Crossing, Yukon (62° 46' N), proved to be adapted to all day lengths from 2 to 24 hr. Those from near Haines Junction, Yukon (60° 47' N), flowered promptly under 4- to 18-hr photoperiods but only much more slowly at 2, 20, and 22 hr. Plants from Swift Current, Sask. (50° 10' N), flowered promptly with 4- to 14-hr photoperiods, but more slowly at 2 and 16 hr, and remained vegetative at 18 hr. Finally, plants from Cachuna Lake, Calif. (34° 20' N), flowered only with 4- to 12-hr photoperiods. Not only have the Yukon plants become conspicuously different in photoperiod response from those of the population from which they were derived, but within southern Yukon there is a substantial difference between populations only two degrees of latitude apart. The Pelly Crossing plants are arctic adapted in terms of photoperiod response. Such a rapid change suggests that the plants that invaded Yukon may have carried a wide selection of genes influencing such a response. A curious finding in Cumming's experiments is that at 30 C flowering is delayed but the curves generally show double optima, one at 8 to 10 hr and one at 22 to 24 hr, with much less distinction between the geographic races than at 15 C. Although several explanations are possible, this effect suggests that some genes influencing photoperiod response in *C. rubrum* are expressed only under certain conditions. Such an explanation may partly explain, through threshold selection (Mayr, 1963), the rapid latitude response of the Yukon plants. *C. rubrum* is nearly circumpolar. In spreading from Eurasia to North America, or the reverse, it probably crossed the Bering Bridge, at which time it must have been adapted to long days. It may well have carried such genes ever since, although they are not always expressed.

It will be noticed that the Pelly Crossing plants of *Chenopodium rubrum* are indifferent to photoperiod rather than specifically adapted to long days. It is clear that a substantial number of temperate species, or particular strains of them, are indifferent to day length. Hadač (1941) listed no less than 52 temperate species, including both weeds and cultivated plants, that had become established in Spitzbergen (ca. 77° to 80° N).

Photoperiodic requirements are probably seldom critical for arctic plants that spread far south of their normal ranges, either along mountain systems or, during glacial advances, through lowlands. However, Mooney and Johnson (1965) found that the arctic population of *Thalictrum alpinum* grew best under long photoperiods, and it is probable that many other species have at least some degree of actual adaptation to very long days. Mooney and Billings (1961) found that the arctic race of *Oxyria digyna* made substantially more growth under 24-hr days than 15-hr days, and flowered only under close to 24-hr days, but this behavior may be somewhat exceptional. Over much of the

latitudinal range of North America and Eurasia evidence has been accumulating from various sources, including peat macrofossils, pollen data, soil studies, and relict populations, that many plants have shifted north and south several hundred kilometers under the influence of postglacial climatic fluctuations. Thus the limits of these plants are imposed by climate rather than by day length, and they move northward as soon as climatic restrictions are relaxed. The repeated and much more pronounced climatic fluctuations that have occurred since late Tertiary have guaranteed broad potential photoperiodic adaptation in the majority of northern plants. Montane species may adapt to climatic changes by altitudinal shifts, but species of the plains must move latitudinally or face extinction alternatively through climatic pressure from the north or through competition from the south.

The low light intensity of the Arctic is probably not a critical problem, for intensity is generally much lower on a forest floor. Nevertheless, taken in conjunction with the cold and short summer, low intensity in sites subject to heavy cloud cover must limit the total metabolic capacity substantially. Any physiological or morphological modification that increases photosynthetic efficiency at low light intensity must therefore generally be strongly adaptive. The little available evidence suggests that such modifications are widespread. Mooney and Billings (1961) found the arctic population of *Oxyria digyna* to be adapted to lower light intensities than the Cordilleran alpine population. Similarly Mooney and Johnson (1965) found arctic plants of *Thalictrum alpinum* to have a higher photosynthetic efficiency at low light levels than alpine plants from California. They also found arctic triploid plants to have substantially higher efficiency and lower reflectance than arctic diploids. These differences seem to be at least partly structural. The arctic plants lack the glaucousness of the alpine ones and have somewhat thicker leaves. The triploids have particularly thick leaves with the chlorenchyma tissue markedly denser than in either arctic or alpine diploids. The low leaf reflectance of the triploids probably results from both surface and internal structure.

Many high-arctic plants have been grown at Ottawa under moderate light intensities, using winter daylight with supplementary evening lights, or shaded greenhouses in summer, usually without obvious morphological effects due to light conditions. However, Dr. Jens Clausen (personal communication) grew some of the same arctic grasses that we have grown at Ottawa under the intense insolation of southern California and found them to become severely stunted. Such evidence as is available thus supports the belief that most arctic plants are genetically adapted to light of low intensity.

6 Adaptation to low nitrogen supply

Nearly all arctic soils are markedly deficient in nitrogen in comparison with temperate arable land. Russell et al. (1940) found inorganic nitrogen universally low in the soils of Jan Mayen Island, and nitrate nitrogen generally absent in open areas. They considered slow bacterial action, due to both low temperature and low nutrient supply, to be the main cause of the

deficiency. They also concluded that nitrogen deficiency was of great importance in determining the distribution and development of various types of communities. It is tempting to regard nitrogen deficiency as a critical limiting factor in both the low stature and limited occurrence of many arctic plants. However, any such generalization would be extremely dangerous, for there is good reason to believe that many species have become adapted to a low nitrogen supply.

It is true that in the low arctic, especially in areas of ample rainfall, some grasses react conspicuously to additions of nitrogen, as, for example, around owl roosts. However, the stimulus seems to last for hundreds of years at very old campsites, suggesting that the nitrogen is very gradually released (as is to be expected under conditions of meager bacterial action) and that the amount of nitrogen that causes the original stimulus may be extremely small. In the more continental conditions of much of the Canadian high arctic, water supply is often a more critical factor in limiting growth. On limestone barrens, which retain little water once the active layer becomes deep in midsummer, a ring of vigorous growth may be seen about large boulders. However, the stimulus is just as marked around boulders that are flush with the ground as with those that are erect, which indicates that nitrification by perching owls or visiting foxes is not the main stimulus. On the contrary, the stimulus is roughly proportional to the area of the boulder and is greatest on the side that receives most runoff. Thus these boulders act largely by catching precipitation and delivering it to narrow zones about their margins, a very conspicuous addition in regions where the summer precipitation is largely fog or drizzle (Savile 1959, p. 967). The initial stimulus builds up humus, which increases the water-holding capacity of the soil and further improves conditions of growth. One accordingly wonders whether the stimulus from manuring is not also often partly one of added water-holding capacity rather than only of nitrification.

On arid sites at Hazen Camp it appeared that nitrification had no effect on plant development, because lack of water both limited plant growth and limited the already slow bacterial action in making organic nitrogen available. In a nitrified depression near the camp, the grass *Puccinellia angustata* showed the effect of nitrification in abundant leaf production and in being heavily attacked by the mildew *Erysiphe graminis* to which it is generally resistant (Savile, 1964c). But culm height and abundance were not increased, and it appears that the nitrogen supply was above optimum. A considerable number of high-arctic plants have recently been grown at Ottawa under temperate conditions, in a standard soil mixture and with fertilization according to a regime that promotes flowering of most temperate plants. Under these conditions a number of the arctic species have made rapid vegetative growth but have produced few or no flowers. The leaves are abnormally lax and green and the internodes of some species unusually long. These reactions, which have been pronounced in *Oxyria digyna*, *Saxifraga* spp., and various Caryophyllaceae and Gramineae, indicate excessive nitrogen. It seems clear that such plants are specifically adapted to the conditions of low nitrogen that are prevalent in the Arctic. Other plants that we have grown, notably *Taraxacum*

spp., and many Cruciferae, seem to be indifferent to the amount of nitrogen, their morphology in "normal" soil being closely comparable with that in the Arctic although the growth rate is greatly accelerated under the higher temperature.

Other species will doubtless prove to make better growth with modest additions of nitrogen, but our experience at Ottawa suggests that few high-arctic plants will justify the epithet "nitrophilous."

D Dispersal

A thorough appreciation of dispersal mechanisms and their efficiency in the Arctic is essential both to round out our survey of adaptations in arctic plants and to allow us to estimate the age of the arctic flora (Section I, B). Several authors have recently demonstrated a lack of such appreciation. Hadač (1963) assumed that plants move only in associations, that they must therefore have spread through the Arctic by land connections, and accordingly that much of the arctic flora is of great age. Even in temperate regions many plants move as individual species, as we see in tracing the spread of adventives. In the Arctic, where most habitats are very incompletely filled, individual movement is almost universal. Rønning (1963) noted that most of the plants of Svalbard are of wide distribution, and, assuming that only overland spread to this area is possible, claimed the flora to be ancient, as there is no evidence of recent land connections. Dahl (1963) classified arctic plants by their possession or lack of devices that promote long-distance dispersal in temperate regions, showed them to be statistically deficient in such devices, and accordingly declared that most species must date far back into the Tertiary when a land connection probably existed between Europe and Greenland. Löve (1964) speaks of old and isolated arctic islands with little endemism in the flora as indicating very slow subspeciation.

As I have already noted (Savile, 1964*b*), many effective temperate dispersal systems are inadapative under the very different conditions of the Arctic. Burs and fleshy fruits function efficiently only if the population of birds and mammals is high. Table II compares breeding-bird densities at some arctic sites with those in various temperate habitats. It will be seen that even at low-arctic sites the density is less than in any temperate habitats except deserts, and that in the very high arctic the density is extremely low. No density data are available for mammals, but, as with birds, there is unquestionably an abrupt decline in both species and numbers at the tree line and a gradual further decline as we move into the high arctic. The chances of burs and fleshy fruits serving as effective dispersal agents clearly fall off rapidly as the forest is left behind, and it is not surprising that species producing such fruits become correspondingly scarcer. Production of a device that rarely functions is almost certain to be inadapative in the Arctic, where carbohydrate metabolism is strictly limited and the available food is better used to produce more seeds or an alternative device.

A number of plants in the Arctic do possess one or other of the devices recognized as being effective for long-distance dispersal in temperate regions,

TABLE II. Breeding-bird density in arctic and temperate habitats

Locality	Description	Breeding density ^a	
		Birds/10 acres	Birds/km ²
Isachsen	Cold, moist, high-arctic desert	0.15	3.71
Hazen Camp	Warm, dry, high-arctic desert	0.39	9.65
SW Baffin	Grassy low-arctic tundra	6.1, 8.5	151, 210
Chesterfield	Heathy low-arctic tundra	4.8	117
(Various)	Temperate desert and dry short-grass prairie	2.0-10.0	49.5-247
(Various)	Climax spruce forest	60	1482
(Various)	Deciduous woodland	15.6-105	386-2595
(Various)	Deciduous swamp	60-184	1482-4550

^aData from Hickey (1943), Savile (1951, 1961*a*), Savile and Oliver (1964).

but most are primarily temperate or alpine species that have invaded the arctic to varying degrees. Some examples follow.

Plumed seeds and fruits are, significantly, one temperate device that occurs freely throughout the Arctic. They are developed conspicuously in *Eriophorum*, *Salix*, *Dryas*, *Epilobium*, *Erigeron*, and *Taraxacum*. Plumed fruits are probably most effective in the Arctic in plants that exclusively occupy low or otherwise sheltered sites. This is particularly true for *Eriophorum*, which occurs predominantly in bogs and marshes. On upland sites, as we shall see, plumes are of little value. It may be significant that the plumeless nearctic *Geum rossii* has spread farther northward than the plumed palearctic *G. glaciale*.

Winged seeds and fruits are scarce. *Betula nana*, *B. glandulosa*, and *Rumex* spp. occur freely in the low arctic, and *Oxyria digyna* reaches the limit of land.

Small, light seeds are represented by *Diapensia*, *Pyrola*, and some Ericaceae, all essentially low-arctic, and by *Juncus*, with a few widespread species. The seeds of *Juncus* have a loose bitailed coat and are adapted to dispersal by both wind and water, a device found in scattered genera of various families of dicotyledons and monocotyledons.

The inflated nutlets of *Mertensia maritima* adapt this sea-beach species to marine dispersal. It is predominantly temperate to low-arctic, but has reached Svalbard and the White Sea, probably through the agency of the Gulf Stream. It also extends far northward in Baffin Bay, where open water is more extensive than in most of the Canadian Arctic.

