Interrelationships of *Ledum* species and their rust parasites in Western Canada and Alaska[1]

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Ledum glandulosum extends northward from Western United States into southern British Columbia in and east of the Cascade Range and into extreme SE British Columbia and SW Alberta in the Rocky Mts. Further north, within the range of *L. groenlandicum* but beyond that of *L. glandulosum*, hybrids between the two species occur, notably in and near Banff National Park, indicating that *L. glandulosum* formerly extended further north. The hybrids form an irregular swarm among typical *L. groenlandicum* rather than a cline; for this reason, and because of numerous morphological and other distinctions, the taxa are maintained as species. *L. groenlandicum* and *L. palustre* ssp. *decumbens* overlap in Alaska, Yukon, and Mackenzie in a belt up to 700 miles wide. Six definite hybrids were detected out of ca. 300 specimens from the sympatric zone, and ca. 30 specimens showed signs of probable minor introgression. The marked sympatry with minimal hybridization makes it necessary to maintain *L. groenlandicum* at specific rank. A rust, *Chrysomyxa ledicola*, that freely attacks *L. palustre* ssp. *decumbens* and *L. groenlandicum* does not infect *L. glandulosum*, but it attacks the hybrids in the Banff region except those closely approaching *L. glandulosum*. Another rust, *C. ledi*, has developed morphologically distinct varieties each specialized to a single *Ledum*. In the Banff region hybrids have been found between *C. ledi* var. *glandulosi* and *C. l.* var. *groenlandici* on *L. glandulosum* × *groenlandicum*. *C. ledi* var. *ledi*, on *L. palustre* (including ssp. *decumbens*) is morphologically distinct from *C. ledi* var. *groenlandici*, further emphasizing the sharp distinctness of *L. groenlandicum* from *L. palustre* ssp. *decumbens*.

Introduction

Most recent authors have recognized three species of *Ledum* in North America: *L. glandulosum* Nutt. is predominantly a plant of mesic coniferous forests in the Cordilleran region, just reaching southern British Columbia and southwestern Alberta (Fig. 1). *L. groenlandicum* Oeder occurs chiefly in sphagnum bogs from coast to coast in Canada. It is common in the northwestern United States and follows the Pacific coast south to northwest Oregon. Northward it is mainly subarctic but occasionally surpasses the arctic tree line. *L. palustre* L. ssp. *decumbens* (Ait.) Hult. is a dwarf, small-leaved shrub predominantly found in mesic tundra but also invading the drier parts of bogs. It occurs from coast to coast in the lowarctic and subarctic, pushing further south on exposed coasts or in mountains. The relationship of this third taxon to *L. palustre* of Eurasia remains in doubt and is beyond the scope of this paper. Porsild (1951, 1955, 1957) treats it as a species, *L. decumbens* (Ait.) Lodd. It differs from *L. p. palustre* mainly in its decumbent habit. The latter usually has larger leaves, which may be largely a phenotypic response to its generally more temperate environment, and the fruiting pedicels seem to be less uniformly decurved than in *decumbens*. However, the two taxa have several other characters in common, including rust relationship, and I am accordingly following Hultén (1930) in treating *decumbens* as a subspecies. I argued (1955) against the action of Hultén (1948) in reducing *L. groenlandicum* to subspecific rank under *L. palustre*, in view of its wide sympatry with *L. p. decumbens*, lack of intergradation in the Hudson Bay region, and possession of a distinct variety of the rust *Chrysomyxa ledi*. This view was echoed in Calder and Taylor (1968) in the hope that the relationship would be reassessed. However, after recently collecting in Banff National Park a palpable hybrid between *L. glandulosum* and *L. groenlandicum*, bearing what proved to be a hybrid rust, I became aware of a complex relationship between these two species, whose elucidation was needed for a better understanding of the rusts. It consequently seemed advisable to undertake a detailed study of the relationships of the three North American taxa.

Hitchcock (1956) indicated, from stamen number, capsule shape, and occasional rusty lanate hairs, that what had been called *L. columbianum* Piper in southwestern Washington

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was actually a swarm of variable hybrids between *L. glandulosum* and *L. groenlandicum*. Perhaps because he was working in a region dominated by *L. glandulosum*, Hitchcock made *columbianum* a subspecies of *glandulosum*. However, in parts of British Columbia and Alberta north of the contemporary limits of *L. glandulosum* we see the other side of the coin: a variable population with *groenlandicum* predominating. It is remarkable that these hybrids, which are most conspicuous in and near Banff National Park, have escaped prior comment. It appears that most collectors have been content to assign specimens to one species or the other on the basis of a single key character, such as presence or absence of rusty tomentum on the lower leaf surface.

Methods

Although this study is based predominantly on material in this institute (DAO), supplementary material from eastern British Columbia and western Alberta was borrowed from University of Alberta (ALTA), University of Calgary (UAC), University of British Columbia (UBC), and British Columbia Provincial Museum (V). Material from Alaska and Yukon was borrowed from the National Museum of Canada (CAN). Finally, mycological specimens from this institute (DAOM) and the Calgary Forest Research Laboratory (CFB), Department of Forestry and Rural Development, were used to supplement range data of hosts as well as parasites. Most specimens seen (a few were inadequate) have been annotated regarding disposition, many with detailed assessment. To save space and for greater clarity most specimens will not be cited, except those needed to illustrate particular points.

In the search for reliable distinctive characters, two points soon became clear. First, most available characters are quantitative rather than qualitative, and random variation makes it impossible to rely on them individually. Second, phenotypic variation, not only in stature and leaf size, but in petal size, stamen length, and anther length, is so great that these characters must be used with great caution if at all. In the next section all available characters, biological and morphological, are listed and discussed. A few, such as the occurrence of glands, are of little practical value but are included because examination of a few specimens may give a false impression of their utility. (The yellow glands are of intrinsic interest because of their physical properties.) Of the rest, several reinforce the distinctness of the species, and thus demand consideration, but are of limited value in the identification of individual specimens because they are not routinely available (e.g. parasites) or require data often lacking from the label.

The characters available for each specimen were recorded in uniform sequence on the specimen card, which allowed prompt retrieval of data with minimal handling of specimens.

Available Characters

Habitat

Ledum glandulosum occurs mainly in mesic to moderately dry coniferous forest, but occasionally in moist, somewhat boggy forest where it might make contact with *L. groenlandicum*. It is rare in fully open situations except near tree line.

L. groenlandicum occurs predominantly in open sphagnum bogs. However, in places of frequent and sustained high humidity it freely invades closed coniferous forest. This condition is well illustrated in the narrow belt of advection fog on the shores of L. Superior, where the steady drip of condensing fog from the tree canopy causes a thick layer of sphagnum to form even on rocky slopes; and this carpet is exploited by *L. groenlandicum* and other bog plants (and often by their parasites). In the otherwise relatively dry montane forest of the Alberta Rockies, waterfalls and cataracts deluge narrow bands of forest with mist and induce a somewhat similar situation; and in such a site (Paradise Creek at Moraine Lake road, Banff National Park, *D.B.O. & C.E. Savile 4934B*, DAOM) the hybrid specimen of *Chrysomyxa ledi* on *L. glandulosum* × *groenlandicum* was taken that precipitated this study.

The habitats of *L. groenlandicum* and *L. palustre decumbens* overlap slightly, but the latter is predominantly a plant of dry to moist tundra and penetrates only the drier parts of bogs.

Habit

Ledum glandulosum and *L. groenlandicum* are both erect shrubs, generally more than 1 m high in favorable habitats. *L. p. decumbens*, as its subspecific epithet implies, is typically decumbent (apparently its principal distinction from *L. p. palustre*), and is typically less than half the height of *L. groenlandicum* where they grow together. This distinction is clearly important, but herbarium specimens so often bear inadequate data that it can seldom be used in identifications.

