# The Biological Flora of Canada.

## 3. *Vaccinium vitis-idaea* L. var. *minus* Lodd. Supplementary Account..*

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*Vaccinium vitis-idaea* var. *minus* is a widely distributed evergreen dwarf shrub of northern temperate, boreal and arctic areas in North America. Rapid dispersal of seeds by birds and mammals through their droppings, followed by good seed germination and seedling establishment, permits this species to colonise burned forests and open habitats. Its evergreen characteristics and low growth form permit effective photosynthesis and growth in northern climates because its niche is the warmer microclimate at the soil surface. Plants flower in Canada from mid-June to early August depending on location, and the berries generally mature in late August or early September. Berries are of low pH, moderate caloric content and are high in tannin and anthocyanin.

Key Words: *Vaccinium vitis-idaea* var. *minus*, Partridgeberry, Fox Berry, Lingonberry, biology, ecology, physiology, distribution, economic importance.

### 1. *Name*

*Vaccinium vitis-idaea* L. var. *minus* Lodd., section Vitis-Idaea; Ericaceae
*Vaccinium vitis-idaea* spp. *minor* (Lodd.) Hultén (Hultén 1937, 1949),
*Vaccinium vitis-idaea* L. (Scoggan 1979); Mountain-cranberry, Rock Cranberry, Cowberry, Lingen, Lingberry, pommes de terre (Fernald 1950), Partridgeberry (Rouleau 1956), airelle-d'Ida (Marie-Victorin 1964), Lingonberry (Hultén 1968), Fox Berry (Roland and Smith 1969), Redberries (Bourchard et al. 1978); Dry-ground Cranberry (Looman and Best 1979); berris, graines rouges (Scoggan 1979).

### 2. *Description of the Mature Plant*

*a) Raunkiaer life-form.* Chamaephyte. Evergreen dwarf creeping shrub, reproducing by seeds and rhizomes.

(b) *Shoot morphology.* Stems semi-woody, up to 15 cm high, 1-2 mm diameter, puberulous, the bark with a reddish tinge in late autumn; terminal flower buds larger than the vegetative buds; evergreen leaves alternate in a spiral (Figure 1), simple, petiolate, 5-18 mm long, 3-9 mm wide, somewhat leathery, pinnately net veined, margin slightly revolute, obovate, apex mucronate to emarginate, base cuneate, the upper surface dark green, purplish in autumn, the lower surface waxy, pale green with black glandular dots; slender creeping stems semi-woody, bearing numerous shoots, new growth white or pinkish. Occasionally produces rhizomes not morphologically distinct from stems (Shaver and Cutler 1979).

*(c) Root morphology.* Tap root with finely divided rootlets at the extremities (Hall and Beil 1970) (Figure 2), adventitious roots occurring at nodes along the creeping stems and rhizomes (Viereck and Little 1972). Leiser (1968) has described a mucilaginous root sheath surrounding the root tip.

*(d) Inflorescence.* Flowers occurring singly or in racemose clusters (Figure 1), "the most common numbers being five and six" in Newfoundland (Torrey 1914), at Kentville, Nova Scotia, 5.2 ± 1.6 ($\bar{x}$ ± standard error used throughout paper) (n = 167). Stems bearing inflorescences at anthesis are 9 cm tall (Pojar 1974). Flowers pedicellate; sepals 4, green (pinkish in dried specimens), deltoid, 1.5 ± 0.0 mm diameter (n = 42); petals 4, the corolla pinkish-white, bell shaped, corolla lobes free for half their length, 4.7 ± 0.5 mm long (n = 42), 4.8 ± 0.6 mm wide (n = 42); stamens 8, in 2 whorls, filaments hairy. Pollen is borne in tetrads, and shed from the anther through a terminal pore.

* See J.C. Ritchie (1955).


FIGURE 1. Flowers and leaves of *Vaccinium vitis-idaea* L. var. *minus* Lodd.