Fleshy fruits are represented in the low arctic in North America by *Rubus chamaemorus*, *Empetrum hermaphroditum*, *Arctostaphylos alpina*, *A. rubra*, *Vaccinium uliginosum*, and *V. vitis-idaea*. Only *E. hermaphroditum* and *V. uliginosum* freely penetrate the high arctic; the rock ptarmigan, *Lagopus mutus*, probably carries

overwintered fruits north in spring. A related category is composed of succulent aquatic plants whose seeds are incidentally ingested by the pond ducks (Anatinae) along with the pulpy fruits and vegetative parts. If these ducks penetrated the arctic more freely, such plants as *Potamogeton filiformis* var. *borealis* and *Ranunculus pallasii* might be found farther northward.

Hooked fruits are virtually absent from the Arctic, only *Galium* spp. barely reaching it in a few locations. One plant that may be included in this category is *Carex microglochin*. The slender culms of this species are topped by a spike whose finely pointed perigynia reflex at maturity and are easily detached. When a bird or mammal passes through a stand of *C. microglochin* the culms bend over and the backward-pointing perigynia lodge readily in the feathers or fur of the animal. (The effectiveness of this device, which has evolved independently in such unrelated plants as *Triglochin palustris*, which barely reaches the Arctic, and in the temperate genus *Osmorhiza*, is evident to anyone who has worn exposed woollen socks when walking through mature plants of any of these species.) *C. microglochin* is predominantly temperate, but it extends far northward in Greenland, where the movement of birds is concentrated between the coast and the ice cap. It should be noted that northward spread must be predominantly in spring and from plants in late situations that failed to shed their perigynia before winter.

Some plants of wet situations are carried externally by birds, the wet disseminules clinging to feet or feathers. This mechanism is most highly developed in the minute water plants *Lemna* and *Wolffia*, but only two species are sparingly recorded north of the tree line (Polunin, 1959).

We thus see that the classical long-distance dispersal devices of temperate regions, far from actively developing in the Arctic, tend to be excluded. It is also clear from biogeographic studies (Savile, 1956, 1961*b*) that plants without such devices have generally spread as fast from their Wisconsin refugia as those with them. These observations provide ample warning against reliance on temperate mechanisms to explain arctic dispersal. All these mechanisms function in exceptional cases, but two much more general dispersal agencies, although not strictly confined to the Arctic, are most plentifully developed within it.

The less important mechanism operates through the grazing of geese in spring migration. As the vegetation becomes uncovered by melting snow in the Canadian Arctic it is lush and green for a day or so before it dries. In this stage, the brant goose, *Branta bernicla*, feeds on it voraciously and indiscriminately. Inevitably the birds ingest large numbers of seeds, many of which must be excreted in germinable condition. It has been suggested (Löve, 1963) that the passage rates through the intestinal tract cited by Ridley (1930) are too fast to allow the carriage of seeds across substantial sea barriers. But Ridley emphasized that these are minimum times and that hard-coated seeds may lodge in the gizzard folds for days and emerge in germinable condition. Even seeds that pass through the intestinal tract without delay must often be carried 100 to 300 km, and those that lodge in the gizzard may be carried many times as far. Several species of geese probably contribute to the dispersal of overwintered seeds in this manner. Although the total number of seeds so

transported must be much less than by the next method, ingestion may sometimes be important in dispersing species against the prevailing wind or across open water. This method perhaps should not be regarded as an arctic adaptation, for it is not clear whether any modifications of arctic species, such as unusually impervious seed coats, can be directly linked with it. The evolutionary significance of the mechanism lies rather in the fact that its existence helps to explain the lack of some temperate mechanisms, which, in the circumstances, become unnecessary and generally inadapative.

The second and more important mechanism is dispersal by wind in winter. Appreciation of this mechanism requires some understanding of arctic winter conditions.

Winter dispersal has long been familiar to those who have worked in the Arctic in winter or before the snow softens in late spring. Simmons (1913) recorded scraps of vegetation blowing past him, and quoted Sherard Osborn as distinguishing seeds of poppy, willow, and saxifrage among the abundant material traversing sea ice, often far from land. Lind (1927), in a thorough discussion, often overlooked because it was in a mycological paper, quoted other early observations. He referred further (1934) to the process in discussing the distribution of arctic fungi. Savile (1956, 1961*b*, 1964*b*) has further discussed some aspects of such dispersal.

We have seen (Section II, B) that once winter is fully established most of the snow falls as small, hard crystals, which become firmly locked together by strong winds into an extremely hard and generally smooth layer.

The contours of ridges and beach crests are smoothed (Fig. 5, *a*), so that the wind passes over them with minimal turbulence. In fact, when a ridge lies across the wind direction it acts as a venturi, and the wind sweeps over it with reduced pressure but increased velocity. Such ridges are thus almost perpetually bare, and plants on them are subjected to even more wind than those on level plains.

This is not a completely haphazard means of dispersal, for all material carried across sea ice (or a plain or frozen lake) tends to accumulate below a cliff, bluff, or high bank (Fig. 5, *b*). Seeds deposited by the eddy near the base of such a broad obstruction are accompanied by snow, mineral soil, and plant fragments. These sites are accordingly well watered, both by melting snow and by seepage; they accumulate soil and humus and they are among the most favorable sites for plant growth.

Many fruiting stems of all xerophytes and of most mesophytes are subjected to such wind action. In regions of light snowfall nearly all plants are affected in some degree, but dispersal is particularly favored in regions with low relief and adequate summer rainfall. In such regions mesophytes occur on relatively exposed shallow ridges, from which seed dispersal is highly reliable.

In early May at Chesterfield, when the snow was still too hard to be marked by a boot heel and generally as smooth as an asphalt road, I studied the crests of the marine beaches on which snow never persisted for more than a few hours. If a man or dog crossed a ridge he generally broke loose pieces of *Saxifraga tricuspidata* or *Arenaria peploides*, which dominated these sites. In a

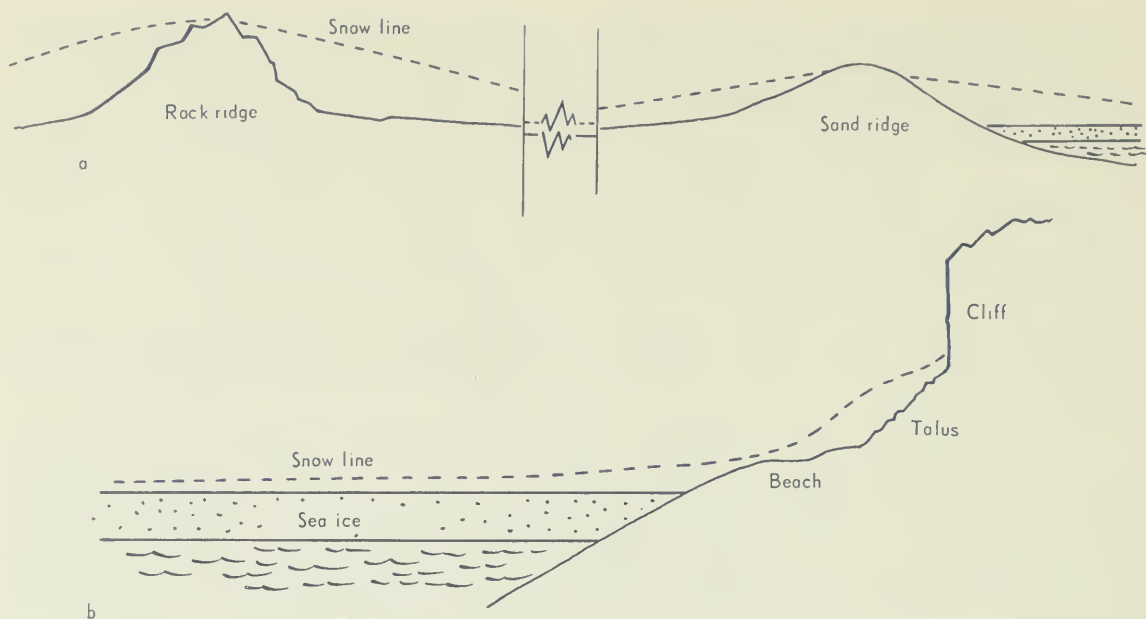


Fig. 5. (a) Smoothing of contours by wind-packed snow. (b) Accumulation of drifted snow and debris, including seeds, at foot of bank or cliff near shore.

moderate breeze such fragments were quickly blown out across the snow-covered sea ice, where they could be followed with field glasses for several hundred meters, traveling apparently little slower than the surface wind.

In regions of small tides, such as the western two-thirds of the Canadian Arctic Archipelago, open leads and high pressure ridges are scarce, and we have, in effect, a series of hills emerging from a level plain for about 9 months of the year. Tides are also very small on the shores of the Palearctic islands. There are thus many opportunities for capsules, seeds, and bulbils to be carried between islands during winter gales. The effectiveness of such dispersal is demonstrated by the distribution patterns of Nearctic plants (Porsild, 1964). Distribution is generally essentially continuous to the limit of the species, rather than sporadic as on islands in ice-free seas. The absence of many species from some of the northwestern Canadian islands is due to their elimination by climatic deterioration since the end of the hypsithermal interval (Savile, 1961*b*). In the Nearctic region we see only two important barriers to dispersal: Davis Strait, in which there is always open water along the Greenland coast; and Hudson Strait, which is choked with ice but which has enormous tides that keep the ice perpetually in motion and prevent the formation of smooth ramps of wind-packed snow along the coasts.

Snow abrasion, the principal scourge of arctic plants, is probably not a serious menace to wind-borne seeds, for the seeds and snow particles move together with very low relative velocities.

Published wind speeds for most arctic stations are not exceptionally high, but the figures are generally misleading, for sustained gentle to moderate breezes are uncommon. Instead prolonged calms commonly alternate with strong winds or gales. Thus the mean velocity, often 4 to 5 m/sec, is far from being a modal velocity. Table III lists the most prolonged gales recorded at

four high-arctic weather stations in the winter months of a single year. Although some of these months were substantially windier than average, stronger and more prolonged gales are far from uncommon at these and many other stations. Even at Eureka, the fifth of the group of high-arctic Canadian stations, which is ringed by high mountains, strong winds are occasionally recorded, although usually for quite short periods. It must be noted that each of the winds recorded in Table III blew from a nearly constant direction. Thus the figures in the last column represent approximately the distance that suspended particles would travel in each gale. Seeds or other macroscopic disseminules blowing along at or close to the surface would travel more slowly. If we assume a speed of travel of only half the average wind speed (probably too low a figure, for wind speeds over unobstructed sea ice must be appreciably higher than at the weather stations), we see that any of these gales might have carried seeds 800 to 2000 km, ample to reach the most isolated arctic island from its nearest neighbor if the ice were continuous. Thus dispersal by this means is easily effected between all the Nearctic islands. In years of heavy ice it must regularly be possible between Greenland and northern Spitzbergen and between the latter and the remaining Palearctic islands. It is probable that occasionally within the last 3000 years over-ice dispersal has been possible between Greenland and Iceland, for we must remember that we need continuous ice initially only against the shore from which the wind is blowing. As the gale continues the ice will be packed against the lee shore and become smoothed by snow before many of the seeds arrive.

Although many of the species dispersed by this means have no obvious

TABLE III
Prolonged strong winter winds at stations in the Queen Elizabeth Islands, 1954

Station	Date	Duration (hr)	Avg wind speed ^a		Km of wind
			(mph)	(m/sec)	
Alert	26-27 Feb	27	42.9	19.2	1860
Alert	5-6 Dec	48	29.1	13.0	2250
Isachsen	24-26 Jan	66	29.5	13.2	3150
Isachsen	8-11 Feb	75	31.7	14.3	3830
Mould Bay	11-13 Jan	72	28.9	12.9	3320
Mould Bay	26-29 Jan	81	30.3	13.5	3950
Mould Bay	10-12 Feb	33	29.9	13.3	1590
Mould Bay	11-13 Mar	51	33.3	14.9	2740
Mould Bay	5-7 Apr	48	35.2	15.7	2730
Resolute	26-27 Feb	36	40.2	17.9	2350

^aData from 3-hourly synoptic readings in Canada Dep. of Transport, Meteorological Branch (1960), measured at mast-head generally ca. 8 m above ground.

morphological modifications to enhance its efficiency, but are simply preadapted, some genera that are almost wholly arctic-alpine do have structures that seem to have developed in response to selective pressure favoring gradual release of the seeds in winter. The genus *Saxifraga* offers a striking example of such an adaptation. The genera of Saxifragaceae are delimited largely through characters that reflect pollination or dispersal mechanisms (Savile, 1961c). In *Saxifraga* we find that, although the flowers may be variously oriented, before maturity the capsules become strictly erect (Fig. 6, a). They are typically bicarpellate, have axile placentae, and open by a limited dehiscence of the narrowed apical part. The upright position and constricted opening ensure that no seeds are shed without considerable agitation of the fruiting stems, which become increasingly rigid as they dry after maturity. Some seeds may be flipped out by animals striking the stems, but we have seen that low bird and mammal density in the Arctic makes such dispersal ineffective even locally. Wind, however, is effective for both local and distant dispersal. The capsules dehisce at any time from August until late winter, but in any species and at almost any site a large proportion open during winter. As the wind increases, the stems begin to vibrate when a velocity determined by their size and stiffness is reached. Probably most seeds are shaken out only when resonant vibration sets in, and certainly none are shed until the wind speed is sufficient to carry them away from the parent plant. Any seeds that are shed in mid or late winter, when the terrain is predominantly smooth and firm, are almost certain to be carried a considerable distance.