Phenology

I have no knowledge of pure *L. glandulosum* and *L. groenlandicum* growing strictly sympatrically, and thus it may be impossible to compare their flowering periods accurately. However, to judge from the specimens examined from Banff National Park, it should be possible to compare *L. groenlandicum* with a range of identically situated *glandulosum* × *groenlandicum* hybrids. Judging from the frequency of such hybrids, flowering in the two species may well be essentially synchronous.

The wide sympatry of *L. groenlandicum* and *L. palustre decumbens* makes it clear that the latter flowers first by a substantial margin when the two plants are strictly adjacent. At humid, subarctic Great Whale River on the east coast of Hudson Bay the difference appeared to be about 7–10 days in 1949, with very little overlap in anthesis within a precise site but perhaps appreciable overlap between shady or late-snow sites for *palustre decumbens* and open ones for *groenlandicum*. Unfortunately, varied obligations (and a failure to realize that anyone might consider these plants conspecific) prevented me from making more detailed studies. It is clear from mixed sheets, and from specimens specifically stated to be contiguous, that *L. p. decumbens* also flowers earlier in the northwest, as the following examples show. In *Anderson 6565* (CAN) from Hope, Alaska, a plant of *L. p. decumbens* ranges from late bud to well past anthesis, and one of *groenlandicum* from early to late bud. In *Cody & Webster 5239* (DAO) from mi 289 Richardson Hwy., Alaska, *L. p. decumbens* is well past anthesis and *groenlandicum* is at about full anthesis. In *Calder & Gillett 26023* (DAO), Cathedral Rocks, Oglivie Mts., Yukon, *L. p. decumbens* is in full flower, whereas, in *26024* from the same site, *groenlandicum* had made virtually no growth by the date of collection (29 June 1960) but bore year-old immature capsules frozen before they could complete their growth. In *Shewell s.n.* (DAO) from Ford L., 63°08′ N 107°24′ W, Mack., *L. p. decumbens* is well past anthesis and *groenlandicum* varies from bud to anthesis. On a specimen of *L. P. decumbens* from Rae, Mack. (*Thieret & Rick 6749*, DAO) in full flower, the collectors note that bloom of *groenlandicum* was just starting.

It is clear that, as the climatic tolerance of *L. groenlandicum* is approached, it falls progressively further behind *p. decumbens* (see *Calder & Gillett 26023*, *26024*, above) until cross-pollination is inconceivable. Conversely we might expect that near the southern (or climatic) limits of *L. p. decumbens*, as we approach optimum conditions for *groenlandicum*, the phenological distinction would be less. I cannot extract the answer to this question from the herbarium specimens, but it may be significant that most of the few definite hybrids are from relatively far south or from the warm interior valleys of Alaska and Yukon. In general, however, *L. p. decumbens* and *groenlandicum* seem to be preponderantly allochronic.

Rust Relationships

Several rust fungi of the genus *Chrysomyxa*, with aecial states on *Picea*, attack *Ledum*. These have been discussed elsewhere (Savile 1950, 1955). The systemic *C. woroninii* attacks *L. groenlandicum*, *L. p. palustre*, and *L. p. decumbens* in boreal and subarctic regions. Its recorded southern limit is far north of the range of *L. glandulosum* and it is not known whether this species is susceptible.

C. ledicola is abundant in North America on *L. groenlandicum* through almost its whole range. It occurs almost equally freely on *L. palustre* ssp. *decumbens*, to far north of tree line, where it persists in the uredinial state (Savile 1953). It is also recorded on *L. p. decumbens* in Kamtchatka and Japan. Whether it occurs on *L. p. palustre* in Siberia remains unknown. It may have simply failed to have spread that far from North America or have been overlooked in a region that has received inadequate mycological study; but the possibility remains that *L. p. palustre* is not susceptible to it. True *L. glandulosum* is resistant to *C. ledicola*, but most of the *glandulosum* × *groenlandicum* hybrids are attacked except those most closely approaching *glandulosum*.

Most interesting are the relationships of the *Chrysomyxa ledi* complex, a group of host-specialized rusts with generally extremely small morphological distinctions. The three North American *Ledum* ssp. take different rusts, which I treated (Savile 1955) as varieties, following the common uredinological practice of a broad species concept, but which might better be regarded as true (biological) species. *L. p. decumbens* takes a rust (*C. ledi* var. *ledi*) indistinguishable from that on *L. p. palustre* in Europe in wall thickness and sculpturing of the urediniospores (the other states of all members of the complex are essentially identical). The spores in the North American specimens tend to be smaller than those in the European specimens examined; but the latter are from maritime and the former from continental regions, and it has long been clear that the spores in other *Chrysomyxa* spp. are largest from maritime sites (Savile 1950). Accordingly it is not likely that the size difference is of genetic origin. *L. glandulosum* takes a rust with spore-wall characters subtly but regularly different from *C. ledi* var. *ledi*, which I segregated as *C. ledi* var. *glandulosi*. Fortunately the rust on *L. groenlandicum* is amply distinct, with shallow tesselate rather than delicate cylindrical warts on the urediniospore walls. Thus, not only are the two varieties easily separated in the hybrid *Ledum* swarm in Banff National Park, but it has even been possible to detect hybrid rust specimens.

Glands and Hairs

Two types of glands and three basic types of hairs are seen on various parts of *Ledum* plants.

The more conspicuous gland is a large, yellow, sessile structure, generally ca. 90–135 μ diameter, flattened ellipsoidal in form, and probably generally about 50 μ high. The yellow color is in the outer wall, which is generally 1.5–2.5 μ thick. In casual examination these glands appear to be 1-celled, but several very thin, hyaline partitions may be discerned in cleared specimens studied at high magnification, preferably with phase contrast. The most remarkable characteristic of these glands is that, despite their thin wall, their contents remain fluid indefinitely, on leaves that were formed within a month or two of the date of collection and in specimens dried quickly enough to give good color retention. This property is most easily demonstrated on the under surface of young leaves of *L. glandulosum* in which the glands nestle in hairs bearing abundant scales of wax. When such a gland is pierced with a scalpel tip, under about ×30 magnification, abrupt wetting (and staining) of the adjacent waxy hairs is often seen. Such mobile fluid contents have been demonstrated in specimens up to nearly 70 years old, e.g. *L. glandulosum* (× *groenlandicum*), Banff, Alta., 24 July 1899, *McCalla 2163* (ALTA).

A smaller, sessile to short-stalked, deep red or rarely deep yellow gland occurs sporadically on all three species of *Ledum*. These red glands are generally less than half the diameter of the yellow glands on herbarium specimens, partly because they are seldom turgid. When warmed in lactophenol they range from 35 to 110 μ diameter. They are clearly multicellular, the septa being thicker than those of the yellow glands and pigmented. They apparently do not retain fluid contents for any great length of time. The occurrence, and distribution on the plant, of the red glands seems to reflect the occurrence of localized genotypes, but is of little value in specific identification, although they tend to be most abundant on *L. palustre decumbens*.

The most conspicuous type of hair is the coarse, contorted rusty hair that produces the familiar dense lanate tomentum on the under surface of the leaves of *Ledum groenlandicum*. These rusty lanate hairs, generally about 20 to 25 μ in diameter, are often substantially over 1 mm in length but their tight convolutions make exact measurement difficult. They occur freely on *L. palustre* ssp. *decumbens* as well as *L. groenlandicum*, but are completely lacking in pure *L. glandulosum*. These hairs are regularly present on the pedicels and often fringe the calyx lobes of *L. palustre decumbens*; but never occur on these parts of *L. groenlandicum*. They are thus a valuable aid in the assessment of all *Ledum* specimens.

The calyx lobes of *L. glandulosum* are generally, and those of hybrids with *L. groenlandicum* occasionally, fringed with conspicuous cilia, somewhat more slender than the rusty lanate hairs, and subhyaline to pale yellow in well-prepared specimens. In badly dried specimens with poor color retention these cilia are often deep brown, which increases their resemblance to the rusty hairs of the other two species.