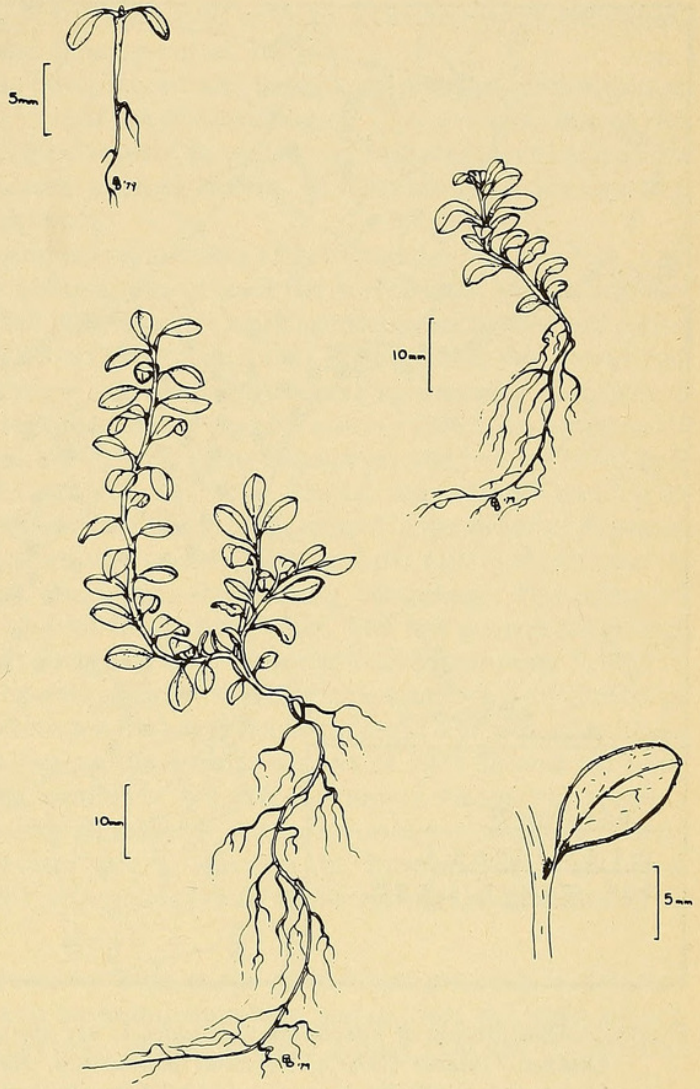

FIGURE 2. Seedlings of *Vaccinium vitis-idaea* L. var. *minus* Lodd. Approximate age of largest plant 1 yr.

The stigma and part of the style protrude beyond the corolla (Figure 1). The ovary is inferior with many ovules and together with the calyx produce a true berry. Berries are carmine in colour when ripe, globose, nearly 1 cm diameter (Gleason 1958), acid, and have several small seeds per berry (see 7b); seeds are dark brown, elliptic to semicircular, 1.0 × 0.6× 0.5 mm, with a reticulate surface (Montgomery 1977).

*(e) Subspecies.* Hultén (1949) treats *V. vitis-idaea* L. var *minus* as a subspecies.

*(f) Varieties.* We have followed Fernald (1950) who considered the smaller North American form as a variety (*Vaccinium Vitis-Idaea* L. var. *minus* Lodd.) and the larger European plant as variety *vitis-idaea.*

*(g) Ecotypes.* None recognized in North America.

*(h) Chromosome numbers.* 2n = 24 has been reported by Newcomer (1941) from plants collected in N. Carolina and Tennessee, by Taylor and Mulligan (1968) from a collection southeast of Port Clements in the Queen Charlotte Islands, B.C., and from the IBP sites at Barrow Alaska by Packer and McPherson (1974). The European *V.vitis-idaea* var. *vitis-idaea* also has 2n = 24 (Ritchie 1955, Sorsa 1962, Hedberg and Hedberg 1964, Rousi 1966, 1967, Laane 1969).

## 3. *Distribution and Abundance.*

*(a) Geographic range. Vaccinium vitis-idaea* var. *minus*, a native species listed by Macoun (1884), occurs widely in north temperate, boreal and arctic regions. In North America it extends from eastern Newfoundland to Alaska and British Columbia (Figure 3, Table 1). It has been collected along the north coast of Alaska, in the