Saxifraga seedlings are rarely found at the base of the parent plant, as frequently happens in some arctic plants, which supports the view that the mechanism is efficient. Further support comes from the distribution pattern of *S. tricuspidata*, a xerophyte often found on exposed ridges. It is abundant in Alaska and Yukon and spreads eastward across northern Canada, occupying most of the archipelago. It is abundant in west Greenland but is restricted to a small area in east Greenland and is virtually absent from Peary Land.* If the east Greenland population were a relict we would expect the plant to have spread far north and south and to occur in Peary Land. However, as Calder and Savile (1959) have indicated, the entire population of the species seems to have spread since the end of the Pleistocene from the refugia in Alaska, Yukon, and western Mackenzie, with the Scoresby Sound population originating from seeds (perhaps stems and capsules) blown across the Greenland ice sheet. It is noteworthy that the distribution of this species nearly matches that of *Dryas integrifolia* and is substantially wider than that of *Taraxacum lacerum*, both with plumed achenes, and both apparently originating from Alaska and Yukon. This mechanism is probably less effective in *S. hirculus*, predominantly a marsh plant, than in any other arctic saxifrage, but even this species sometimes occupies springy gravel flats or slopes from which the seeds are readily blown. The same capsule structure occurs with minor differences throughout the genus *Saxifraga* and must be regarded as alpine in origin although most

*The discovery of a single small colony, probably clonal, was recently reported by B. Fredskild (1966). The apparent isolation of this colony in an area that has been vigorously studied by biologists in recent years supports the view that it was established from a single immigrant seed within the last 50 to 100 years.

effective on the arctic plains.

Essentially similar mechanisms have evolved independently in *Papaver* and in some Caryophyllaceae, notably *Lychnis*. In these genera, however, there is no sharp distinction between the censer mechanism, in which a flexuous stem swings when struck and throws out the seeds, and the vibratory mechanism. The censer mechanism, which is a means for local dispersal, probably predominates in temperate species of these genera, and the vibratory mechanism evolved from it as representatives penetrated the Arctic. In *Papaver radicum* the tallest scapes are somewhat flexuous and may shed some seeds in gentle breezes, but the shorter ones are rigid. The habit of producing successive scapes through the summer ensures that some capsules will open in winter.

Most other arctic flowering plants release their seeds gradually, which guarantees that some are shed during winter, but in most genera there is no guarantee that they will be shed only when the wind is strong.

The siliques of Cruciferae are well adapted to gradual release of the seeds. The process is most evident in species with long siliques, such as *Braya humilis*, *Cardamine bellidifolia* (Fig. 6, b), *Arabis arenicola*, *Erysimum pallasii*, and *Eutrema edwardsii*, in which, with increasing desiccation, the valves gradually curve away from the supporting frame or replum, separating from the top, bottom, or occasionally both ends. By this means a considerable period elapses between the release of the first and last seeds. At sites with very severe climates the last seeds of *Cardamine bellidifolia* are not released until the following spring. Gales are likely to complete removal of the valves, at which time the remaining seeds are either freed or carried away with the valve. Thus there is some tendency for the seeds to be carried away from the parent plant at release. However, they are often found in the base of the plant, and the process is less reliable than that of *Saxifraga*. In short-podded crucifers, such as *Cochlearia*, *Draba*, *Lesquerella*, and *Parrya*, the release of the individual valves is more abrupt, but successive ripening of the siliques ensures that some seed is released in winter.

The pods of most arctic species of *Astragalus* and *Oxytropis* split at maturity and eject their seeds, as in many temperate and tropical Leguminosae. If the pods split after the onset of winter the round seeds are readily carried by wind. The inflated pods of *O. nigrescens* var. *uniflora* (*O. arctobia*) frequently absciss unopened and are freely blown about on sandy ground. It is probable that some pods are also blown over snow and ice before releasing their seeds. The same habit is known in a few temperate species of *Oxytropis* of sandy habitats.

Gradual release of seeds seems to be general in most other arctic plants, but it is not effective under all circumstances. If heavy snow comes early in the winter plants with weak or decumbent stems, such as *Puccinellia angustata*, may be pressed against the ground, and all the fruits are found lying close to the panicles in spring. But such suppression of dispersal seems to be unusual except at very unfavorable sites.

Even in species with plumed fruits, the release may be greatly delayed, occasionally until the succeeding summer in *Dryas* and *Eriophorum* (Savile, 1964c).

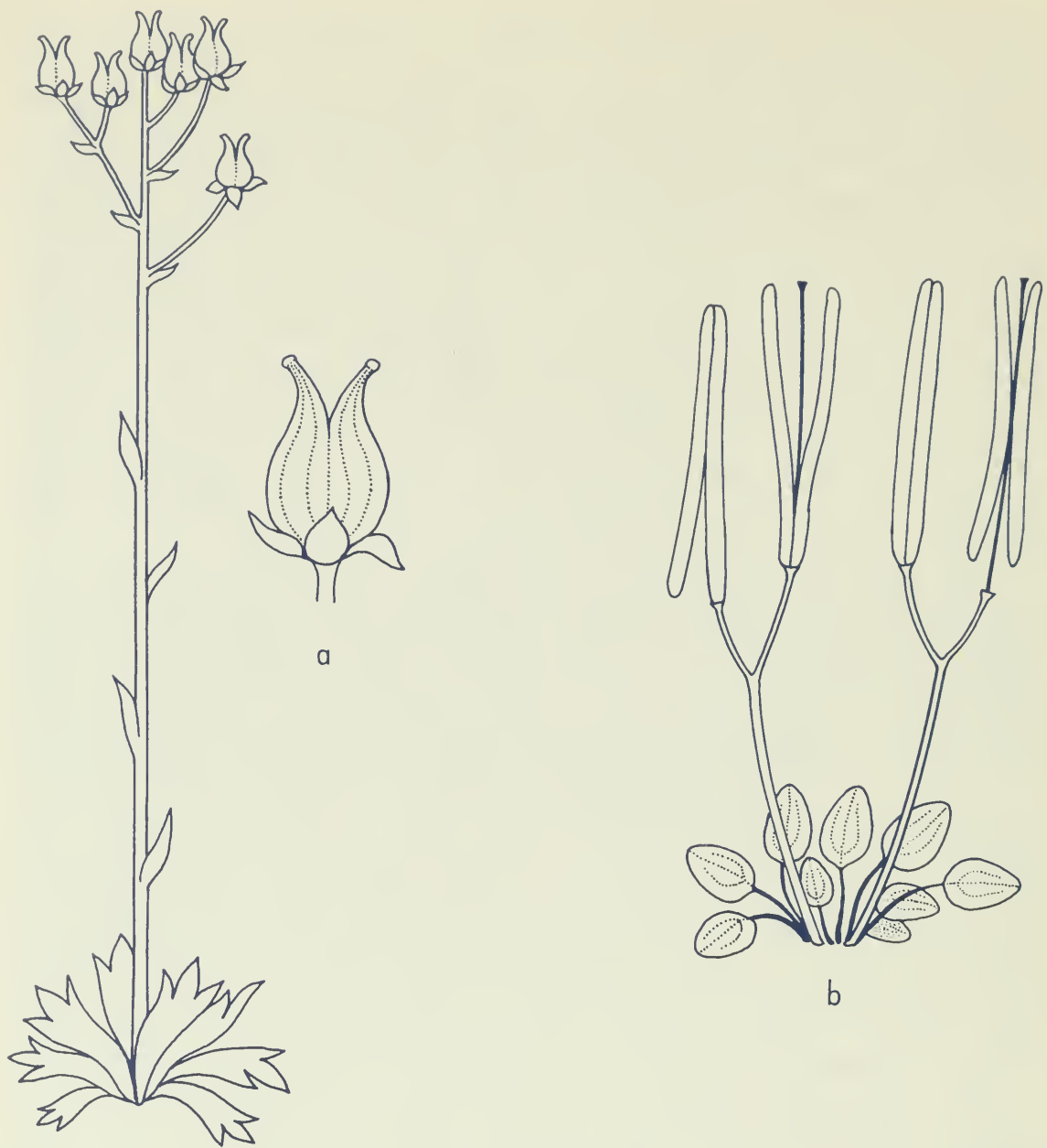


Fig. 6. Adaptations assisting in dispersal of seeds by winter gales: (a) *Saxifraga tricuspidata*, showing erect capsules; and enlarged view of capsule, showing constricted apical opening; (b) Fruiting stem of *Cardamine bellidifolia* with valves of silique curving away from replum.

Most arctic plants that reproduce by bulbils, including *Polygonum viviparum*, *Saxifraga cernua*, and viviparous forms of several grasses, are subject to winter dispersal to varying degrees. *Saxifraga foliolosa* generally grows in marshes where it is overtopped by grasses and sedges and its bulbils must generally be spread by water. However, it also occurs occasionally on springy slopes where wind dispersal may function, for the bulbils are gradually released.

Finally we must briefly discuss local dispersal, which ensures that some

seeds are carried clear of the parent plant. Although devices for long-distance dispersal have this effect, other devices operate only over distances of a meter or so. No such devices are peculiar to the Arctic, but several are found within it. In *Montia* and *Claytonia*, of which several species reach the Arctic, the mature capsules point upward at 45°, the valves dehisce, and their margins curve together to press against the smooth seeds and flip them often more than a meter. The same mechanism operates in some species of *Viola*. These genera occur in the Arctic in low-lying situations or beneath shrubs where wind dispersal is least effective.

Dispersal in the predominantly temperate genus *Chrysosplenium* is by splash cup (Brodie, 1951; Savile, 1953*b*), in which the kinetic energy of falling water drops throws the seeds out from the flared lip of the open capsule. This mechanism works best where large drops fall vertically from trees or cliffs. Near their northern limits *C. rosendahlii* and *C. tetrandrum* most often occur in open marshes, where rain usually falls obliquely and in small drops. Vertically falling large drops must generally fall only 30 cm or less from pendulous grasses and sedges in such sites and the seeds are probably thrown laterally no more than 15 cm.

The censer mechanism, mentioned above, may operate to some degree in a number of plants in the low arctic, where stems are tall and relatively flexible, including: *Juncus*, *Luzula*, *Tofieldia*, *Sisyrinchium*, *Lychnis*, *Papaver*, *Parnassia*, *Primula*, *Gentiana*, *Castilleja*, *Pedicularis*, *Rhinanthus*, and *Campanula*. However, the stems become progressively reduced with increasingly severe conditions until they can be flexed only very slightly and presumably the seeds must be bounced out by vibration as in *Saxifraga*. Comparative studies of the genera of Saxifragaceae suggest that the vibratory mechanism in *Saxifraga* is derived from a censer mechanism in an ancestral genus (Savile, 1961*c*). The same trend is apparent in various genera in the Arctic, but in many species it may be simply conditioned by the environment rather than genetically fixed.

Studies in the Canadian Arctic have shown not only that many plants have traveled several thousand kilometers since the end of the last glaciation, but that a number covered more than their present range during the hypsithermal and have since retreated substantially (Savile, 1961*b*; Blake, 1964; Bryson et al., 1965). It is clear that significant spread may sometimes be measured in centuries, or even decades, rather than millennia. Plant distributions indicate that glacierization of some islands has occurred once or more in the last 3000 years, and Ives (1962) has dated the end of an extensive glacierization in Baffin Island at about 300 years B.P. However, there has been a modest recolonization of all these areas. Although various dispersal mechanisms contributed to this rapid recolonization, winter dispersal by wind must have been predominant, for few birds would visit these areas until some vegetation existed.