The last type of hair, common to all three species, is a fine subhyaline to white hair, varying considerably in size. In their most conspicuous development these fine white hairs may be 150 μ long, (or longer on the filaments) 7–12 μ diameter near the base, tapering to 3 to 5 μ just below the rounded apex. They may be smooth (and then almost hyaline) or irregularly roughened (and consequently whiter in appearance). The lumen is narrow and does not extend the full length of the hair. When weakly developed, the fine white hairs are often less than 50 μ long and about 7 μ wide at the base, and are very inconspicuous. They must then be sought under bright, preferably oblique illumination and at ×30–40 magnification.

The hairs on the undersides of, especially young, leaves of *L. glandulosum* are dazzlingly white, suggesting an affinity to those on the leaves of *Andromeda glaucophylla*. However, the latter owe their high albedo largely to closely spaced transverse septa, whereas the hairs on *L. glandulosum* owe their equally high albedo to the presence of numerous small flakes of waxy material presumed to be cutin. The hairs, generally about 35–55 μ long by 7.5–12 μ wide near the base, with rough or smooth surface and narrow lumen, appear to be identical with the normal fine white hairs. The under surfaces of the leaves of *L. groenlandicum* often bear wax-coated fine white hairs to various degrees, but they generally seem to be lacking from the leaves of *L. palustre decumbens*. However, it is only occasionally that the under surface of these two species can be examined without plucking off the rusty tomentum; and the presence of the hairs, with or without waxy scales, is thus not a very practical taxonomic character.

The distribution and development of the fine white hairs prove to be of major assistance in distinguishing *L. palustre decumbens* and putative hybrids from *L. groenlandicum*. In *L. groenlandicum* these hairs are sparse to abundant, but often small, on the twigs; generally abundant on petioles and midveins and slightly to conspicuously developed on the lower leaf surface (sometimes with waxy scales); abundant on the peduncles, pedicels, and calyces; and usually abundant on the ovaries and capsules, but often so covered by glandular secretions on the young ovary as to be almost indistinguishable. Their distribution in *L. glandulosum* is very similar, but they are generally better developed, especially on the twigs. In *L. palustre decumbens*, however, although these hairs are moderately well developed on the peduncles, they are lacking or rarely few and very small on twigs, petioles, and lower leaf surfaces; lacking or few and small (and generally only near the base) on the pedicels; lacking on the calyx; and lacking or few and very small on ovary and capsule. The hairs on the stamen filaments are discussed later.

All the epidermal processes, but especially the rusty lanate hairs and yellow glands, tend to weather off in age. Usually they are lost from the twigs after about 2 years. They often occur sparingly on the upper leaf surface in *L. groenlandicum* and *L. palustre decumbens*, but largely disappear before the leaves are fully mature.

Leaf Shape

Although leaf size helps to distinguish *Ledum groenlandicum* from *L. palustre decumbens*, it varies so greatly both within and between specimens that it alone is of little value. However, leaf shape is more constant than size and can be used without inordinate labor by simply recording the ratio of the greatest leaf length to the greatest width (L/W) in each specimen. This process is simple in *L. glandulosum* with its flat to slightly decurved leaf margins; but in the other species, with strongly revolute margins, it is important not to include widths of leaves that lie across twigs or other leaves, for at such points the revolute margin often becomes conspicuously splayed in pressing. Even shape does show some phenotypic variation, and *L. palustre decumbens* occasionally has its leaves so tightly revolute at exposed mountain sites that the length/width ratio becomes abnormally high. In the other two species the reaction to such exposure is generally reflected in reduced size rather than altered shape. One further precaution must be taken in using leaf shape. Under some conditions the leaves of *L. groenlandicum* and *palustre decumbens* may unroll until nearly flat, and thus become conspicuously wider than normal. This unrolling may be accompanied by a partial loss of the hypophyllous tomentum. This effect is occasionally the result of infection by *Chrysomyxa* or *Exobasidium* spp., but it is generally due to growth conditions. It is occasionally confined to heavily shaded lower branches, and is not uncommon in plants of *L. groenlandicum* from the fog forest bordering Lake Superior. Thus low light intensity and possibly sustained high humidity may be involved. The effect is marked in a specimen of *L. groenlandicum* grown from seed (*Calder & Taylor 36897A*, Queen Charlotte Is.) for cytological purposes at this institute, in a greenhouse shaded in summer to reduce the temperature. This is presumably f. *denudatum* Vict. & Rousseau, but, as it is certainly an ecological effect found in two species, it does not merit formal designation. Length/width in pure *L. gladulosum* falls in the range (1.5–)1.7–2.8(–3.2); in *L. groenlandicum*, sampled far from the other two species, the range is (2.5–)3.0–5.0 (–5.7); and in apparently pure *L. palustre decumbens* it is (5.2–)5.7–10.7(–14.0). In definite *glandulosum* × *groenlandicum* hybrids, the range is about 2.7–3.6, intermediate between that of the two parents; but in the few definite hybrids between *groenlandicum* and *palustre decumbens* the range is about 3.3–7.9, covering most of that of *groenlandicum* and half that of *palustre decumbens*.

Pedicels and Calyces

As noted above, the pedicels of *L. palustre decumbens* are sparsely to heavily clothed in rusty lanate hairs, and the calyx lobes usually bear at least a few such hairs on their margins; but fine white hairs are few and small or absent. In *L. groenlandicum* the opposite is true: rusty lanate hairs never occur, and fine white hairs are abundant and conspicuous. This distinction would be clear-cut in almost all specimens but for the copious secretions of the yellow and (or) red glands, which are often very numerous on the pedicels. These secretions may mask the fine white hairs against casual observation; and they occasionally pick up rusty hairs from adjacent vegetative shoots. Generally such transfers occur in localized tufts only, and are easily recognized, but lightly dispersed hairs may occasionally be deceptive. It may be noted that such transfers are much less common in specimens spread out in a field press than in those packed into a vasculum.

In fruit, but not in flower, the pedicels of *L. palustre decumbens* are generally abruptly decurved near the apex, whereas those of the other two species are gradually arcuate. This character is variable in young fruit, but much more constant in mature fruit, even in Alaska and Yukon, than Hultén (1967) maintains.

Apart from their pubescence the calyx lobes of *L. groenlandicum* and *palustre decumbens* are not safely distinguishable. Their lengths in *L. groenlandicum* range from 0.1 to 0.8 mm, with individual specimens ranging from 0.1–0.2 to 0.4–0.8 mm; and in *L. palustre decumbens* the range is 0.1–1.0 mm, with individual specimens 0.1–0.2 to 0.4–1.0 mm. The calyx lobes of *L. glandulosum* are generally about 0.7–1.3 mm long, but individual specimens range from 0.5–0.8 to 0.9–1.5 mm or exceptionally 1.3–1.8 mm. In addition to their greater length the calyx lobes of *glandulosum* are generally distinguishable from those of *groenlandicum* by the possession of yellow cilia.

Petals

Although the petals of *L. glandulosum* are generally larger than those of the other two species, much of the difference appears merely to reflect the preference of this plant for shady forested sites. In such sites the maximum length in *glandulosum* is from (5.0–)5.5 to 7.5(–8.0) mm and maximum width 4.0–5.0 mm; but on an alpine cliff top (near Quinescoe L., B.C., 49°04′ N 120°12′ W, 6800 ft, *Calder*, *Parmelee & Taylor 19639*, DAO) the maxima were 4.5 and 3.2 mm, and leaves, filaments, and anthers were correspondingly stunted. In *L. groenlandicum* maximum length is (4.5–)5.0–6.6(–7.0) mm and width 2.5–3.5(–4.0) mm. In *L. palustre decumbens* maximum length is 4.0–7.0(–7.5) mm and maximum width 2.3–3.8(–4.2) mm, the lowest figures being generally for plants from exposed arctic or alpine sites and the largest from shady forested sites; but variation between specimens from a single site suggests that there may also be appreciable genetic variation in size. Clearly petal size is an unreliable guide to identity despite the somewhat larger size in *L. glandulosum*. Few to many yellow glands occur sporadically along the middle of the abaxial petal surface in all three species. They are generally numerous, but occasionally completely lacking in *L. glandulosum*; regularly abundant, regularly absent or variable in different populations of *L. palustre decumbens* (e.g. abundant in most Baffin Island specimens but absent or rare in many others from the Canadian Eastern Arctic, and varying from none to abundant in Kenai Peninsula, Alaska); lacking in *L. groenlandicum* from much of its range, but sporadically present in some regions. Most of the areas where the petals of *groenlandicum* are appreciably glandular are places of contact with *glandulosum* (Banff National Park) or *palustre decumbens* (Alaska and northwestern Canada). This tendency suggests introgression with the contiguous species; but such an explanation is open to some doubt for two reasons. First, *L. groenlandicum* occasionally has glandular petals far from contact with either of the other species, e.g.