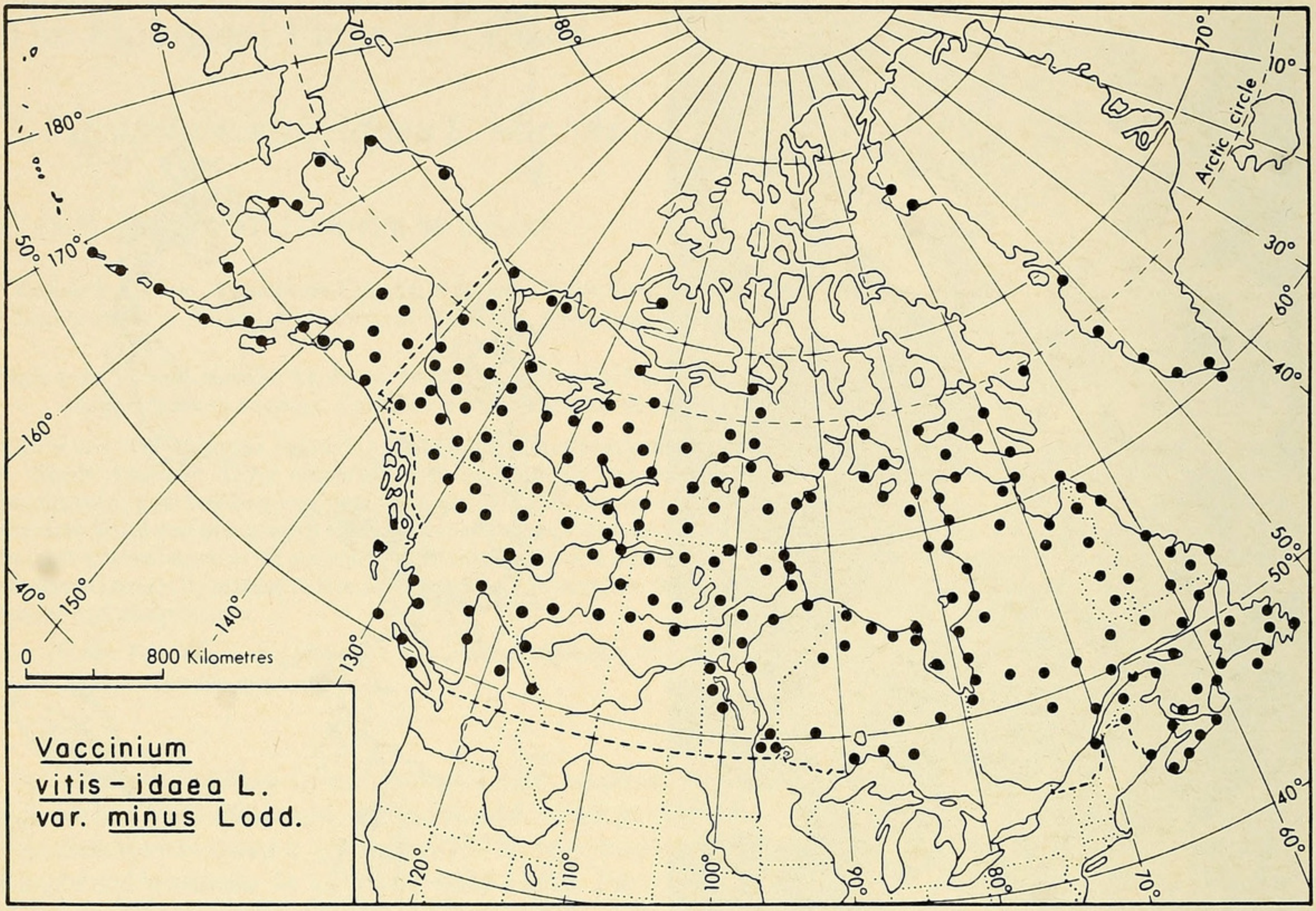


FIGURE 3. Distribution of *Vaccinium vitis-idaea* L. var *minus* Lodd. from specimens in the herbaria of Canada Agriculture, Ottawa, Ontario (DAO), National Herbarium, National Museum of Canada, Ottawa, Ontario (CAN), Acadia University, Wolfville, Nova Scotia (ACAD), University of Manitoba, Winnipeg, Manitoba (WIN), and University of Alberta, Edmonton, Alberta (ALTA).

Mackenzie District, Victoria Island, Keewatin (Scoggan 1979) and southern Baffin Island (Polunin 1948). It ranges southward to northern Minnesota and New England (Scoggan 1979). Porsild and Cody (1980) map the N. American distribution, Ritchie (1962) gives Manitoba sites and a map of Alaska sites is contained in Viereck and Little (1975). Beyond North America it has been recorded in Greenland up to 78° N and in eastern Asia (Hultén 1948). Eurasian distribution of var. *vitis-idaea* is given in Ritchie (1955). Distribution maps are listed in Hultén (1971) and include those of Meusel (1943), Raup (1947) Szczawinski (1962), Porsild (1964), Hultén (1968,1971).

*(b) Altitudinal range.* In Eastern Canada this species extends from about sea level to the summits of the Shickshock (elevation 1290 m), Gaspé Peninsula, and Torngat Mts. (elevation 1200 m), Newfoundland. On Mount Washington (elevation 1700 m), New Hampshire it is found on north and west slopes (Bliss 1963). It occurs from valley bottoms to well above treeline in the Alberta Rockies (elevation 2250 m) (Hrapko and LaRoi 1978). Throughout the northwest it occupies habitats of various altitudes including the lower elevations of the Mackenzie Mts., Northwest Territories, and the Ogilvie (1350m) (See and Bliss 1980), and St. Elias Mts. (up to 1500 m) (Birks 1977), and the Alsek River region (2100-2400 m) in the Yukon (Douglas 1974). Populations of this species at the highest elevations are less vigorous and have small leaves with short internodes. At sea level in southern Alaska it grows vigorously (Cushwa and Coady 1976). It occurs around Hudson Bay on uplands, islands and in estuarine habitats.

## 4. *Physical Habitat*

*(a) Climatic relations.* The major part of the plant's distribution lies within Thornthwaite's (1931) Dfc climatic

region, characterised as semi-arid with short, cool summers and long, cold winters. It occurs within the arctic, subarctic, cryoboreal, boreal and mesic climatic soil classes (Clayton et al. 1977a).