The greater the dispersal distance the greater must be the average distance between disseminules. The successful establishment of a species after dispersal over very long distances thus largely depends on its being self-fertile. Self-fertility presumably became general in arctic plants mainly because of its value in speeding seed development, and its role in promoting rapid migration

must be regarded as secondary in such species. However, it is possible that in some instances the almost unlimited dispersal ability conferred by self-fertility first allowed a species to become established in the Arctic.

III Cryptogamic Plants except Fungi

A Introduction

The bryophytes, lichens, and algae are conveniently considered together, partly, it must be confessed, because we know very little about their biology in the Arctic, but also because their arctic representatives seem principally to be there through chance preadaptation to arctic conditions rather than through specific adaptations. In particular they share the ability to stop growth with impunity at any time and to resume it promptly as soon as conditions permit. In the mosses and lichens this ability may have evolved in temperate or tropical climates as protection from intermittent desiccation. Drought and cold resistance are intimately related and, at the cellular level, scarcely distinguishable. When these organisms invaded alpine and arctic regions, their state of perpetual drought resistance may have served, with the minimum of modification, to confer immediate cold resistance from a state of active metabolism.

The production of small, buoyant spores makes dispersal a minor problem in most terrestrial cryptogamic plants. In those mosses that seldom fruit in the Arctic, dispersal may be severely limited, for many species are confined to low sites that are deeply covered by snow. The majority of lichens are adapted to aerial or over-snow dispersal by wind.

B Bryophytes

Many mosses and liverworts have wide climatic tolerances and are excellently preadapted to the arctic. Holmen (1960) made a distributional analysis of the mosses of Peary Land that illustrates this fact. Of 134 species recorded, only four are strictly Nearctic: *Orthothecium acuminatum* is known only from Peary Land and is probably endemic to it, whereas the other three occur across the continent. Twenty species are Holarctic with only limited penetration of alpine regions. The remaining 110 are widespread in alpine or in boreal lowland regions or even essentially cosmopolitan. Such figures suggest a limited evolution of mosses within the Arctic and reflect both their great mobility there and the ease with which many species have become adapted to arctic conditions.

Many temperate mosses seem to be genetically variable, which suggests the plasticity necessary for establishment in the Arctic. They do not readily invade closed habitats. However, closed habitats, other than those formed by bryophytes, are scarce in the Arctic and lack of aggressiveness is thus not serious. Many species are monoecious and self-fertile, which aids the penetration of new areas without completely sacrificing genetic recombination.

The most important characteristic that adapts mosses to the Arctic is their capability for indefinite vegetative growth. Although some species fruit freely on favorable sites, all can persist vegetatively and many disperse mainly by vegetative means. Vegetative propagules are scattered freely by wind or water in summer, but must occasionally spread by wind in winter. A few

mosses have never been known to fruit in the Arctic, but it is possible that their populations are partly renewed by air-borne spores from temperate regions. In general mosses and liverworts are not dependent on the frequent completion of a seasonal fruiting cycle in anything approaching the degree found in the flowering plants.

Although able to metabolize whenever conditions permit, the bryophytes seem to be in a perpetual state of resistance to cold and drought. They can accordingly make some growth even in the worst of seasons. Some species grow profusely under the peripheral parts of perennial snowdrifts, appearing to be in excellent condition even in places that are uncovered only in mid-August in a warm season. In cold summers that follow a winter of heavy snow such areas must remain covered. It is accordingly clear that some bryophytes can withstand being covered for at least a year by snow and stationary ice. A few years ago Mr. K. C. Arnold recovered a considerable amount of plant material from beneath the retreating edge of the shallow ice cap on Meighen Island. This is stagnant ice, which preserves rather than destroys the surface features. The plants are known, from aerial photographs and ground studies, to have been covered for more than 5 years, but the material is too young for carbon dating and its exact age could not be determined. The flowering plants are completely dead although sometimes well preserved. Among several mosses a large clump of the conspicuous upland species *Rhacomitrium lanuginosum* appeared very fresh and a few cells took up neutral red in the vacuoles, but the plants failed to grow when planted in a cool growth room. However, an unidentified fragment of moss that was bright green when soaked in water was recovered from the middle of a clump of *Phippisia concinna*. Most of the cells of this fragment not only took up neutral red but plasmolyzed and deplasmolyzed repeatedly. It is probable that an intact plant in this condition would have grown under favorable conditions.

The ability to withstand complete coverage by snow or ice for a year or more is of considerable importance to bryophytes, for many of the arctic sites with an adequate supply of water are subject to deep and prolonged burial in snow. There is reason to believe that many mosses not merely persist but make appreciable growth under snow or ice thin enough to transmit light. As the snow becomes macrocrystalline in spring through melting and refreezing, it becomes increasingly transparent. Not only may sufficient light for photosynthesis reach the mosses, but, being generally dark in color, they absorb most of the light and the temperature of the tissues is raised. The outgoing infrared radiation is stopped by the snow (greenhouse effect) and the plants may be in a small snow cave substantially above the ambient temperature. Savich-Lyubitskaya (1960) cites several reports that suggest endogenous production of heat by mosses beneath the snow in the Arctic in spring and at mid-latitude alpine sites in winter. However, it is not clear whether the heat production, deduced from cavities in the snow about the erect sporophytes, is due to anything but the greenhouse effect. Indeed endogenous heat production in the Arctic, where the season for food production is short, appears to be an intolerable waste of food material.

Arctic mosses must obviously be capable of metabolism at low temperatures, but in some species the ability may indicate a tolerance rather than a specific adaptation (Section II, C, 2, *b*). Tallis (1964) studied the physiology of *Racomitrium lanuginosum*, which is widespread in the Arctic, but occurs far southward only on alpine peaks. He showed that maximum elongation occurs at 12–13 C and, with ample water, maximum net assimilation at 14 C. Net assimilation fell off very rapidly above and below 14 C, being less than half the optimum rate at 10 C and 20 C. These optima are very low for land plants and are well below the maximum soil surface temperatures recorded even at such a cold station as Isachsen. Despite the severely depauperate flora at Isachsen, *R. lanuginosum* grows profusely over the rocky hills, partly because frequent fog and rain ensure adequate moisture, but partly, it now seems, because of its low temperature preference. The scarcity of this species at Hazen Camp (Savile, 1964*c*) and at some other sites in mountainous regions may be due as much to high surface temperatures on sunny days as to aridity.

Igumnova and Shamurin (1965) showed that *Sphagnum angustifolium* has a much higher transpiration rate than a variety of mosses, lichens, and vascular plants. Lack of resistance to transpiration may be the principal factor in preventing the occurrence of *Sphagnum* in high-arctic regions with a continental climate where summer aridity is often serious. In most other mosses substantial resistance to water loss allows metabolism to proceed under slight to moderate aridity. However extreme xerophytism is not found in any mosses although most species can withstand indefinite drying and resume metabolism when water becomes available.

Some mosses are essentially cosmopolitan and have enormous ecological tolerance. Hedberg (1964) records several species, widespread in the arctic and reaching 83° N latitude, from the equatorial Afroalpine areas, where the daily temperature fluctuation is enormous and light intensity is extremely high with a constant 12-hr photoperiod. Such species, if they are genetically homogeneous, must have extremely wide physiological tolerances.

Although many bryophytes that occur in the Arctic are somewhat depauperate representatives of the same species as seen in temperate regions, Steere (1953) pointed out that this condition is not universal. He cited a number of mosses and liverworts that are solely or primarily arctic, which, so far from being depauperate, are among the most robust representatives of their genera. It would be of interest to know whether such species have unusual physiological adaptations to low temperature and low light intensity.

C Lichens

The lichens are, in general, poikilohydric; i.e., they readily persist with extremely low metabolic rates when dry. In this condition they withstand extremes of heat and cold with minimal injury.

All lichens seem able to take up moisture from atmospheric water vapor by hygroscopic action of cell-wall material. They cannot retain moisture efficiently in extremely dry air, but dry out without injury. Their water relations have been reviewed by Heatwole (1966). On wetting, they resume

full activity within approximately a minute. Thus they withstand the arctic winter with impunity and can make the most of brief opportunities for growth in the bleakest arctic summers. Although lichens are subject to competition and parasitism, these factors are not serious in the Arctic, where habitats are usually only sparsely filled and populations of a species are low in density or patchy in distribution.

Probably nearly all arctic lichens invaded the newly available arctic plains from adjacent mountain systems or arid temperate situations. Although vast arctic areas are too poorly known to lichenologists to permit a positive statement, it seems nearly certain that lack of competition allows the establishment of some lichens on sites where they would not otherwise survive. A small lichen clump collected on almost completely sterile gravel on the west coast of Meighen Island (80° N), one of the bleakest ice-free sites in the Nearctic Region, proved to be *Metasphaeria decolorella*, stated by Dr. R. Santesson to be not rare in the Scandinavian mountains but previously unreported in North America. More adequate collecting will surely prove this lichen to be much more widespread in North America, but its occurrence at this site seems to reflect extreme tolerance of severe conditions under complete lack of competition.

Because they typically occupy more exposed sites, lichens are more subject to snow abrasion (Section II, B) than are mosses. Closely appressed crustose species predominate on the more exposed sites, the habit evidently being adaptive against both abrasion and desiccation. Weber (1962) showed that continued abrasion by mineral grains may not only check the growth but even reduce the size of lichen colonies. Snow abrasion in the Arctic is probably less violent in its action but must often substantially reduce the net annual growth of exposed colonies.

It is probable that many lichens can survive for one to several years under snow or ice. They appear well fitted to survive on small nunataks that remain covered in unduly cold summers. However, there is no indication that they can survive indefinitely under ice. If a melting ice sheet has been stationary they emerge with a fresh appearance but quickly deteriorate.

D Algae

For a distributional analysis of algae in an arctic region we may use the treatment of Whelden (1947) for the eastern Canadian Arctic. In a treatment that is recognized to be seriously incomplete for the northern islands, Whelden recorded 383 species excluding diatoms and marine phytoplankton. Only 16 of these species are not recorded from outside the Arctic. Most of these 16 species are desmids recorded from a single site, some of which may prove, with more adequate sampling, to occur in the temperate zone, for several species recorded by Whelden were previously known only from the temperate type locality. Some of the more abundant species are virtually cosmopolitan. Despite inadequacy of sampling it is clear that in the algae, as in the bryophytes and lichens, the arctic flora is predominantly an attenuated temperate one. The

attenuation is, however, extremely uneven, with blue-green algae (Cyanophyta), desmids (Desmidiaceae), and diatoms (Bacillariophyceae) making up roughly 95% of the total.

Except for a limited number of species found on wet ground, where snow cover is usually ample, the arctic algae occur in aquatic habitats in which the range of seasonal temperature variation is relatively small. Thus few if any specific winter adaptations are needed. Prescott (1963) suggests that the very wide distribution of most algae reflects their great adaptability, but the comparative uniformity of aquatic habitats is as probable an explanation.

Low light intensity is probably a critical factor for most arctic algae. To the normal loss of light with increasing water depth that occurs at all latitudes must be added: low initial light intensity due to low solar altitude; loss from increased reflection at the surface due to low angle of incidence; and loss of intensity due to ice or ice and snow persisting on lakes until far into summer. Both Prescott (1963) and Hobbie (1964), working in arctic Alaska and studying population density and productivity respectively, have shown that metabolic activity starts in spring before the snow melts and reaches its peak after the snow has melted but while the lakes are still ice-covered. After the ice melts, the water temperature rises quickly but growth drops abruptly, probably not because of the increased temperature but because turbulence prevents the algae from remaining in the euphotic zone. Prescott suggested that the large chloroplasts of the desmids, which are especially abundant in the arctic, are adaptive to low light intensity.

Little has been reported on specific temperature requirements of arctic algae, but it is clear that most species must be able to metabolize at low temperatures. Not only are the water temperatures little above 0 C for much of the summer, during which time, as we have seen, metabolism is relatively high; but low light intensity limits the heat that can be absorbed by the algal cells.

Prescott (1963) noted that vegetative algal cells revived promptly when thawed from ice, which is reminiscent of the behavior of bryophytes and lichens and, indeed, of the flowering plants in summer. He also observed that in some species of algae large numbers of encysted cells persisted through the summer, and suggested that some species may be permanently encysted under local conditions. He was not able to revive and grow enough of these encysted cells to determine whether any wholly arctic species are involved in this behavior, but it appears that encystment is generally a phenotypic modification of predominantly temperate or subarctic species.