in Nova Scotia. Second, glandular *groenlandicum* may occur, e.g. in central Yukon, in proximity to predominantly eglandular *p. decumbens.*

Stamens

The stamen number in *L. glandulosum* is 8–10(–11), rarely 7 or 12, and the filaments are conspicuously ciliate in the lower (1.0–)1.5–2.0 (–2.5) mm with white hairs up to 300 μ long. In *L. p. decumbens* the number is similarly 8–10(–11) or rarely 12; and the filaments are usually slightly to moderately ciliate in the lower 0.7–1.5 mm with hairs to ca. 200 μ long, but are rarely essentially glabrate. In *L. groenlandicum* the number is generally 5–7, but occasionally 6–8 and rarely 6–9 in, for example, southern Quebec and Nova Scotia, far from contact with the other species. The filaments in *groenlandicum* are often essentially glabrous and are at most lightly ciliate in approximately the lowest 1.0 mm with hairs to ca. 150 μ long. The variation is not clearly correlated with proximity to the other species. In southwestern British Columbia, stamen number in *L. groenlandicum* may reach 8–10, possibly reflecting former contact with *L. glandulosum;* and in Alaska, Yukon, and Mackenzie the number ranges from 5–6 to 9–10. Occasionally most of this variation is covered in different plants on the same sheet: thus in a sheet from Carcross, Yukon (*Gillett 3792*, DAO) different shoots, otherwise in close agreement, yield stamen counts of 5–6, 6–8, and 8–10. It seems probable that some of this variation represents slight introgression from *p. decumbens*. However, diminutive, more or less abortive stamens, which are rare in *L. p. decumbens* and which I have not seen in *glandulosum*, are relatively common in *groenlandicum*, 1–2 or rarely 3 being seen in a flower. To include these small stamens, as I have done in my counts, involves lifting at least one petal in many flowers, for they do not protrude beyond an upright petal. This condition of somewhat unstable stamen development suggests that the genes controlling stamen number may not be fully expressed under all conditions. Consequently some of the high stamen counts in northwestern *groenlandicum* may reflect some factor in the environment rather than introgression from *p. decumbens.*

Anthers

Anther length is decidedly variable in all three species, much of the variation being phenotypic. In *L. glandulosum* the range in normal habitats is 0.8–1.3(–1.4) mm, but, in the alpine collection (*Calder et al. 19639*) cited under Petals, it is 0.5–0.7 mm. In *L. groenlandicum* the range is (0.6–)0.7–1.0(–1.1) mm; and in *L. p. decumbens* it is 0.5–0.9(–1.0) mm. Although the smaller size in the latter partly reflects exposure in arctic and alpine sites, the lengths tend to be less than in strictly sympatric *groenlandicum.*

Ovary

The ovary is subglobose in all species. Approximately the upper three-quarters is closely covered by yellow or yellow and red glands, and in very glandular plants of any species the glands may extend slightly up the style. A ring-shaped nectary encircles the basal part of the ovary and there is typically a very narrow gland-free belt immediately above it. In *L. glandulosum* and *groenlandicum* fine white hairs are freely interspersed between the glands, but copious secretion from glands and nectary often make them hard to see. In *L. p. decumbens* such hairs are few and small or even absent. The five stigmatic lobes tend at first to be erect and to turn outward as the style shrivels after anthesis. Possible interspecific differences are thus masked. Style length is too variable to be of value.

Capsule

Capsule size varies greatly with environmental conditions, but, as with the leaves, shape is relatively constant in each species. The capsules dehisce promptly from the base and the valves spread widely. Those that are very young when the specimen is taken often shrivel or become distorted in the press. However, a substantial number of specimens yield capsules with only incipient basal dehiscence, which does not affect the width. From such material *L. groenlandicum* is seen to have conspicuously elongate capsules, (3.5–)4.0–6.0(–6.8) × (1.8–)2.0–3.0(–3.3) mm, with the apex slightly to moderately retuse or even tapering into the style (*L*/*W* 2.0 or slightly more). In *L. glandulosum* the capsules are broadly ellipsoid to globoid, (2.7–)3.0–4.5(–5.0) × 2.5–3.7(–4.0) mm, not tapering to style (*L*/*W* under 1.5 and usually 1.2–1.3). In *L. p. decumbens* the capsules are intermediate in shape, (2.5–)3.0–5.0 × (1.8–)2.2–3.2(–3.7) mm, nearly always strongly retuse at the apex and the style arising from a pronounced cavity (*L/W* (1.1–)1.3–1.8(–2.0) av. 1.5).

Despite variability in capsule shape in *L. p. decumbens*, nearly all fruiting specimens are distinguishable from *groenlandicum* both by proportions and by the strongly retuse apex. The capsules of *glandulosum* and *groenlandicum* bear many fine white hairs, as noted for the ovary, but such hairs are few and small or lacking in *L. p. decumbens*. As these hairs persist over winter, except on severely exposed sites, they may provide an extra character for use in flowering specimens.

It may also be noted that the long calyx lobes of *L. glandulosum* are almost always reflexed on old capsules, which is not true of the shorter lobes in the other two species.

On the basis of the characters discussed above the three *Ledum* taxa may be assessed as follows.

Ledum glandulosum Nutt., Trans. Am. Phil. Soc. II, 8: 270. 1843.

Habitat: mainly moderately dry coniferous forest. Habit: erect shrub, generally over 1 m in favorable habitats. Phenology: probably flowers more or less synchronously with *L. groenlandicum*. Rust relationships; takes *Chrysomyxa ledi* var. *glandulosi*; immune to *C. ledicola*. White hairs: abundant and well developed on twigs, peduncles, pedicels, capsules. Rusty lanate hairs: nil. Leaves: flat or margin slightly decurved, *L/W* (1.5–)1.7–2.8(–3.2). Pedicels slightly arcuate in fruit. Calyx lobes: (0.5–)0.7–1.5(–1.8) mm long, slightly to strongly ciliate with coarse subhyaline to pale yellow hairs (often brown in badly prepared specimens). Petals: (5.0–)5.5–7.5(–8.0) × 4.0–5.0 mm max. (or smaller on severely exposed sites), yellow glands (nil–)occasional–many. Stamens: ((7–))8–10(–11)((–12)); filaments conspicuously ciliate in lower (1.0–)1.5–2.0(–2.5) mm with white hairs to 300 μ long. Anthers: 0.8–1.3(–1.4) mm long in normal habitats, but may be only 0.5–0.7 mm long in severe exposures. Capsules: (2.7–)3.0–4.5(–5.0) × 2.5–3.7(–4.0) mm (*L/W* 1.2–1.3) at incipient dehiscence, rounded at apex.

Ledum groenlandicum Oeder, Fl. Danica 4: 5. 1777.