Larsen (1971a) suggests that in central northern Canada boreal forest and tundra, correlations with air mass frequencies are sufficiently high to warrant the conclusion that the distribution of *V. vitis-idaea,* one of the dominant species in Black Spruce, White Spruce and Jack Pine forests, is related to arctic air mass distribution and frequency. But in rock field (fell-field) tundra and tussock muskeg tundra, *V. vitis-idaea* distribution and frequency are related to warm, moist Pacific air mass frequency.

Due to their northerly distribution, plants must withstand extreme cold and prolonged cover by snow. The latter may be an advantage because ample snowcover is necessary to protect the leaves from snow abrasion (Savile 1972). On Mt. Washington it dominates dwarf shrub communities where winter snow is deep but melts early in the spring (Bliss 1966). In contrast, Hrapko and LaRoi (1978) report that *V. vitis-idaea* var. *minus* has high cover in the *Dryas octopetala** (Dryas) — *Empetrum nigrum* (Crowberry) community type where snowmelt is late. In Greenland it can survive snow cover for more than a year (Warming 1908). Resumption of growth is governed by the timing of snow melt (Wielgolaski 1974). Both light (Oldemeyer and Seemel 1976) and moisture are important influences on development and growth. In Nova Scotia, maximum flower bud formation occurs in open exposed sites, although in Alberta bud formation was greatest in the shade of *Populus tremuloides* (Trembling Aspen) (Smith 1962) where moisture was greater. Lehmushovi (1977) states that in Finland the more open and better illumined the habitat, the higher the fruiting percentage. The effect of temperature is shown by later flower anthesis in coastal and more northerly sites. The low growth habit and shallow root system of *V. vitis-idaea* enable it to take advantage of the warmer microenvironment found at ground level. Ritchie (1955) suggests that temperature is the critical factor that limits its southern distribution in England. He reported significant temperature differences between the southern heath areas where *V. vitis-idaea* was present and absent. In field plantings at Kentville following the normal winters of 1978-79 and 1979-80, when maximum January temperature was 15°C and the minimum -19.5°C, all native *Vaccinium* species, including *V. boreale* (Sweet Hurts), *V. myrtilloides* (Sour-top Blueberry), *V. angustifolium* (Lowbush Blueberry) and *V. vitis-idaea* var. *minus* survived without winter injury, whereas the European *V. vitis-idaea* (Cowberry) plants had mostly brown, withered leaves and *V. myrtillus* (Dwarf Bilberry) had the stems killed to ground level (personal observation I.V.H.).

*(b) Physiographic relations.* *Vaccinium vitis-idaea* occupies a wide range of habitats growing in extreme exposure on headlands, sea cliffs, rocky hilltops, eskers and mountain summits, and in more sheltered sites in Black and White spruce forests. It is found on low flat areas, gentle to steep slopes (Larsen 1972b) and mountainous terrain (Hrapko and LaRoi 1978).

At Caribou Lake, northern Manitoba, it was a principal component of the south- and east-facing slopes of eskers and moraines but was absent on the snowless northwest side (Ritchie 1960a). In contrast, near Inuvik (Ritchie 1977) *V. vitis-idaea* was absent in the open forest on south-facing slopes and had a frequency of 40% and cover of 3% on north-facing slopes. North-facing slopes in the Pelly Lake area had the greatest moisture and supported more or less continuous vegetation which included *V. vitis-idaea* with a mean frequency of 80% (Larsen 1972b).

Parent material may be sandstone (Hall *et al.* 1964), limestone (Polunin 1948, Rickard *et al.* 1965) schist, gneisic or granite rock, glacial outwash plains of coarse sand and gravel (Larsen 1971a) or peat (Ritchie 1960a, Haag 1974). *Vaccinium vitis-idaea* is found on gray luvisols, humoferric podsols, dystric brunisols, orthic and cryic regosols, gleysols and cryic gleysols, fibrisols, mesisols, and rockland (soil classification after Clayton *et al.* 1977a) and histic cryaquepts (peaty phase of orthic gleysol) with 15 cm peat (Haag and Bliss 1974). Ritchie (1960a) reports it on peat up to 1.5 m deep. Soil pH is generally acid, it may be 3.0-3.9 (Dugle 1972), 4.5-4.7 (Barclay-Estrup and Nuttall 1974), 4.9 (Swan and Dix 1966), or 5.4 (Haag 1974). *Vaccinium vitis-idaea* var. *minus* was common in a Larch fen (*Larix laricina*) with a pH 7.0-8.2 (Ritchie 1960b).