The blue-green algae are found abundantly on moist soil at cold arctic sites where nitrogen deficiency is pronounced. Many blue-green algae, about half of those tested, according to Fogg (1962), are capable of fixing nitrogen. It is probable that this ability largely accounts for their comparative abundance in these unpromising situations.

E Vascular cryptogams

Many ferns, horsetails, and clubmosses invade the Arctic to varying degrees, along with a few species of *Isoetes* and *Selaginella*. A few species virtually reach the limit of land in appropriate habitats. There are, however, no fully arctic species. In fact, those that reach farthest north include *Equisetum arvense* and *Cystopteris fragilis*, which are widespread in temperate lowlands.* Apart from the great mobility assured by their buoyant spores, the occurrence of these species in the Arctic seems to be due principally to their tolerance of marginal habitats where competition is slight. They grow in the temperate zone in habitats too severe for other plants to occupy freely (e.g., leached sandy soil or exposed subsoil for *E. arvense* and dry cliffs for *C. fragilis*). In the Arctic they are relatively widespread and occupy more diversified habitats, because the severity of the climate causes many habitats to be incompletely filled and biological competition is slight or sometimes nonexistent.

Although it is probable that physiological adaptations to low temperature, low light intensity, and long photoperiod have occurred in arctic populations of some species, the lack of morphological distinctions suggests that the vascular cryptogams have undergone less evolutionary change in the Arctic than any other group of plants.

**Equisetum calderi*, described from the Canadian Arctic, is a depauperate form of *E. arvense*, which appears, from field observations, to be without genetic distinction.

IV Fungi

A Introduction

The great majority of arctic fungi are parasitic or saprophytic upon leaves and stems of flowering plants. Because they are heterotrophic in their nutrition they are more dependent upon appropriate substrate than are most cryptogams. Some of the completely terrestrial species, and possibly some aquatic species, may be able to persist and spread indefinitely by vegetative means. But most fungi are restricted, as individual colonies, to a plant that is spatially isolated from its neighbors. This is true whether they are plurivorous, like many saprophytes, or confined to one or a few host species, like some saprophytes and almost all parasites. Within these confines some fungi might conceivably persist for substantial periods by vegetative spread. This condition may be approached by a few saprophytes that occur on the oldest, partly decayed leaves, which are packed closely together. But most higher plants do not have an unlimited existence as individuals, and ultimately even such fungi must sporulate to survive. Most fungi grow on living or recently killed plant parts, which are not in contact with each other, and in such species regular sporulation is essential for immediate survival as well as dispersal.

Because of these limitations, selection in arctic fungi has favored devices that promote reliable sporulation, and we find fully as close parallels with the flowering plants as we do with the other cryptogams.

No elaborate morphological devices are known to have been specifically evolved in response to arctic conditions. However, modifications of the life cycle and physiological changes, which are of great importance although probably involving a few mutations, are common.

Light is essential for sporulation in some temperate fungi and may well be for some arctic species, but no critical photoperiod requirements are known, and it is unlikely that the continuous daylight of the arctic summer has hindered any fungi from entering the region. Light is of great indirect importance in that its absorption raises the temperature of the fungal cells and allows metabolism when the ambient temperature is very low (Section II, C, 2, *a*). Deeply pigmented walls of mycelium, sporocarps, and even spores are predominant in the fungi that attack the aerial parts of plants. One function of such pigment is certainly heat absorption, but it also shields protoplasm of air-borne spores from injury by ultraviolet radiation, and it or some associated material reduces water loss. Raising temperature and reducing desiccation seem to be the chief functions of wall pigments in the Arctic.

Coldhardiness has not been specifically studied in the fungi, but it is presumably very similar to that found in the higher plants and will not be discussed. We must remember that, as in other arctic plants, summer coldhardiness is a more important problem than winterhardiness, for metabolism must be resumed promptly whenever conditions permit.

B Adaptations to cold, short summer

The production of spores despite low temperature and a short growing season is the principal limitation to survival of fungi in the Arctic. It will be most convenient to treat the obligate parasites separately from the saprophytes and facultative parasites, because their dependence on living host tissues throughout their development imposes additional restrictions.

1 Saprophytes and facultative parasites

Although facultative parasites generally attack living leaves and stems, they are able to complete their growth and development after the death of these organs. They are often very restricted in host range, but in most other respects closely resemble the saprophytes.

a Simplification of life cycle and breeding system. A large proportion of the ascomycetes possess asexual conidia (spores dispersed by wind, rain, or occasionally insects) in addition to the sexual state (the ascus, from which ascospores, the immediate products of meiosis, are discharged). In most temperate species there is a succession of conidial generations during the summer. The asocarps start to develop in late summer, mature in late winter, and discharge their spores in spring, completing a regular annual cycle. The conidial generations serve to multiply and disperse the fungus, whereas the ascigerous state overwinters it and is the seat of genetic recombination, but its roles of multiplication and dispersal are less pronounced.

In the Arctic there is no time for such a succession of states in a single year. Four tendencies have been noticed: (i) The conidial state is completely suppressed. (ii) The conidial state develops independently from the ascigerous state, behaving as, and perhaps eventually becoming, an independent species. For example, the common saprophyte *Mycosphaerella tassiana* has *Cladosporium herbarum* for its conidial state but, although both are common, they are almost never associated in the Arctic. In fact the two states are not regularly associated even outside the Arctic and divergence may have started long ago. (iii) A conidial state is produced upon living or 1 year-old leaves of the host and the ascigerous state develops gradually in the succeeding one or more years. (iv) The conidial state develops simultaneously with the ascigerous state, the conidiophores often arising from the asocarps.

As far as is known all arctic fungi are self-fertile. Spermatia are known to be formed rarely by at least two arctic ascomycetes, *Mycosphaerella pyrenaica* and *M. saxifragae*, but it is probable that they simply have not yet been completely eliminated. Self-sterility both delays development of the sexual state of a fungus and decreases the likelihood of its establishment after dispersal over a great distance, closely paralleling its effects in the flowering plants (Sections II, C, 3, b, and II, D).

In compensation for the substantial reduction of genetic recombination caused by the adoption of self-fertility and its apparent elimination in the separation of conidial states as independent species, the fungi have developed substitute mechanisms. (i) Heterokaryosis and vegetative nuclear exchange.

The mycelial cells contain two to many nuclei; through hyphal fusion nuclei are exchanged between genetically different mycelia. (ii) Parasexuality. This process, reviewed by Pontecorvo (1956), was first demonstrated in 1952. It goes further than heterokaryosis, allowing complete segregation and recombination of genes carried in different nuclei of heterokaryons. The steps in the cycle are: fusion of two dissimilar haploid nuclei in a heterokaryotic mycelium; multiplication of the resulting diploid heterozygous nucleus together with the parental haploid nuclei; eventual sorting out of a homokaryotic diploid mycelium, which becomes established as a strain; mitotic crossing over during multiplication of the diploid nuclei; progressive, gradual, vegetative haploidization of the diploid nuclei. As Pontecorvo has remarked, the parasexual cycle is less perfect but more flexible than the sexual cycle. The sequence of steps is not as precisely fixed as in the sexual cycle. The system provides for storage of genetic diversity in both heterokaryotic and heterozygotic condition in a single mycelium, and it provides reassortment of all this diversity in haploid and diploid conditions "ready for the sieve of natural selection." The process may seem complex and unduly prolonged, but we should remember that all the steps are incidental to normal vegetative growth and that actually no time is wasted by it at all. It must be emphasized that the demonstrations of parasexuality have all used temperate fungi, but the very nature of the process suits it perfectly to arctic fungi, in which it almost certainly occurs. The assumption that it does occur freely in the Arctic makes the speciation of independent conidial states comprehensible.

Detection of parasexuality requires a substantial body of genetic information about a species, considerable skill, and a great deal of work. Consequently it has been demonstrated in relatively few fungi, generally important crop pathogens or species used in biochemical genetics. However, it was found in the first four species tested by Pontecorvo and his colleagues and may be general in all classes of fungi.

It is apparent that in simplifying their life histories and breeding systems, the fungi have gained a great deal and lost very little. The deletion of conidia by an ascomycete reduces its potential dispersal, but as we shall see in Section IV, C, dispersal is no great problem in the Arctic. The time saved by adopting self-fertility more than compensates for the reduced rate of recombination.

b Gradual development of sporocarps. At high-arctic sites it is clear that sporocarps of nearly all ascomycetes and some conidial fungi never mature in a single year (Savile, 1963*a*). Generally the tissues are invaded by the fungus with almost no symptoms in the first year, very immature asocarps are formed in the second year, and the spores are produced in the third or fourth year. *Isothea rhytismoides*, which attacks the leaves of *Dryas*, may mature in the second year near the tree line, but requires an extra year or two farther north. This ability is shared by six orders of ascomycetes, including nearly all the arctic species of this class. The apothecia of the discomycetous genus *Sclerotinia*, of which three species grow on arctic sedges, mature in a single summer. However, they develop from food stored in large sclerotia and it is probable that at very cold sites, such as Isachsen where *S. vahliana* grows freely, the sclerotia take more than 1 year to develop, although some mature each year.

In ascomycetes that do produce conidia the sequence is often variable. In species of *Mycosphaerella* that are initially parasitic, such as *M. oxyriae*, *M. pyrenaica*, *M. saxifragae*, and *M. taraxaci*, we often see the conidiophores arising from the ascocarps (Savile and Parmelee, 1964), but the conidia may also precede the ascocarps by a year or more. *M. chamaenerii* produces conidia on living leaves north approximately to the tree line, but in the Arctic the conidia and ascocarps may occur together on leaves at least 2 years old. In these fungi we see both the repeated cessation and resumption of growth until the ascocarp finally matures, and a telescoping of the life cycle, so that conidia and ascocarps mature simultaneously rather than in succession. A few of these fungi occur in temperate regions, where they behave in an orthodox manner. It is not known whether the arctic modifications are simply induced by the climate in species of great plasticity, or whether genetically distinct races occupy the arctic and temperate zones.

This delayed development is made possible by the fact that bacterial decay is so slow in the Arctic that leaves and herbaceous stems persist for several years. The slight bacterial action also increases the ecological scope of the fungi.

The fruit bodies of at least some arctic puffballs (Lycoperdaceae) take more than 1 year to mature, as may readily be seen when sporocarps are produced contiguously in several successive summers. In southern Somerset Island (72° N), in a colony of *Calvatia tatrensis*, very immature sporocarps were found in late July mixed with ones that were shedding spores but, from the weathered peridium, had clearly overwintered. At Hazen Camp in 1962, a clump of *C. cretacea* contained an immature sporocarp of 1961, one of 1960 that was starting to shed spores, and one of 1959 in which the peridium was severely weathered and the majority of spores had been shed. Owing to extreme aridity no sporocarps were initiated in 1962 (Savile, 1964c).

c Prolonged development of mycelium in soil. Although such small mushrooms (Agaricales) as grow among mosses on perennially wet sites seem to fruit annually, fruiting is evidently intermittent on upland sites, as is often true in temperate habitats. The mycelium may develop in the soil for several years, gradually accumulating nutrients, but fruits only when conditions of moisture and temperature are favorable. In some years *Agaricus arvensis* at Hazen Camp has produced numerous sporocarps nearly as large as it forms in temperate grasslands, but in the very dry season of 1962 it produced none. The same behavior is suspected in a few large discomycetes (*Paxina* spp.). This behavior, which largely prevents waste from abortive fruit-bodies, seems adaptive against both drought and cold in the Arctic.

Although indefinite delay in fruiting is not possible in most of the microfungi that invade herbaceous plants, it may be approached in some species that take part in the final stages of decomposition, such as *Acrospermum compressum* and *Cephalosporium* spp., for which a continually renewed supply of old leaves permits prolonged vegetative growth. In some of the obligate parasites we shall see an analogous form of vegetative persistence (Section IV, B, 2).

2 Obligate parasites

Dependence on living host tissues for nutrition complicates the problem of arctic survival for the obligately parasitic fungi, which are predominantly rusts (Uredinales) or smuts (Ustilaginales), but include a few leaf-gall fungi (Exobasidiaceae), downy mildews (Peronosporaceae), powdery mildews (Erysiphaceae), and Chytridiaceae. These fungi have three choices: completion of the life cycle in one summer; growth upon hosts with evergreen or winter-green leaves; or adoption of a systemic-perennial habit, which allows the fungus to persist for the life of the host plant whether it fruits or not. Simplification of the life cycle may accompany any of these choices.