Habitat: predominantly sphagnum bogs or wet coniferous forest. Habit: erect shrub, generally over 1 m in favorable habitat. Phenology: anthesis later than *L. p. decumbens* by ?7–10 days av., much more at northern or altitudinal limits of *groenlandicum*, probably less near southern limits of *p. decumbens*; probably nearly synchronous with *glandulosum*. Rust relationships: takes *C. ledi* var. *groenlandici*; susceptible to *C. ledicola*. White hairs: sparse to frequent on twigs, abundant and moderately large on peduncles, pedicels, and capsules. Rusty lanate hairs: abundant on twigs and leaves, never on pedicels and calyx lobes; those on leaves typically covering lower surface. Leaves: normally strongly revolute; *L/W* (margins undistorted) (2.5–)3.0–5.0(–5.7). Pedicels slightly arcuate in fruit. Calyx lobes: 0.1–0.8 mm long, with only glands and fine white hairs. Petals: (4.5–)5.0–6.6(–7.0) × 2.5–3.5(–4.0) mm max., yellow glands often nil but sporadically few to moderately numerous. Stamens: 5–7(–8)((–10)); filaments glabrous to lightly ciliate in lower 1.0 mm with hairs to 150 μ long. Anthers (0.6–)0.7–1.0(–1.1) mm long. Capsules: (3.5–)4.0–6.0(–6.8) × (1.8–)2.0–3.0(–3.3) mm (*L/W* 2.0 +) at incipient dehiscence, apex slightly to moderately retuse or tapering to style.

Ledum palustre L. ssp. *decumbens* (Ait.) Hult., Flora of Kamtchatka, 4: 8. 1930.

Habitat: moderately dry tundra, occasionally penetrating bogs or coniferous forest. Habit: decumbent shrub generally much less than 0.5 m and less than half height of adjacent *L. groenlandicum*. Phenology: see under *L. groenlandicum*. Rust relationship: takes *Chrysomyxa ledi* var. *ledi*; susceptible to *C. ledicola*. White hairs: moderately developed on peduncles, few and small or none on twigs, pedicels, and capsules. Rusty lanate hairs: abundant on twigs and leaves, scarce to abundant on pedicels, usually present on calyx lobe margins; those on leaves mainly on lower surface of midrib and near margin. Leaves: normally strongly revolute; *L/W* (margins undistorted) (5.2–)5.7–10.7(–14.0). Pedicels: abruptly decurved near apex in full fruit. Calyx lobes: 0.1–1.0 mm long, glandular and usually fringed with rusty lanate hairs, fine white hairs lacking. Petals: 4.0–7.0(–7.5) × 2.3–3.8(–4.2) mm max., yellow (and (or) red) glands varying locally from nil to many. Stamens: 8–10(–11)((–12)); filaments (glabrate or) slightly to moderately ciliate in lower 0.7–1.5 mm with white hairs to 200 μ long. Anthers: 0.5–0.9(–1.0) mm long, generally shorter than in contiguous *groenlandicum*. Capsules: (2.5–)3.0–5.0 × (1.8–)2.2–3.2(–3.7) mm (L/W (1.1–)1.3–1.8(–2.0), av. 1.5) at incipient dehiscence, apex nearly always strongly retuse.

From this summary it may be seen that each species has numerous morphological and biological distinctions, far more than are commonly seen in subspecies (populations that intergrade smoothly at points of contact). Unfortunately many of the characters are quantitative or not readily usable in the assessment of individual specimens. However, difficulty in identifying taxa does not affect their actual status. To judge the status of the *Ledum* populations we must study their behavior in areas of contact or overlap.

Results

Ledum glandulosum and *L. groenlandicum*

Figure 1 shows that essentially pure *Ledum glandulosum* penetrates western Canada in two areas: in the northern Cascades and, somewhat further east, the southern Monashees; and along both flanks of the Rockies. It is not truly continuous in the more western area, for aridity excludes it from the Similkameen and Okanagan valley floors. Substantially further north, and generally disjunct from pure *L. glandulosum*, many *glandulosum* × *groenlandicum* hybrids occur.

Most of the hybrid specimens are from Yoho, Kootenay, and Banff National Parks, within the limits from 50°30′ to 51°30′ N and 115°20′ to 116°40′ W. Most of these specimens are plotted in Fig. 2, but space does not permit inclusion of all those recorded from especially Lake Louise and Banff. Few specimens are available except from near roads and improved trails; and the northeastern part of Banff Park and the adjoining areas beyond the park boundary are so inaccessible that the limits of the hybrid swarm cannot yet be defined. However, specimens from just north of the map area are all

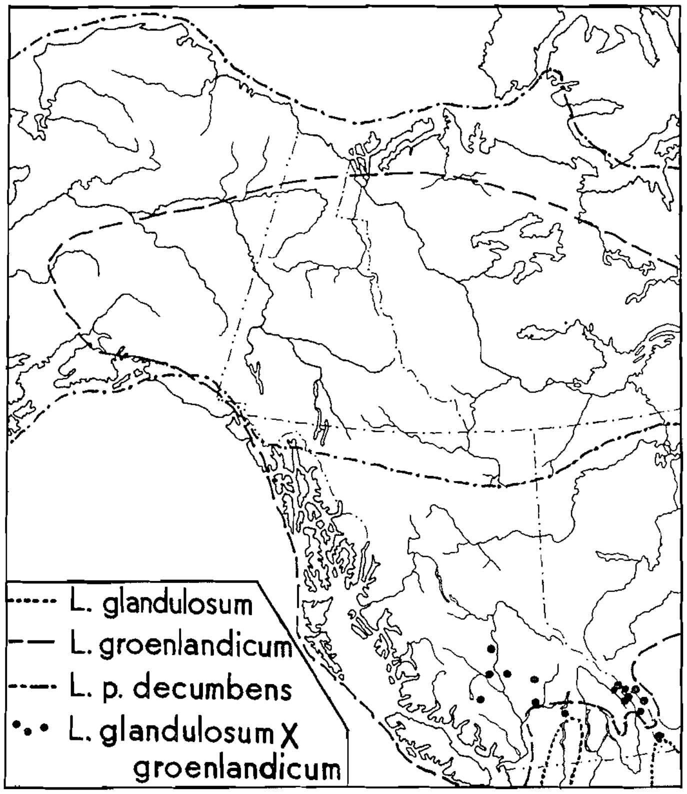

FIG. 1. Approximate limits of *Ledum* spp. in western Canada and Alaska, and locations of hybrids between *L. glandulosum* and *L. groenlandicum*.

pure *L. groenlandicum*. All phanerogamic and mycological specimens seen from the map area (except various *C. ledicola* on *L. groenlandicum* that duplicate phanerogamic collections) are cited below, graded roughly from pure *groenlandicum* to predominant *glandulosum*.

Ledum groenlandicum: B.C.: Yoho Natl. Park: L. Wapta, *Cormack* (ALTA); Kicking Horse Pass, *Taylor & Ferguson 2395* (DAO). Kootenay Natl. Park: Marble Canyon, *Nobles* (DAOM, *C. ledicola*); Paint Pots, *Fodor 273* (UBC); Dog L. Trail, *Seel 215* (DAO); Radium Hot Springs, *Fodor 157* (UBC, 2 plants). Sheep Mtn., 34 mi N of Natal, *Weber 2313* (V, UBC). Alta.: Banff Natl. Park: Bow L., *McCalla 7728* (ALTA, UBC); Lake Louise, *Malte & Watson 1045* (UAC), *Dudley 126* (DAO), *Fyles* (DAO); Mt. Eisenhower, *A. & D. Löve 6678* (DAO); Hillsdale, *Mair 31* (UBC); Vermilion Lakes, *Lewis* (ALTA); Banff, *McCalla 2164* (ALTA), *Brinkman*, *Holway* (both DAOM, *C. ledicola*); Bankhead, *Moss* (DAOM p.p., *C. ledicola*); road to Cave Basin, *Malte & Watson 774* (UAC). Forty miles W of Calgary, *Seaborn* (UAC).