The Orthic Gleysols described by Hrapko and LaRoi (1978) had the following characteristics: pH 5.2, N = 0 ppm, p = 5 ppm, and K = 127 ppm. Their field capacity was 46%, permanent wilting point 27% and available water 19%. Eutric Brunisols and Orthic Gleysols at Tuktoyaktuk had a 10-15 cm organic layer with a total exchange capacity of 77.4 meq/100 g overlying a thin, discontinuous Bg horizon (total exchange capacity 118.1 meq/100 g). The permafrost maximum active layer was 35-50 cm at the end of the summer (Haag 1974), and ranged from 29-112 cm.

In the southern part of its range *V. vitis-idaea* var. *minus* occurs most frequently in bogs and relatively moist

*Nomenclature follows Scoggan 1979

sites, although further north it frequents dry to moist sites (Polunin 1948, Larsen 1971b, 1972a) or those that are well to moderately drained (Ritchie 1960b; Lavkulich 1973). It grows in moist sites as well as those with a slight moisture deficit. Larsen (1972b) pointed out that differences in moisture rather than soil type governed *V. vitis-idaea* distribution at Pelly Lake, for it flourishes best where there is some moisture retention. In the peat soils around Little Catalina on the Bonavista Peninsula, Newfoundland, the linear growth was three to four times that on the drier mineral soils nearby (personal observation I.V.H.).

*(c) Nutrient and water relations. Vaccinium vitis-idaea* nutrient requirements are low being satisfied by soils that are shallow or of low fertility. It is generally shallowly rooting (Shaver and Chapin III 1980) but may root from 0-30 cm (Hrapko and LaRoi 1978). Rhizomes and roots grow well in peat, but often penetrate and grow in mineral layers (Weber 1974, Shaver and Cutler 1979), the latter also found roots concentrated in the structured dead zone, below the living moss. In Britain the rhizomes are invariably confined to the humus layer (Ritchie 1955).

Haag (1974) fertilized a dwarf shrub-heath community dominated by *Betula nana* ssp. *exilis* (Dwarf Birch) and *Salix glauca* (Willow) with a prostrate ground cover of *V. vitis-idaea* var. *minus, Ledum palustre* (Northern Labrador-tea) and *Empetrum nigrum* var. *nigrum* using 100 and 200 kg/ha ammonium nitrate (34% N) and 100 and 200 kg/ha superphosphate (20% P). The applications of N increased production by 15% and 30% by 12 July, and to 45% and 68% by 6 August at low and high rates respectively. Phosphorus at low rates decreased total production 20% but increased it 4% at high rates. When N and P were combined, total production increased 15% and 30% on 7 July and 35% and 75% by 6 August. This indicates that total primary production is limited more by available soil N than P.

## 5. *Plant Communities*

*Vaccinium vitis-idaea* var. *minus* is a northern plant and like its European counterpart (Ritchie 1955) occurs primarily in the Boreal Forest and Tundra regions (Rowe 1972). It is found in a range of communities including forests (Moss 1953a, 1953b; Ritchie 1956, 1959, 1960a, 1960b; LaRoi 1967., Blouin and Grandtner 1971, Bouchard et al. 1978), various types of muskeg (Larsen 1965, Ritchie 1960b), bog, fen (Ritchie 1960b), peatlands with feather mosses and/or Sphagna (Calder and Taylor 1968, Railton and Sparling 1973); arctic-alpine tundra (Porsild 1937; Bliss 1966; Porsild and Cody 1980), and other communities characterized by their physiography such as rock outcrops, eskers and rockfields (Larsen 1965), dunes (Grandtner 1977), and heath barrens along coasts (Torrey 1974; Marie-Victorin 1964).

Data showing the abundance of *Vaccinium vitis-idaea* var. *minus* and the location of a selection of communities containing it are given in Tables 1 and 2. LaRoi (1967) found it present in 35% of the White Spruce and 42% of the Black Spruce stands in an east-west arc across the Boreal Forest. In the east its presence in the Acadian (Roland and Smith 1969) and Great Lakes-St.Lawrence Forest Regions (Blouin and Grandtner 1971) is more limited. In the west it forms part of Rowe's (1972) Mixedwood Forest Region (Swan and Dix, 1966, LaRoi 1967, Larsen 1972a, Shay and Shay 1979) and it occurs westwards to the Northern Pacific Coast (Pojar 1974). Many studies have reported it in arctic and alpine locations (Polunin 1948, Cody 1954b, Bliss 1963, 1966, Birks 1977, Hrapko and LaRoi 1978).