Obligate completion of the life cycle in 1 year embodies the same risk as the annual cycle in flowering plants. Persistence at high latitudes accordingly demands rapid growth at very low temperatures.

In the smut genus *Anthracoidea*, of which several species penetrate the high arctic, infection is always localized, and, because the annual florets of *Carex* and *Kobresia* are the site of infection, the cycle must be regularly completed in a single year. Infection takes place through the stigma at the time of anthesis and the fungus replaces the achene by a sorus (largely a mass of closely packed spores), which ruptures the perigynium. Self-fertility is apparently universal in the genus (Kukkonen, 1963) even in temperate species, and genetic recombination probably occurs only when double infection of a floret allows nuclear reassociation. The overwintered spores largely remain in place on the old inflorescences and are gradually released in spring, often being blown to stigmas of adjacent new inflorescences where high humidity aided by moisture on the stigmatic surface allows prompt germination. It is possible that some of the arctic species are particularly adapted to rapid development at low temperature, but in general the adaptations seem to be those in common with the temperate species. Some arctic species may be directly restricted by temperature, but in others very sparse fruiting of the hosts, which enormously decreases the chance of a spore landing upon a stigma, seems to limit the range (Savile, 1963*a*). This situation closely parallels that seen in parasitic and predacious insects in the Arctic (Downes, 1964). When the host population becomes greatly reduced in density, the parasite has little chance of surviving unless it can broaden its host spectrum or be dispersed with the host and so maintain the association. The latter device has been employed by some fungi, as described in Section IV, C.

A few rusts with localized mycelium occur in the Arctic on hosts whose leaves die after a single season. In these species the teliospores mature before the onset of winter and germinate in spring as soon as adequate warmth and moisture are available, using stored food to produce basidia and the small, forcibly discharged basidiospores; the latter infect the new leaves. One such species is *Puccinia eutremae*, which may be limited to the low arctic by the lack of overwintering leaves on its host, *Eutrema edwardsii*, which extends much farther north. *Cochlearia officinalis* takes what is thought to be the same rust, but, although it has some winter-green leaves, the plants live only a few years and are, perhaps, too precarious a substrate to allow persistence of the rust far north of the tree line. On the other hand *P. bistortae*, with localized sori on

Polygonum viviparum (which has no winter-green leaves at least in continental climates), reaches northern Ellesmere Island, whereas some rusts whose hosts have winter-green leaves drop out at quite low latitudes. Clearly this host character is far from being of universal importance.

Only two powdery mildews occur extensively in the Arctic. *Erysiphe graminis* occurs on several grasses, principally *Poa* spp., but produces only conidia on simple conidiophores without any elaborate fruiting bodies and readily matures these spores even at some high-arctic sites. *Sphaerotheca fuliginea*, which, like most powdery mildews, demands a relatively dry climate, produced ascocarps profusely on several dicotyledons at Hazen Camp, maturing them by late July in the warm season of 1962, about 50 days from the initiation of growth. This species certainly has a capacity for rapid growth at low temperatures, for it also had fruited profusely in the much colder summer of 1961.

There is little doubt that the occurrence of evergreen or conspicuously winter-green leaves permits the survival of several parasites in the high arctic, where they would otherwise be eliminated by short seasons. The leaf smut *Ustilentyloma pleuropogonis* survives at Isachsen only because some leaves of *Pleuropogon sabinei* stay green for most of their second summer, allowing the sori to mature with certainty (Savile and Parmelee, 1964). *Puccinia cruciferarum* on the substantially winter-green *Cardamine bellidifolia*, *P. heucherae* var. *saxifragae* on the strongly winter-green *Saxifraga nivalis* and *S. tenuis*, and *P. pazschkei* var. *tricuspidatae* on the evergreen *S. tricuspidata* can follow their hosts almost to the limit of land because sori that fail to mature in 1 year can do so in the next.

The systemic-perennial habit in parasitic fungi is closely analogous to the perennial habit in flowering plants: occasional failure to fruit does not wipe out the population. The proportion of systemic species in the Arctic is much higher than in temperate regions. Three parasites of the nearly ubiquitous *Saxifraga oppositifolia* follow it almost to the limit of land in the Canadian Arctic, and all three, *Melampsora epitea*, *Puccinia fischeri*, and *Arcticomyces warmingii*, are systemic-perennial. The last two of these fungi barely completed fruiting in an average summer at Isachsen, and at such sites winter must often set in before they fruit. The sori of *P. fischeri* can probably resume development in the following spring, but the leaves infected by *A. warmingii* do not seem to live through the winter and further development of the basidia and spores must therefore be impossible. The systemic habit generally permits the fungus to produce substantially more spores than localized infection allows, but this advantage is partly counterbalanced by conditions for infection being more critical.

As noted by Savile and Parmelee (1964), *Ustilago bistortarum*, which has systemic and localized phases at low-arctic, subarctic and alpine sites in nearly equal abundance, is almost exclusively systemic in the high arctic. It is not believed that these phases represent genetic races, although they were originally given distinctive names. The conditions for infection of the young leaves are seldom met under high-arctic conditions, but the production of numerous spores on systemically infected plants year after year allows occasional infection in exceptionally favorable seasons. The systemic-perennial

habit allows a related smut, *Ustilago oxyriae*, to flourish on decidedly arid sites where conditions suitable for infection must often be lacking, and the same is true of a systemic rust, *Puccinia holboellii*, on *Erysimum pallasii*.

Modifications of life history and breeding system in the Arctic are most conspicuous in the rust fungi (Savile, 1953*a*), whose orthodox cycle is very complex. To appreciate these modifications we must briefly review the full cycle (Fig. 7). In the primary full cycle possessed by many temperate rusts, including nearly all primitive species, overwintered teliospores germinate in spring to produce basidia from which four basidiospores are forcibly discharged. In heteroecious species, such as *Puccinia graminis* and other important cereal pathogens, the basidiospores must drift to leaves of the alternate (aecial) host, which they infect to produce haploid pycnia of two strains. The pycnia secrete pycniospores and copious nectar. Insects attracted by the nectar transfer pycniospores to receptive hyphae in pycnia of the opposite mating type, to which they fuse, and their nuclei pass through the mycelium to the incipient aecium. Binucleate cells in the base of the aecium produce chains of binucleate aeciospores, which infect the telial host to initiate usually several generations of uredinia (also with binucleate spores). Late in the summer the uredinia are replaced by telia, whose spores are generally deeply pigmented and serve two main functions: they house the fusion and subsequent meiotic divisions of the paired nuclei, and they overwinter the fungus. The aeciospores and urediniospores are diaspores, serving to disperse and multiply the fungus. The basidiospores possess delicate unpigmented walls, providing little protection from desiccation or ultraviolet radiation. Consequently these spores can generally disperse the fungus for only very short distances.

The orthodox full-cycled rust is found north approximately to the tree

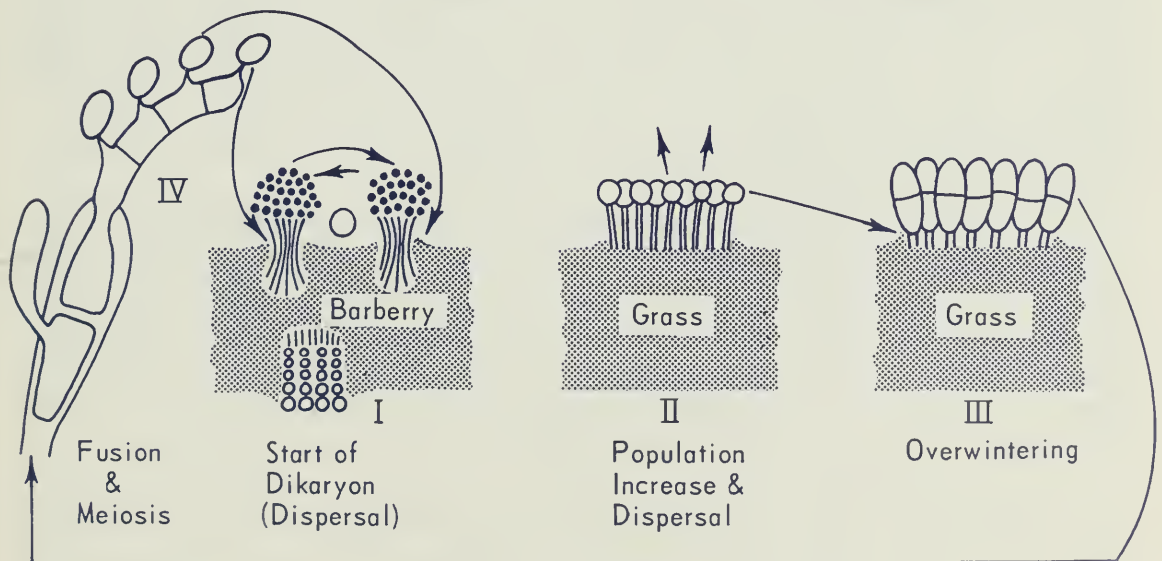


Fig. 7. Life cycle of temperate, heteroecious, long-cycled rust (e.g., *Puccinia graminis*). Symbols O, I, II, III, and IV represent pycnia, aecia, uredinia, telia, and basidia, respectively, and their spores.

line, where there is time for at most one uredinial generation and the small population increase makes persistence impossible unless the aecial and telial hosts grow virtually in contact. Some heteroecious species that occur close to the tree line, such as *Puccinia karelica* and *P. praegracilis*, have become self-fertile and lost their pycnia. This elision is estimated to save about 15 days under subarctic conditions in the time needed for maturation of the aecia. However, even this device seems inadequate to allow orthodox heteroecious rusts to spread far into the tundra. Heteroecism so reduces the chances of basidiospores or aeciospores landing upon the appropriate host that persistence is impossible without a substantial uredinial buildup, for which there is no time.

A few heteroecious rusts persist in the Arctic through the ability of their urediniospores to overwinter, the cycle being reduced to an unlimited succession of uredinial generations, one or more of which occur each year. The best example of such a rust is *Puccinia poae-nemoralis*, which attacks *Poa* spp. nearly throughout the Arctic. It never forms telia in the Arctic, rarely does so in the temperate zone, and is completely independent of aecial hosts. Until the discovery of parasexuality it was assumed that genetic recombination was impossible in rusts that persist solely in the uredinial state. In recent years pathologists have investigated the question of gene exchange in uredinial cultures of the cereal rusts, in which the problem is of great practical importance and for which much genetic information is available. Several authors (Watson, 1957; Vakili and Caldwell, 1957; Ellingboe, 1961; Johnson, 1961) have published reports that strongly suggest genetic recombination in such cultures at low frequency. The results are not all unequivocal, for it is difficult to distinguish between somewhat rare recombinations and contaminated cultures, which are a perpetual hazard in laboratories where many rust races are handled routinely. However, Watson's results seem to be beyond question. Population studies of *P. poae-nemoralis* strongly support the occurrence of somatic recombination in this species. A subspecies, *hyparctica*, occurs in northern Ellesmere Island and probably Peary Land, which can only have been isolated from the typical species since the onset of the Wisconsin glaciation, but which differs in host specialization and in pigmentation, size, wall thickness, and sculpturing of the spores (Savile and Parmelee, 1964). It is inconceivable that the many mutations needed for these changes could have accumulated in this population without gene flow.

In the genus *Chrysomyxa*, whose species alternate between spruce and various evergreen dicotyledonous shrubs, an interesting telescoping of the life cycle has occurred, described in detail by Savile (1953*a*). Dikaryotic mycelium overwinters in the green leaves of the telial host and produces uredinia and telia simultaneously in spring. Because of this habit several species are abundant at the tree line, and uredinial succession allows them to persist on *Pyrola*, *Ledum*, *Rhododendron*, and *Empetrum* for some 500 to 700 km beyond it.