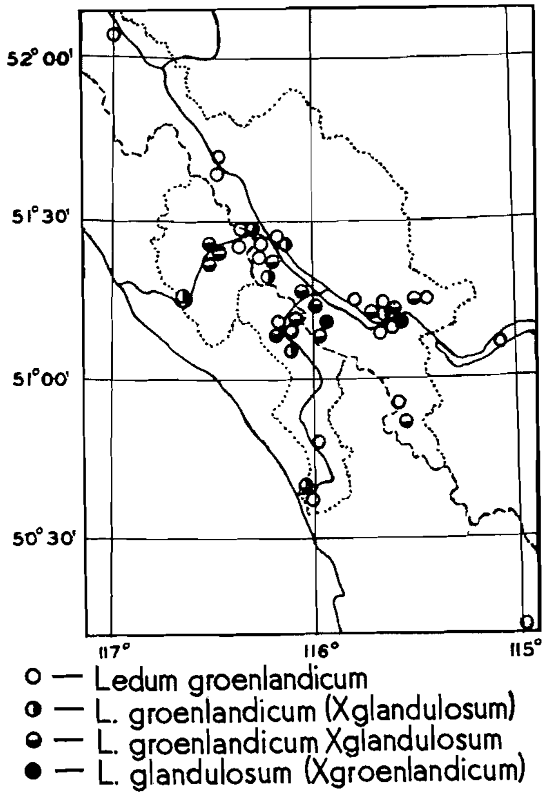

FIG. 2. Locations of *Ledum groenlandicum* and *groenlandicum–glandulosum* intergrades in Yoho, Kootenay, and Banff National Parks.

L. groenlandicum (× *glandulosum*): B.C.: Yoho Natl. Park: Kicking Horse Gorge, *McCalla 7528* (UBC); Kicking Horse Pass, *Fowler* (DAO). Kootenay Natl. Park: Numa Creek Trail, *Patterson* (CFB 6810, *C. ledi* var. *groenlandici* ?tending to var. *glandulosi*); Radium Hot Springs, *Fodor 157* (UBC, 1 plant). Alta.: Banff Natl. Park: Lake Louise Sta. (Laggan), *Holway* (DAOM, *C. ledicola*); Consolation Valley, *Beamish & Vrugtman* 620170 (UBC); Middle Spring, Banff, *Fletcher* (DAO); Banff, *Sanson* (DAO, two sheets, not identical).

L. groenlandicum × *glandulosum*: B.C.: Yoho Natl. Park: Natural Bridge, Kicking Horse Valley, *McCalla 7017* (UBC); Mt. Steven, nr. Field, *Calder & Savile 12047* (DAOM, *C. ledicola*); Field, *Henry* (UBC). Kootenay Natl. Park: Marble Canyon, *Moss* (DAOM, *C. ledicola*); trail to Stanley Peak, *Calder & MacKay 32776* (DAO). Alta.: Banff Natl. Park: Paradise Creek, Moraine L. road, *D.B.O. & C.E. Savile 4934A* (DAOM, *C. ledicola*) and *B* (DAOM, *C. ledi* var. *groenlandici* × var. *glandulosi*); Smith L. trail, *Patterson* (CFB 7650, *C. ledi* var. *groenlandici* × var. *glandulosi*); 3 mi W of Eisenhower Junct., *Ogilvie* (DAO); Red Earth Creek, *Ogilvie* (UBC); Squaw-Norquay Col, *Lewis* (ALTA); nr. Banff, *McCalla 2163* (ALTA, 2 collns., flower and fruit), *Anderson 484* (V); Bankhead, *Moss* (DAOM p.p., *C. ledicola*); Marvel Creek, *Barclay 285* (UAC).

L. glandulosum (× *groenlandicum*): Alta.: Banff Natl. Park: Redearth Fire Road, *Patterson* (CFB 7399, *C. ledi* ± *glandulosi*); Mt. Norquay, *Hardy* (V).

In addition to the mixed specimens noted in the citations, several sheets bear shoots clearly from shrubs with different genotypes, the differences sometimes indicating different degrees of hybridity. Thus *McCalla 7528*, cited as *groenlandicum* (× *glandulosum*), bears three plants, all with moderately ciliate stamens; the left one has mostly 5 stamens and *groenlandicum* calyx lobes; the center one 6–9 stamens and more or less *glandulosum* calyx lobes; and the right one 6–9 stamens and *groenlandicum* calyx lobes. It is quite impossible to indicate all such variations in the citations, but they are recorded on the sheets.

A few hybrids have been noted elsewhere, as shown on Fig. 1. These include two specimens that I rate as median: B.C.: Taseko L., E of Mt. Waddington, *Sugden 334* (DAO); and Enderby, north Okanagan Valley, *Lawes 484* (V). One specimen from the Crowsnest area, Alta., west of Castle R., *Ogilvie* (UBC), is vegetative but apparently predominantly *glandulosum*; the leaves are long and narrow and, on one of three sheets, some are fringed with rusty hairs. Finally, in the Cariboo District of southcentral B.C., several specimens (in poor flower or wholly vegetative) are predominantly *groenlandicum* but almost certainly with appreciable *glandulosum*: Tranquille Range, nr. Kamloops, *Tisdale 40-604* (DAO); 5½ mi E of Bridge L., *Calder, Parmelee & Taylor 20001* (DAOM, *C. ledicola*); nr. Alexandria, *Calder, Parmelee &*

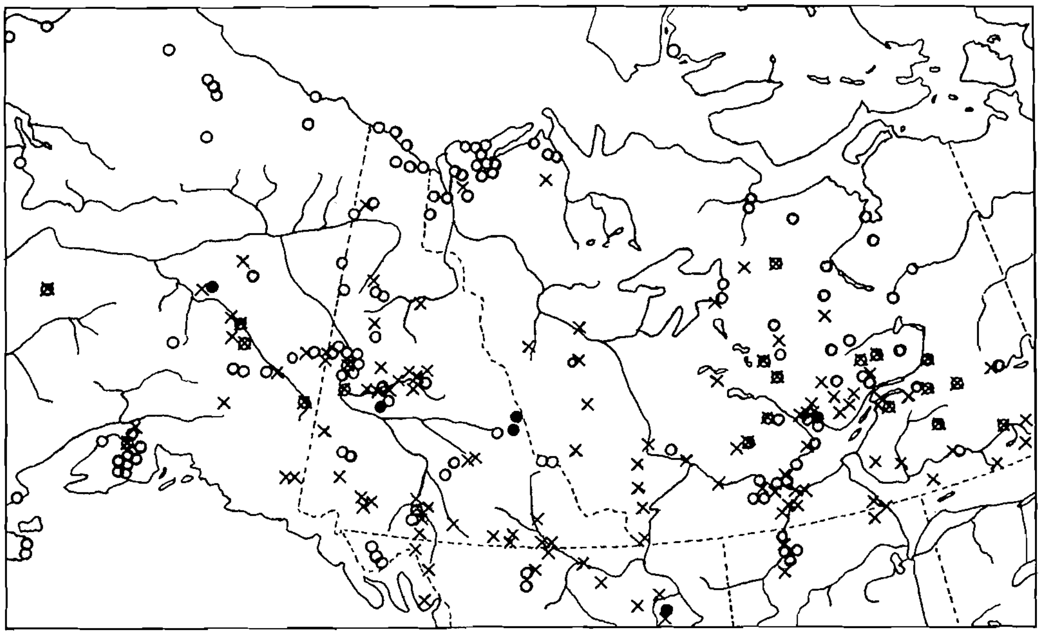

FIG. 3. Distribution of *Ledum groenlandicum* (crosses), *L. palustre* ssp. *decumbens* (open circles), and hybrids (solid circles) in Alaska and northwestern Canada.

TABLE I

Characters of hybrids between *Ledum groenlandicum* and *L. palustre decumbens*

Specimen	Twigs	Leaves	Pedicels	Calyx lobes	Stamen no.	Filaments	Anthers	Capsules
Argus 286	i–p*	±g	i	±p	10	i	g	—
Campbell 151	g	i	i	±g	10	g	g	—
Porsild & B 11257	i	i	i–p	i	—	—	—	i–p
Calder & K 22734	±g	±g	i	i	—	—	—	i–p
Cody 2446	±g	±g	±p	i	9–10	i	i	—
Calder & G 25410	i	g	i–p	g	10	g	±g	—

* g = *groenlandicum* type, i = intermediate, p = *palustre decumbens* type.