## 6. *Growth and Development*

*(a) Morphology.* The oblong-elliptical cotyledons are ca. 2 mm in length. The first true leaves are nearly ovate and less than one-third the size of fully mature leaves. Rhizomes begin to grow on seedlings 5 cm in height (Figure 2). Lateral growth of plants is slow, being ca. 2 to 4 cm per year at Kentville. Bliss (1966) studied growth at 1600 -1800 m on Mt. Washington, New Hampshire and found that plants elongated 0.05-0.1 cm in 3-day periods, and that over four years, mean shoot elongation in *V. vitis-idaea* ranged from 0.8-1.8 cm per year. Bliss (1962b), in a review article on the adaptations of arctic and alpine plants to environmental conditions, states that work in Russia by Zhuikova showed that most plants of *V. uliginosum* (Alpine Bilberry), *V. myrtillus*, and *V. vitis-idaea* did not flower until 14-20 years of age. Ritchie (1955) indicated that, in cultivation, few flowers are formed in *V. vitis-idaea* before plants are 5-10 years old.

In a pine forest in Sweden, Teär (1972) found that in four year old plants, stems of *V. vitis-idaea* were monopodial with 2 to 3 shoots per stem and 3 to 4 stems per plant. At least one stem (approximately 4 cm long) is produced each year, the number depending on plant size. Fertile shoots have more leaves than sterile ones and produce one flower bud containing 5-6 flowers. On the other hand, plants on farmland were more branched and stems were sympodial with 6 to 12 stems per plant ( 2 cm long). The number of leaves per running cm was greater than in the pine forest and two flower buds per stem were produced instead of one. *Vaccinium vitis-idaea* from

TABLE 1. *Vaccinium vitis-idaea* L. var. *minus* Lodd. in various North American plant communities. Relative abundance based on author's estimates: a = abundant, f = frequent, o = occasional, r = rare, x = present.