Autoecious long-cycled rusts might be expected to spread farther north than heteroecious species, but our distribution data do not allow a thorough assessment of their potential. *Uromyces armeriae*, which lacks pycnia and is presumably self-fertile, has been recorded slightly beyond the tree line in the western Canadian Arctic. It and *Phragmidium arcticum* were found abundantly

enough at Great Whale River, near the tree line on Hudson Bay, to suggest that they might persist some distance beyond it. Some autoecious species have dropped either uredinia (e.g., *Uromyces lapponicus*) or aecia (e.g., *Puccinia hieracii*). *U. lapponicus*, which has systemic-perennial aecia, occurs, almost exclusively in the aecial state, at least 700 km beyond the tree line, and may reach almost the limits of its hosts, *Astragalus* and *Oxytropis* spp. It is suspected that aeciospores may produce further aecia rather than only telia, a modification known in a few temperate and alpine rusts. *P. hieracii* is known on *Taraxacum* nearly 500 km beyond the tree line in sufficient abundance to suggest that it extends appreciably farther.

In the ultimate reduction of the life cycle only telia are produced whose spores germinate to produce basidia and basidiospores. Infection by a single haploid basidiospore gives rise to dikaryotic mycelium of paired sister nuclei and ultimately teliospores. This life cycle, which is of relatively minor importance in temperate regions, is the major one found in the Arctic. A few species, *Puccinia drabae*, *P. fischeri*, *P. holboellii*, and *Uromyces phacae-frigidae*, have systemic-perennial mycelium, and at least a dozen have localized sori. Repeatedly in *Puccinia* and *Uromyces*, the teliospores have developed delicate and freely deciduous pedicels, together with wall sculpturing and other changes that permit the spores to serve efficiently as diaspores and to germinate while lying free on a leaf rather than attached to the sorus (Savile, 1954*b*). These changes are desirable in short-cycled rusts, in which they allow the teliospores effectively to replace the aeciospores and urediniospores in promoting dispersal, and especially in the Arctic, where the short season permits at most one generation per annum and thus restricts dispersal. Of the microcyclic rusts that extend far into the Arctic only *P. holboellii* has firm-pedicelled teliospores, relying mainly (Section IV, C) on the basidiospores for dispersal, and only it and *P. fischeri* have smooth teliospore walls. Both these species are systemic and perennial in their hosts, and we may suppose that these aids to dispersal are less strongly adaptive in such rusts than in species with localized infection in which some degree of dispersal is necessary for survival and total spore production is generally much lower (Savile, 1954*a*).

In an early discussion of short-season adaptations in the rusts (Savile, 1953*a*), I assumed (and probably no mycologist would have disagreed with me) that elimination of the pycnia was tantamount to the loss of all opportunity for gene exchange. But, as geographic and evolutionary studies of several microcyclic rusts developed, some of them were found to possess great morphological uniformity over wide areas, and it seemed probable that gene flow occurred by some means. These rusts are difficult to study experimentally, but gene flow was finally demonstrated in a natural experiment. *Puccinia cruciferarum*, a microcyclic rust without pycnia, attacks several arctic and alpine species of *Cardamine*. It is divisible into four well-defined geographic subspecies (Savile, 1964*a*). Three of these subspecies are morphologically homogeneous. However, ssp. *nearctica*, although uniform in Axel Heiberg Island, Ellesmere Island, and northern Greenland, varies clinally southward to Hudson Bay where it approaches the nearly circumpolar ssp. *borealis*. Contact between these two subspecies is now prevented, because forests in the Hudson Bay lowlands

have eliminated *Cardamine bellidifolia* from a wide belt, but such a contact evidently existed early in postglacial time. This deduction has very recently been supported by the observation by G. A. Mulligan (unpublished) that the plants from the west coast of Hudson Bay, about 150 km north of the tree line, more closely resemble those of the Cordillera than those of the high arctic (Section II, C, 2, *a*). This clinal variation can only be the result of substantial gene flow between the two rust populations. It is believed that, if two mycelia with any genetic difference are contiguous in a leaf, they will tend preferentially to exchange nuclei through hyphal fusions, for it will be recalled that the dikaryotic cells of the mycelium in such a rust ordinarily contain sister nuclei (Fig. 8). Probably any dissimilar nucleus will be more attractive than a sister nucleus. Cytological studies of self-sterile rusts have shown that affinity between nuclei of opposite strains may be a matter of degree and that a third nucleus may enter a cell that already has a pair and seemingly displace one of them. If this happens in *P. cruciferarum*, recombination will occur during nuclear fusion and meiosis in the teliospore.

The demonstration of gene flow in *P. cruciferarum* clarifies the adaptations of arctic rusts in general. Far from sacrificing genetic recombination as the price of shortening the generation time, these rusts have merely abandoned self-sterility and a method of cross-fertilization that is effective in warmer climates but dangerously slow or uncertain in the Arctic, and have retained and perhaps perfected an alternative device, which sharply reduces the rate of

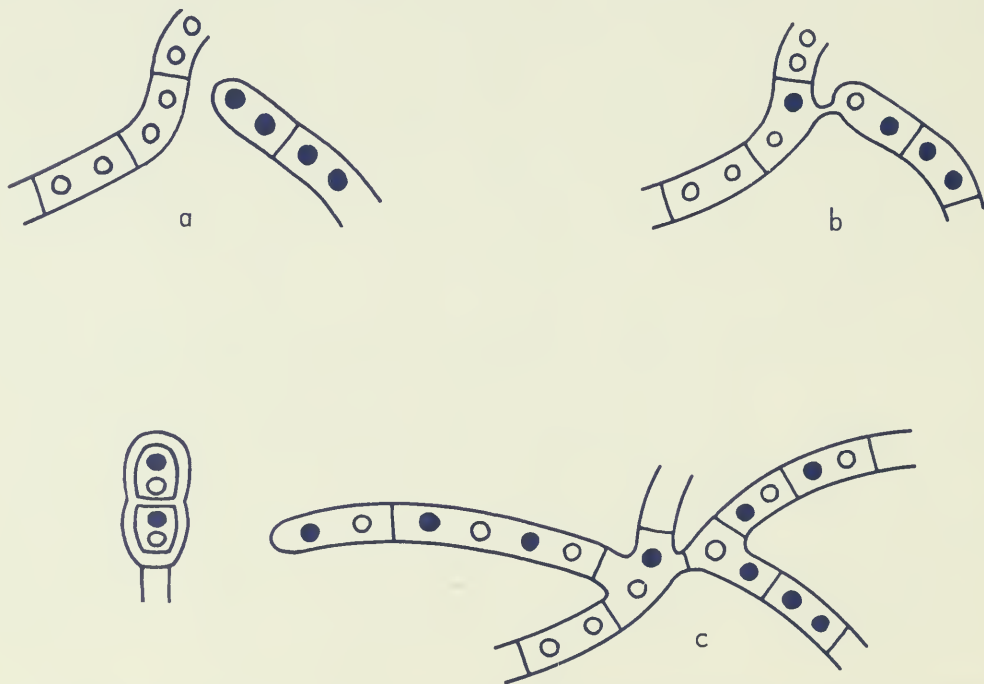


Fig. 8. Probable mechanism of gene exchange in *Puccinia cruciferarum*. (*a*) Genetically dissimilar mycelia meet in leaf; (*b*) Hyphal fusion allows exchange of nuclei; (*c*) Mixed mycelium produces teliospores in which nuclear fusion and meiosis allow genetic recombination.

recombination but whose adequacy is demonstrated by the population structure in *P. cruciferarum*. This process also explains the persistence of nuclear fusion and meiosis in rusts devoid of pycnia in which it once seemed to be a functionless relic.

We must consider two other rusts that seem to be conspicuous exceptions to the rule that heteroecious rusts stop at the tree line. A member of a complex that must all be called *Melampsora epitea*, until experimental work allows it to be split realistically, attacks *Salix arctica* virtually to the limit of land. Its aecial hosts are *Saxifraga caespitosa* and *S. oppositifolia*. Three modifications of the life cycle enable this rust to flourish in the high arctic: the first is rarely found in *Melampsora* in temperate regions; the second is occasionally, and the third rarely, found in other genera. The telia form on *Salix* in late summer and germinate in the following spring, nominally infecting *Saxifraga*, but only occasionally doing so (Fig. 9). The aeciospores formed on *Saxifraga* nominally

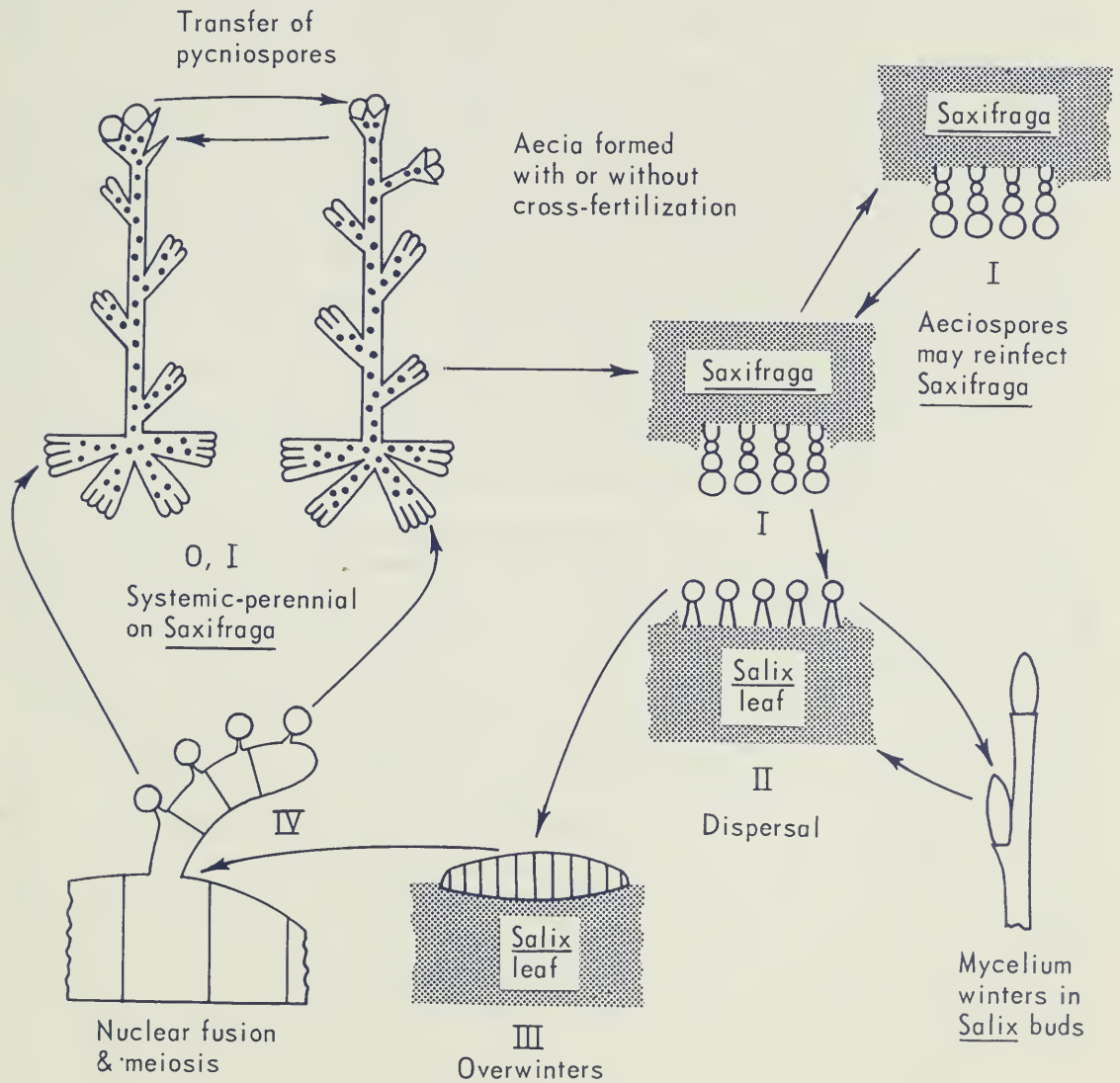


Fig. 9. Modification of life cycle in *Melampsora epitea* on *Salix arctica* and *Saxifraga caespitosa*. In addition to orthodox alternation between *Salix* and *Saxifraga*, rust may persist and spread on *Salix*, persist on *Saxifraga* with or without cross-fertilization, and spread from *Saxifraga* to *Saxifraga*.

reinfect *Salix* and give rise to uredinia, but even as far south as Chesterfield Inlet such infection was only observed when the two hosts were in contact. One or more uredinial generations occur, depending on weather conditions. In late summer appreciable numbers of urediniospores infect the embryonic leaf or catkin tissues of the winter buds, apparently penetrating them before the hard bud scales fully seal them. The mycelium overwinters in the bud tissues, grows with them in spring, and the leaves or catkins emerge with large or numerous sori almost fully developed. This first modification ensures persistence without infection of the aecial host and gives the fungus an early start in the spring. Secondly, the aecial state is systemic and perennial in *Saxifraga*, which ensures its survival. Pycnia are produced, but the aecia always develop so promptly that the rust may be self-fertile, and cross-fertilization may be relatively rare. The third modification, which occurs occasionally in autoecious rusts but only rarely in heteroecious ones, is repetition of the aecia whereby the aeciospores infect other *Saxifraga* plants instead of *Salix*. This ability has not been confirmed by controlled inoculations, but observations leave little doubt that it can occur. In separate parts of the Arctic, once with *Saxifraga caespitosa* and once with *S. oppositifolia*, extensive rusted colonies have been found in which the infected plants ranged from very small to very large and clearly represented a succession of new infections over a long period. In neither instance was any *Salix*, rusted or healthy, living or dead, found close to the rusted *Saxifraga*. In fact at each site willows were substantially closer to healthy saxifrages than to the rusted part of the colony. These three modifications of the orthodox life cycle combine to make this the most successful rust in the Arctic. Incidentally, it has the potential to diverge into two species, somewhat as has been postulated for *Mycosphaerella tassiana* and its conidial state (Section IV, B, 1, a). However, only extensive experimental work can show whether such a divergence has actually started.