Taylor 17896 (DAOM, *C. ledicola*); 10 mi on road to Horsefly from 150 Mile House, *Calder, Parmelee & Taylor 19041* (DAOM, *C. ledicola*); 10 mi W of Puntacheskut L., W of Quesnel, *Calder, Parmelee & Taylor 18248* (DAOM, *C. ledicola*). Whether the lack of phanerogamic vouchers for these mycological specimens reflects sparse flowering in some of the hybrids, or merely the overwhelming commonness of *L. groenlandicum* in a region of over 25 000 sq. mi that the collectors were trying to cover fully in a single season, cannot now be decided; but, in retrospect, it is clear that we were all singularly blind to the occurrence of *Ledum* hybrids in the early years of our work in British Columbia.

It must also be noted that in most of the essentially typical *Ledum glandulosum* specimens from Flathead Valley and Waterton Lakes National Park, close to the Montana border, careful examination of young leaves often reveals a few marginal rusty hairs toward the apex. Such hairs, always shed before the leaves are fully mature and lacking in specimens from further south, presumably are a legacy of earlier contact with *L. groenlandicum.*

Ledum groenlandicum and L. palustre decumbens

In contrast with the situation in *Ledum glandulosum* and *L. groenlandicum*, there is a pronounced contemporary overlap between *L. groenlandicum* and *L. palustre decumbens* continuously from Alaska to Labrador and Greenland.

Random checking of sympatric specimens from various specimens in stations in eastern Canada confirms my observation at Great Whale River that these plants maintain their separate identities. Because Hultén (1967) has suggested that the eastern distinctness is not duplicated in Alaska and Yukon, I have studied in detail all the locally available material from Alaska, Yukon, Mackenzie, and northernmost British Columbia and Alberta. Of the 350 specimens examined, some specimens of *L. p. decumbens* were from north of the limits of *groenlandicum*, but about 300, nearly equally divided between the species, are from the area of sympatry. Most of these specimens are plotted in Fig. 3, but space does not permit recording all from a few heavily collected areas, notably Dawson, Yellowknife, and the west end of Great Slave L.

Figure 3 shows that the two species overlap by up to 10° of latitude (ca. 700 mi). In this vast sympatric area (roughly 800 000 sq. mi) I have found six specimens that are clearly hybrid, i.e. not readily assignable to either species; and these are cited herewith. *Ledum groenlandicum* × *L. palustre* ssp. *decumbens*: Alaska: Fairbanks Quadrangle, 1 mi W of Smith L., *Argus 286* (DAO; A = *L. p. decumbens*, B = hybrid, C = *groenlandicum*). Yukon: White Mtn., McQuesten area, *Campbell 151* (CAN, A = *L. p. decumbens*, C = ? *L. p. decumbens*, B and D = hybrid); Macmillan Pass, Canol Road, *Porsild & Breitung 11257* (CAN); nr. Mackenzie border, 62° 57′ N 130° 09′ W, *Calder & Kukkonen 22734* (DAO). Mack.: Yellowknife, *Cody 2446* (DAO, one of two plants). B.C.: S of Ft. Nelson, *Calder & Gillett 25410* (DAO, one of four plants). The characters of these specimens are summarized in Table I. It will be seen that the characters vary independently and generally unpredictably. Stamen numbers tend to be those of *L. p. decumbens*, favoring the suspicion that *L. groenlandicum* is potentially capable of reaching this number.

In addition to these definite hybrids, which, it must be noted, are often individuals among one or both parents rather than a uniform population, about 17 *groenlandicum* specimens were suspected to contain some *decumbens* genes and about 13 *decumbens* were suspected to contain a little *groenlandicum*. Because most of the characters are quantitative, with considerable variation in genetic makeup or expression, slight introgression is often impossible to identify with certainty. Each time that I sorted the 300 specimen cards I inevitably arrived at slightly different totals. One specimen may be cited with some confidence: *Cody & Loan 3906*, 1 mi S of Ft. Smith, Alta., is typical *groenlandicum* except that the lower plant on the sheet has some rusty cilia on most calyx lobes. As this character is apparently never seen in pure *groenlandicum* it almost certainly represents a trace of *palustre decumbens*, here at its southern limit. Most of the specimens are assigned on less reliable characters, such as high stamen number in *groenlandicum* (low stamen number in nearly pure *p. decumbens* seems to be very rare), or slightly atypical leaf shape or pubescence in either species, which may in some cases only reflect extreme variation within the species.

Nevertheless it appears probable that backcrosses to either parent are more abundant and better adapted than more or less median (perhaps including F_1) hybrids.

It is notable that *L. groenlandicum* and *L. p. decumbens* were strictly sympatric, as indicated by label data or mixed collections, on at least 22 sites. (The hybrid symbol in Alaska actually represents a mixture of the hybrid and both parents.) As many more collections were essentially contiguous but with inadequate data (e.g. "Dawson") to tell whether separation was to be measured in yards or miles. Under the circumstances the number of definite or possible hybrids is impressively small.

One specimen from far beyond the recorded southern limits of *L. p. decumbens* must be mentioned here. *Jenkins 5991* (DAO), nr. Miette Hot Springs, Jasper Natl. Park, Alta. (53°37′ N 117°46′ W), is typical *L. groenlandicum* in most respects, but the pedicels uniformly show traces of rusty pubescence. Available specimens indicate that *L. p. decumbens* currently extends south to about 58°30′ N. Unfortunately, from where the Alaska Hwy. swings east from the Rockies at ca. 58°40′ N southeast to Jasper National Park, the range is cut only by route B.C. 97 at Pine Pass (55°30′ N). Accordingly we have little assurance that no relict colonies of *L. p. decumbens* (and other northern plants) occur along this sparingly botanized section. Whatever the true contemporary limits of *L. p. decumbens*, the anomalous Jenkins specimen suggests that in late-glacial or early postglacial times it occurred further south on the east flank of the Rockies.

Finally it may be noted that, in some specimens of both these species that show no suggestion of hybridity (even far from the sympatric zone), two genotypes are represented on a sheet, as indicated by variation in characters (e.g. pubescence or stamen number) not subject to phenotypic variation. Conversely (e.g. *Calder 5237* (DAO), *L. p. decumbens*, 2 mi E of Hope, Kenai Pen., Alaska) genetic uniformity is occasionally indicated by pubescence characters and stamen number; but correlated differences in leaf size, calyx lobe length, and petal size indicate that the plants came from both open and shady sites. This particular shade-grown plant also bears leaves that are only slightly revolute, revealing the localized disposition of the rusty hairs on margins and midrib, and, with their exaggerated maximum width, an L/W of 5.4 in contrast to 7.1 for the rest of the sheet. Such specimens point to the difficulty of being certain that minor deviations from the norm actually represent hybridity.

Conclusions

A chromosome number of $n = 13$ has been exclusively reported for *Ledum glandulosum* and *L. groenlandicum*, as far as can be ascertained from all the available reports. In contrast the few counts reported for *L. p. palustre* indicate it to be tetraploid ($n = 26$). Unfortunately no count of *L. p. decumbens* seems to have been published. That reported by Böcher, Holmen, and Jakobsen (1968) was not from Greenland material and seems actually to be for *L. p. palustre*. Dr. Holmen (in litt.) states that the number was taken from Jørgensen, Sørensen, and Westergaard (1958), who misread Hagerup (1941). Hagerup stated his material of *L. palustre* was from the Botanical Garden in Copenhagen, and that the Greenland var. *decumbens* should be closely examined.

Although numerous recently discovered examples of two or more levels of ploidy in single homogeneous populations of flowering plants make it inadvisable to draw sweeping conclusions from limited counts, there seems to be no obvious barrier to the production of fertile hybrids between *glandulosum* and *groenlandicum*. These taxa have clearly been kept distinct mainly by geographic and ecological separation. Although field collections do not allow accurate comparison of their phenology, the assorted hybrids in the Banff region suggest nearly synchronous anthesis.