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| BOREAL FOREST | | | | | |
| B.2 Gaspé | Bic and Gaspé peninsula | 48°-49° N<br>64°-68° W | Bog, alpine cliff | x | Scoggan (1950) |
| B.8 Central Plateau | Klotz Lake, Ontario | 60°50′ N<br>73°40′ W | Black Spruce forest | | Larsen (1972a) |
| B.9 Superior | Bowman Island, Ontario | 48°44′ N<br>87°59′ W | Black Spruce, Balsam Fir | o | Barclay-Estrup & Nuttall (1974) |
| | | | Krummholtz | a | |
| | | | Lichen heath | o | |
| B.11 Upper English River | Raven Lake, Ontario | 49°16′ N<br>91°12′ W | Black Spruce forest | r | Larsen (1972a) |
| B.14 Lower English River | West Hawk Lake, Manitoba | 49°53′ N<br>95°15′ W | Black Spruce forest | f | Larsen (1972a) |
| B.15 Manitoba Lowlands | Elma, Manitoba | 49°53′ N<br>95°54′ W | open bog | o | Reader and Stewart (1971) |
| B.18a Mixed wood | Clear Lake, Manitoba | 50°43′ N<br>100°01′ W | Black Spruce forest | o | Larsen (1972a) |
| | Deep Lake, Manitoba | 50°53′ N<br>100°51′ W | Black Spruce bog | f | Shay & Shay (1979) |
| | Prince Albert Nat. Park, Sask. (600 m) | 53°55′ N<br>106°37′ W | Black Spruce forest | r | LaRoi (1967) |
| | Waskesiu Lake, Saskatchewan | 53°55′ N<br>106°15′ W | Black Spruce forest | f | Larsen (1972a) |
| B.18a Mixed wood | Candle Lake, Sask. | 53°50′ N<br>105°20′ W | Trembling Aspen forest | r | Swan & Dix (1966) |
| | | | White Birch forest | r | |
| | | | Jack Pine forest | a | |
| | | | White Spruce forest | o | |
| | | | Black Spruce forest | o | |
| | (600 m) Sask. | 53°57′ N<br>106°29′ N | White Spruce forest | r | LaRoi (1967) |
| B.18ab Mixed wood — Hay River | (480 m) Alta. | 57°36′ N<br>117°31′ W | Black Spruce forest | r | LaRoi (1967) |
| B.18b Hay River | Fort Providence, N.W.T. | 61°13′ N<br>117°31′ W | White Spruce forest | a | Larsen (1972a) |
| | (300 m) Alta. | 59°28′ N<br>117°11′ W | White Spruce forest | r | LaRoi (1967) |
| | Horn Plateau, N.W.T. | 62°08′ N<br>118°07′ W | Black Spruce forest | o | Thieret (1961) |
| | | | Lichen tundra | f | |
| | Northwestern Alta. | 55-60° N<br>114-120° W | White Spruce forest | o-f | Moss (1953a) |
| | | | Black Spruce forest | f-a | |
| | | | Sphagnum bog | f | Moss (1953b) |
| B.19a Lower Foot-hills | Northwestern Alta. | 55-60° N<br>114-120° W | White Spruce forest | f | Moss (1953a) |
| | | | Pine forests | r-f | |
| | | | Poplar forests | r-f | |
| | | | Black Spruce bog forest | f-a | |
| | | | Spagnum bog | f | Moss (1953b) |
| | Crimson Lake, Alta. (950-1010 m) | 52°26′ N<br>115°01′ W | String fen w/Tamarack | r | Slack *et al.* (1980) |
| | Swan Hills, Alta. (1300 m) | 55° N<br>116° W | Patterned fen w/Black Spruce | r | Vitt *et al.* (1975) |
| | (870 m) Alta. | 54°24′ N<br>116°47′ W | Black Spruce | r | LaRoi (1967) |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| BOREAL FOREST (continued) | | | | | |
| B.19b Northern Foothills | (750 m) B.C. | 58°42′ N 123°40′ W | Black Spruce | r | LaRoi (1967) |
| | (840 m) N.W.T. | 58°59′ N 125°47′ W | White Spruce | f | LaRoi (1967) |
| B.21 Nelson River, Manitoba | | 54°36′ N 100°12′ W | White Spruce forest | r | LaRoi (1967) |
| B.22a Northern Coniferous | Cranberry Portage, Manitoba | 54°35′ N 101°23′ W | Black Spruce | o | Zoltai and Tarnocai (1971) |
| | Gods Lake, Manitoba | 54°23′ N 94°26′ W | Black Spruce forest | o | Larsen (1972a) |
| | Ilford, Manitoba | 56°07′ N 95°20′ W | Black Spruce forest | a | Larsen (1972a) |
| | (360 m) Sask. | 55°20′ N 105°05′ W | Black Spruce forest | r | LaRoi (1967) |
| | (375 m) Sask. | 55°20′ N 104°58′ W | White Spruce forest | r | LaRoi (1967) |
| | McBride and Tod Lakes, Manitoba | 56°52′ N 99°57′ W | Black Spruce forests | f-a | Ritchie (1956) |
| | | | Jack Pine woodland | o-f | |
| | | 56°45′ N 101°48′ W | White Spruce forest | a | |
| B.22b Athabasca South | Wapata Lake, Sask. | 58°55′ N 105°37′ W | Black Spruce forest | a | Larsen (1972a) |
| | Cluff Lake, Sask. | 58°20′ N 104°35′ W | Trembling Aspen forest | f-a | Harms (1978) |
| | | | Mixed conifer-deciduous forest | f-a | |
| | | | Black Spruce-Tamarack bog forest | f | |
| | | | Shrub, shoreline | o-f | |
| B.23a Upper Mackenzie | (240 m) N.W.T. | 60°35′ N 116°07′ W | Black Spruce forest | f | Larsen (1972a) |
| | (240 m) N.W.T. | 61°03′ N 117°22′ W | White Spruce forest | f | Larsen (1972a) |
| | Norman Wells, N.W.T. | 65°17′ N 126°51′ W | Black Spruce forest | f | Cody (1960) |
| B.23a Upper Mackenzie | Lower Liard River, N.W.T. | 60-61° N 123°30′ W to 124° W | Black Spruce-feathermoss forest on flood plains | a | Jeffrey (1961) |
| | | | Black Spruce-Tamarack forest on floodplains | a | |
| | | | Deciduous forest on flood plains | o | |
| | | | Black Spruce-Trembling Aspen forest | o-f | |
| | | | Black Spruce forest | f | |
| | (540-690 m) | | Lodgepole Pine-lichen woodland | a | |
| | (480-780 m) | | Mixed coniferous forest | | |
| | (780-1140 m) | | Subalpine fir | f | |