The remaining rust to be considered is *Puccinia bistortae*, which attacks *Polygonum viviparum* in cool-temperate and arctic regions, and it and related species in alpine regions. Its aecia develop on several genera of Umbelliferae, all essentially temperate. In northern Newfoundland, at only 51° 20' N but subarctic owing to the proximity of the ice-laden Labrador Current, the aecia occur freely on *Conioselinum chinense* and occasionally on *Ligusticum scoticum* in close association with *Polygonum viviparum*. Only rarely did rust appear in early summer on isolated *Polygonum*, which suggests that in this region the full cycle at least predominates if it is not universal. At Great Whale River, close to the tree line on Hudson Bay at 55° 20' N, *Polygonum viviparum* was freely rusted, but no aecia were seen on adjacent *Ligusticum scoticum*. *P. viviparum* is often freely rusted in the low arctic, where it has been assumed that uredinia may persist on winter-green leaves. I. Jorstad (personal communication) believed that this happens in parts of Norway. In maritime regions with ample snow it is highly likely that some leaves remain green in winter, but in more continental regions it is doubtful if any green tissues persist. Sorensen (1941) was emphatic that none persisted in northeast Greenland, and I could find no sign of any in northern Ellesmere Island or in specimens from other high-arctic sites. *Puccinia bistortae* has been found repeatedly near Hazen Camp in northern Ellesmere, in

western Axel Heiberg Island, and on Somerset Island. At Hazen Camp a specific search was made for both overwintering uredinia and green tissue, without success. Uredinia, or more generally a few urediniospores in predominantly telial sori, were found until late July, but by August only telia could be found. In the absence of winter-green tissues it seemed inconceivable that any telia could resume growth in the spring and transform partly into uredinia. No trace of uredinia could be found on any overwintered leaves and, in fact, even the first sori on new leaves were often predominantly telial. It is thus almost certain that, in the high arctic at least, the basidiospores of *P. bistortae* have the ability to reinfect *Polygonum*. Whether the arctic rust is genetically distinct or this behavior is merely conditioned by the climate must be decided by experiment. It does appear, however, that at least one population of *P. bistortae* is following the course taken by the related *P. oxyriae* on *Oxyria digyna*, which forms only uredinia and telia at any latitude and in which uredinia are often scarce or absent. It is not known whether the immediate ancestor of *P. oxyriae* was autoecious or heteroecious.

In other groups of parasitic fungi the simpler basic life cycle makes modifications more difficult to observe. *Entyloma compositarum*, a leaf smut that attacks various Compositae, produces abundant conidia as well as teliospores in temperate regions. It occurs sparingly in the subarctic and low arctic, but produces only teliospores. The powdery mildew *Sphaerotheca fuliginea* produced numerous ascocarps on *Braya*, *Arnica*, and *Taraxacum* at Hazen Camp, but few or no conidia. On *Pedicularis arctica* it produced only conidia both at Hazen Camp and in western Axel Heiberg Island (Savile and Parmelee, 1964). Although extremely well adapted to low temperature, this fungus thus tends to produce one state or the other in the arctic according to host. The same strain seems, from repeated field associations, to attack *Braya* and *Taraxacum*, but it is possible that the fungus on *Pedicularis arctica* is genetically distinct.

In conclusion we may remark that most of the arctic adaptations of fungi are comparatively minor, and most of them are also known outside the Arctic. However, the accumulation of several adaptations in *Melampsora epitea* and the marked morphological distinctions that have occurred in the high-arctic races of *Puccinia poae-nemoralis* and *P. cruciferarum* suggest that evolution may be proceeding at a substantial rate. Alternative means of genetic recombination seem to have provided satisfactory substitutes for the devices that accompanied self-sterility in the ancestral species. Although there are substantial numbers of arctic species and subspecies, few, if any strictly arctic genera of fungi exist. *Arcticomycetes* is represented only by *A. warmingii*, which attacks several *Saxifraga* spp. apparently throughout the nearctic, but reaches the subarctic in Iceland and northern Quebec and the alpine zone in Switzerland. In *Ustilentyloma* only *U. pleuropogonis*, on *Pleuropogon sabinei*, is known in the high arctic. But the genus can be distinguished from *Entyloma* only by the germination pattern of the teliospores. Other species may exist among the various described species of *Entyloma* whose germination has not been studied.

C Dispersal

The fungi in general have ample means of dispersal and many that possess air-borne spores are found in almost any part of the world that offers suitable substrates. In such species dispersal is seldom a limiting factor in determining range. Unfortunately recorded distributions give us little idea of the true range of some very inconspicuous saprophytes. For example, *Coremiella ulmariae*, otherwise known only from Ireland and England, has been found at Hazen Camp and at Isachsen. It is probably widespread, but distinguishing it among the vast number of species in a temperate flora might be very difficult unless it were unusually abundant.

Some parasitic fungi are nearly coextensive with their hosts. Others drop out as soon as the population density of the host becomes markedly reduced, as was noted for *Anthracoidea* (Section IV, B, 2), for if the distance between infection courts is multiplied by ten, the chance of a spore landing on an appropriate substrate is reduced to one hundredth. Other fungi may drop out because of climatic limitations, far short of the limits of their hosts.

Although aerial dispersal in summer is clearly important for many arctic fungi, it seems to be less important than in warmer climates. Dry, airborne conidia, such as many ascomycetes produce in temperate summer conditions, are relatively scarce in the Arctic, as are the urediniospores of rust fungi. Ascospores are usually forcibly discharged, but they are sticky, either from the contents of the ascus or through possession of a mucous sheath, and the majority adhere to adjacent vegetation. The basidiospores of rusts and smuts have thin, unpigmented walls, and are subject to injury from desiccation and ultraviolet light if carried far. Overcast and humid weather reduces such injury but introduces an increased risk of the spores being quickly washed out of the atmosphere. In partial compensation, the teliospores of many arctic rusts have become modified to serve as diaspores, the pedicel being readily deciduous and the wall often becoming sculptured, which gives added buoyancy. The teliospores of many smut fungi also serve as diaspores and in one arctic species, *Ustilago violacea*, which fruits in the anthers of *Silene acaulis*, *Stellaria*, and *Lychnis* spp., spread may be largely by blossom-visiting insects.

There can be little doubt that many saprophytes are dispersed in winter over snow in the tissues of fragments of their host plants, as Lind (1927, 1934) suggested. Immature fruit-bodies must often be carried by this means into the proximity of established plants, where they can mature and discharge their spores upon an appropriate substrate. Numerous large and deeply pigmented ascospores of such genera as *Pleospora* or *Clathrospora* are seen under the dissecting microscope on senescent or dead leaves and stems, which may become detached and carry the spores with them as they drift across the snow. This means of dispersal with parts of the host is less likely to be effective in the obligate parasites, which can develop only on living tissue. It is, however, applicable to rust telia that have completed their development and need only appropriate conditions of moisture and temperature to germinate and discharge basidiospores. Thus rusted leaves of *Erysimum pallasii* probably spread

Puccinia holboellii over great distances. It is probable that the mature ascocarps of *Sphaerotheca fuliginea* are successfully transported on old leaves of its hosts.

Long-range dispersal of some ascomycetes is almost certainly achieved through the spores sticking to seeds, fruits, or bulbils, being dispersed with them over the snow in winter, and developing on the seed coats, cotyledons, or other parts of the young plants. Some fungi with extremely narrow host ranges, such as *Wettsteinina eucarpa* on *Polygonum viviparum* and *W. macrotheca* on *Arctagrostis latifolia*, are found to the limits of their hosts (Savile, 1963a), where the latter are so scarce (one small colony of each, for the species cited, in a minimum of 40 km²) as to present a fantastically small target for randomly and independently dispersed spores arriving from a distant source. This secondary utilization by fungi of the principal means of arctic dispersal of the flowering plants (Section II, D) explains the successful penetration of the Arctic by some ascomycetes that lack conidia. Parasites of some temperate plants are carried within the seed coats as mycelium or sporocarps. However, no example of such dispersal is definitely known in the Arctic and dispersal by adherent spores is probably more important. Spores of the stripe smut, *Ustilago striiformis*, which occurs sparingly in the high arctic, are known to be carried on the seed coats of some temperate grasses and to infect the young seedlings. It and *Urocystis junci* are probably spread in part by this means in the Arctic.

V Conclusions

The arctic flora is drawn from many sources: Nearctic and Palearctic; alpine and lowland; bog, thicket, cliff, and shore. Within well-represented genera, we find this mixed origin demonstrated repeatedly. The flora is a young one. Some of the species, notably the vascular cryptogams, are of ancient affinity, but they are primarily temperate species that have entered the arctic environment to various degrees.

The morphological characters of purely arctic species are generally not spectacular, most of them being shared by alpine or temperate species. Physiological adaptations may be more critical to arctic survival than most morphological ones, but their detection and assessment are too difficult to permit a useful comparison. The almost complete lack of arctic genera emphasizes the relative simplicity of arctic adaptations. In the Arctic we are chiefly concerned with short-term evolutionary changes.

The most important modifications involve the maintenance of coldhardiness in summer even at the peak of growth, and various devices to speed reproduction. In the flowering plants the latter include: effective growth at low temperature and low light intensity; low stature to keep the organs within a warm stratum of air; modifications in structure and pigmentation that raise the temperature of leaves, pistils, or other organs; self-fertility and other means of speeding seed set. In the fungi, self-fertility and other aids to reliable sporulation are widespread; but in some other cryptogams there is a stronger tendency for vegetative reproduction to be dominant.

The modifications in reproductive systems all tend to reduce genetic variability, although its complete elimination is exceptional. Genetic uniformity may be adaptive under special circumstances, as at the limit of the range where unrestricted gene exchange may swamp out locally adapted genotypes. In many plants it is probably merely tolerable on balance as the price of rapid production of disseminules and the establishment of species from solitary immigrants. It can be tolerated because habitats are sparsely occupied and biological competition in the Arctic is thus usually less of a challenge than the physical environment. The physical environment does not evolve in response to adaptation by a plant to it, as competing species do in closed communities, and the need for genetic flexibility in the Arctic is consequently less than in more benign environments.

The rapid differentiation of local races of flowering plants and fungi within Wisconsin refugia in Peary Land or Alaska and Yukon may be largely ascribed to reduced gene pools and changed selective pressure, but both their homogeneity and their rapid evolution emphasize the occurrence of adequate genetic recombination within them.

No real understanding of the age and evolution of the arctic flora, particularly the phanerogamic flora, is possible without a proper understanding of dispersal under arctic conditions. Attempts to explain arctic dispersal in terms of temperate mechanisms can only cause confusion. Rapid dispersal of seeds over great distances is clearly effected mainly by wind over ice and packed snow, but geese and other birds play a part, and other mechanisms

may occasionally be involved. Self-fertility and incompletely filled habitats greatly simplify the establishment of immigrants.

In studying the evolution of any group of organisms we commonly find that a single function may be achieved by several means, and that a single mechanism may serve more than one function, especially in the early stages of a new adaptation. Nowhere is this truer than in the Arctic, where novel and severe habitats have been quite recently occupied by plants from various sources and many adaptations are still rudimentary. Under these circumstances it is particularly dangerous to assume that any one explanation has universal application.

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