In the Banff region pure *L. glandulosum* seems to be absent, plants approaching *glandulosum* are relatively scarce, and plants ranging from median hybrids to pure *L. groenlandicum* are abundant. Because *L. glandulosum* is a relatively southern plant, predominantly of warm mesic upland forests, it is most probable that it extended into the Banff region during the postglacial Hypsithermal Interval; and that, with the onset of marked cooling about 3500 years B.P., it was eliminated from the northern part of its range except for relict colonies on favorable sites. Similar extensions and withdrawals are indicated by disjunct ranges in various plants of British Columbia. The cooling trend must have stimulated the southward spread of *L. groenlandicum*, which will presumably finally swamp out the remaining traces of *glandulosum* unless a marked new climatic warming occurs.

The limited data for *Chrysomyxa ledi* in the Banff region indicate that the morphology of the urediniospores varies more or less in proportion to that of the hosts. There is no question about the assignment of the two definitely hybrid specimens on nearly median host hybrids; but the paucity of characters and inevitable random variation in each rust variety makes unequivocal assignment of the other two collections as nearly pure var. *glandulosi* and nearly pure *groenlandici* impossible. Only a long series of specimens in each class and statistical treatment of the variations (almost impossible in this relatively uncommon species) would allow firm disposition. Nevertheless the finding of even two hybrid rust specimens, apparently well adjusted to their hybrid host, indicates some degree of stability in the association and persistence of the *Ledum* hybrid swarm for a substantial time. Thus we have indirect support for this population having persisted since the end of the Hypsithermal Interval.

Turning to the hybrids in south central British Columbia, it is clear that *L. glandulosum* must have extended, in the Hypsithermal, substantially beyond its present limits in the northern Cascades and southern Monashees. On Vancouver Island and the adjoining mainland stamen numbers in essentially typical *L. groenlandicum* range from 5–7 to 8–10, and filament pubescence is quite variable. In view of the definite hybrid from Taseko L. and the findings of Hitchcock (1956) in southwestern Washington, it is probable that some of these coastal plants carry a trace of *glandulosum*.

It will be noticed that there is a substantial area between the scattered outlying hybrids in southcentral British Columbia and the limits of *L. glandulosum*. Although systematic collecting would doubtless reduce this area, much of the country is too arid to support *L. glandulosum*. When this species spread north in the Hypsithermal it must have done so in the Coast Range and the Monashee Mts.

The purity of the population of *Ledum glandulosum* in the northern Cascades and southern Monashees reflects the apparently complete lack of sphagnum bogs, necessary for the support of *L. groenlandicum*. The closest stand of *groenlandicum* known to me was at a small lake between Hope and Manning Provincial Park. This stand was destroyed by a vast rock slide in 1965.

When the total populations of both taxa are considered, most of the specimens are clearly assignable to *L. glandulosum* or *L. groenlandicum*, which have numerous biological and morphological distinctions. Where they meet, and the ecological barrier is overcome, they produce a haphazard swarm of hybrids rather than intergrading clinally. On balance it seems most realistic to maintain them at specific rank. It also seems best not to assign varietal or other names to the hybrids, of which generally no two plants in an area are identical, but simply to record them as hybrids. The predominant parent is often clear and may be indicated on annotation labels. The species are clearly separated by an ecogeographic barrier rather than a genetic one. The case is parallel to that of *Saxifraga lyallii* and *S. odontoloma*, described by Calder and Savile (1960), which generally occupy alpine and moist coniferous forest niches respectively. Hybrids are found where the species overlap near the 49th parallel, but only because *S. lyallii* comes down the alpine brooks into the habitat of *S. odontoloma*.

Turning to the relationship of *L. groenlandicum* and *L. palustre decumbens* we find a contrasting situation. The geographic overlap is very great; and the ecological overlap is appreciable, as numerous strictly sympatric specimens show. However, the species, though evidently not fully allochronic, are markedly different in time of anthesis. We do not yet know whether this phenological difference is the major barrier to hybridization, but it probably plays a part. The extreme rarity of approximately median hybrids and somewhat greater frequency of specimens showing only slight introgression suggest that there may be a genetic barrier to hybridization. If *L. p. decumbens* does prove to be tetraploid, we need scarcely search further for the cause of such a barrier. Whatever the cause, F_1 hybrids are probably relatively poorly adapted (and may also produce little viable pollen, which would restrict further reproduction). However, the slight introgression observed in both species indicates that hybrids do occasionally persist long enough to backcross to both parents. Incidentally, the hybrids are probably usually intermediate in time of anthesis, which would facilitate backcrossing.

It is clear that taxa that are sympatric to the extent of *Ledum groenlandicum* and *L. palustre decumbens* with minimal hybridization must be regarded as specifically distinct. To most zoologists and an increasing number of botanists subspecies are geographic populations that intergrade clinally on contact. Admittedly, this interpretation must be applied with some flexibility. In arctic and alpine situations, where most flowering plants are highly self-fertile and insect activity is often reduced by weather conditions, fully interfertile populations may interdigitate appreciably. With the *Ledum* taxa, in contrast, we see broadly sympatric populaions occurring, among other places, in the interior valleys of Alaska and Yukon where high summer temperatures ensure abundant insect activity. To regard *groenlandicum* and *palustre decumbens* as only subspecifically distinct under these circumstances is to deprive the subspecies concept of all utility.

The basis of the belief that *L. groenlandicum* and *L. p. decumbens* intergrade freely in Alaska and Yukon is not wholly clear. Both Hultén (1967) and Calder and Taylor (1968) mention the sharply decurved upper part of the pedicel in *L. p. decumbens*, first pointed out by Porsild (1951). As noted in the discussion of characters, the pedicel shape is reliable only at maturity: the flowering pedicels are straight to arcuate and those of young fruits are variable. Undoubtedly the frequent dwarfing of leaves of *groenlandicum* in the northwest has caused some confusion. Some of the dwarfing may be genetic, but much is certainly phenotypic. Almost any deleterious factor in the environment except shading tends to reduce leaf size. A few small-leaved plants bear copious mineral dust, indicating proximity to a road; and such plants were probably injured through road drainage lowering the water table. Leaves are generally stunted on severely exposed sites, which are inevitably most frequent in mountainous country. Thus in Alaska, Yukon, and northern British Columbia we see many small-leaved specimens, but also large-leaved ones interspersed with them. Even if some of the stunting is genetic it need not indicate hybridity, for most small leaves fall in the normal L/W range of *groenlandicum*. It is important to use all characters in assessing specimens, but little reliance can be placed on size of an organ except in comparing contiguous specimens of the two species. Leaf and capsule shape are much more reliable than mere size; and the importance of the distribution of both hair types cannot be overemphasized. Study of the hairs requires somewhat higher magnifications than most phanerogamic botanists use routinely.

It is hoped that this somewhat preliminary study, based mainly on herbarium material, will illustrate the need for experimental work. It is clearly desirable that the three species be grown together for phenological comparison, preferably at several temperatures.

It is desirable that crosses be made, using pure material of each species gathered far from areas of overlap. This, at least, would show the range of variation in the F_1 hybrids. However, backcrossing may be possible. Plants of *L. groenlandicum* grown in a greenhouse at Ottawa from Queen Charlotte Islands seed flowered about 21 months after the seed was sown. Thus breeding experiments need not take an inordinate time.

Several chromosome counts should be secured for *Ledum palustre decumbens*. G. A. Mulligan (personal communication) warns me that *Ledum* buds, like those of some other Ericaceae, resist the penetration of fixing fluids, and that the buds should be teased open before fixing.

Finally, the genus seems to offer great promise in the field of pollination biology. *Ledum* flowers attract great numbers of insects in the south, but what happens in the north? What function, if any, have the cilia near the bases of the filaments? What is the constitution of the nectar in the curious annular nectary? In some herbarium specimens the nectary surface is viscid, which would not be expected of a dried sugar solution, but this effect may be due to admixed secretions from the glands higher on the ovary.

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