| | (1050-1110 m) | | Mixed coniferous forest to timberline | o | |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| BOREAL FOREST (continued) | | | | | |
| B.23a Upper Mackenzie | Lower Liard River, N.W.T. | | | | |
| | (1140 m) | | Alpine dwarf scrub tundra | a | |
| B.24 Upper Liard | Nahanni National Park & vicinity, N.W.T. | 61°03′ to 61°58′ N 123°30′ to 128°14′ W | Spruce forest | f | Scotter and Cody (1974) |
| | (510 m) N.W.T. | 60° N 127°43′ W | Black Spruce forest | f | LaRoi (1967) |
| | (420 m) N.W.T. | 59°38′ N 126°50′ W | White Spruce forest | f | |
| B.26b Central Yukon | Atlin Provincial Park, B.C. - Birch Mountain (2061 m) | 59° N 133° W | Alpine fell fields | f | Buttrick (1977) |
| | | | Alpine meadow and scrub | o | |
| B.26c Eastern Yukon | (900 m) B.C. | 59°55′ N 131°41′ W | White Spruce forest | o | |
| | (1290 m) N.W.T. | 60°07′ N 130°44′ W | White Spruce forest | r | |
| B.26d Kluane | St. Elias Mountains, N.W.T. | 61°32′ N 140°30′ W | Open Black Spruce forest | o | Birks (1977) |
| | | | Dwarf Birch scrub tundra | r-o | |
| | Alsek River, N.W.T. | 60°30′ N 137°30′ W | White Spruce forest | o | Douglas (1974) |
| | | | White Spruce treed fen | r | |
| | | | White Spruce-Trembling Aspen forest | r | |
| | | | Willow shrub | r | |
| B.27 Northwestern Transition | Caribou Lake, River, Manitoba | 59°20′ N 95°10′ W | White Spruce forest | f | Ritchie (1960a) |
| | | | Open Black Spruce forest with lichen scrub | f | |
| | | | Open Black Spruce forest with moss scrub | a | |
| | | | Tamarack forest | o | |
| | Long Bay, Southern Indian Lake, Man. | 56°40′ N 100°10′ W | Black Spruce forest | o-a | Shay *et al.* (nd) |
| | | | Open Black Spruce bog | f | |
| | Seal River, Man. | 59° N 96°45′ W | Open Black Spruce forest with lichen scrub | o-a | Ritchie (1959) |
| | | | Dwarf scrub heath | a | |
| | | | White Spruce forest on flood plains | x | |
| | Lynn Lake, Man. | 56°50′ N 101°30′ W | Black Spruce forest | a | |
| | Yellowknife, N.W.T. | 62°54′ N 114°56′ W | Black Spruce forest | a | Larsen (1972a) |
| | | | White Spruce forest | o | |
| | Abitau-Dunvegan Lakes, N.W.T. | 62° N 110° W | Post-fire succession Moss-lichen to closed spruce forest | o-f | Maikawa and Kershaw (1976) |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| BOREAL FOREST (continued) | | | | | |
| B.27 Northwestern Transition | Fort Reliance, N.W.T. | 62°40′ N 109°07′ W | Black Spruce forest | a | Larsen (1972a) |
| | | | White Spruce forest | f | |
| | | | Tussock muskeg tundra | a | |
| | Aubrey & Colville Lakes, N.W.T. | 67°20′ N 126°15′ W | Open White Spruce with lichen scrub | x | Riewe (1979) |
| | | | Cottongrass-sedge on shores and river margins | x | |
| | | | Dwarf scrub-lichen heath | x | |
| | | | Fens and bogs | x | |
| B.28a Grand Falls | (270 m) Nfld. | 48°46′ N 56°14′ W | Black Spruce forest | r | LaRoi (1967) |
| B.29 Northern Peninsula | St. Barbe South District, Nfld. | 49°30′ to 50°50′ N 56°40′ to 58°20′ W | Raised bogs of coastal plain | f | Bouchard *et al.* (1978) |
| | Gros Morne National Park, Nfld. | 49°40′ to 50° N 57°40′ to 58° W | Black Spruce dwarf laurel dwarf scrub | a | Bouchard and Hay (1976) |
| | | | Ericaceous dwarf scrub | a | |
| | | | Black Spruce scrub | f | |
| | | | Bog | o | |
| | | | Herbaceous communities along sea shore barrens | o | |
| | | | Balsam Fir forest | r | |
| B.30 Avalon | Western Bay, Nfld. | 47°50′ N 53°10′ W | Coastal barren | f | Hall (unpublished) |
| | Little Catalina, Nfld. | 48°40′ N 53°05′ W | Coastal barren | f | |
| B.31 Newfoundland-Labrador Barrens | St. Barbe South District, Nfld. | 49°30′ to 50°50′ N 56°40′ to 58°20′ W | Alpine scrub "tuckamoor" | x | Bouchard *et al.* (1978) |
| | | | Juniper scrub on serpentine tableland | f | |
| | Buchans Plateau, Nfld. | 48°45′ N 57°10′ W | Black Spruce forest | r | Bergerud (1971) |
| B.32 Forest tundra | Great Whale River, Quebec | 55°17′ N 77°46′ W | Open forest with lichen or moss | f | Forest and Legault (1977) |
| | E. Pen Island Coast of Hudson Bay, Ontario | 57° N 88° W | Bare rock on coast | | |
| | | | Moss heath hummocks | r | Kershaw (1974) |
| | | | Lichen heath | r-f | Kershaw and Rouse (1973) |
| | Lower Hayes River, Manitoba | 57° N 92°20′ W | White Spruce forest on flood plains | f | Ritchie (1960b) |
| | | | Open White Spruce with lichen or moss scrub | f | |
| | | | Tamarack forest | o | |
| | Churchill, Manitoba | 58°47′ N 94°10′ W | Black Spruce forest | a | Larsen (1972a) |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| BOREAL FOREST (continued— | | | | | |
| B.32 Forest tundra | Ennadai Lake, N.W.T. | 60°42′ to 61°10′ N 100°55′ to 101°45′ W | Black Spruce forest | a | |
| | | | White Spruce forest | a | |
| | | | Tussock muskeg tundra | a | |
| | | | Rock field | a | |
| | Artillery Lake, N.W.T. | 63°05′ N 108°05′ W | Black Spruce forest | a | |
| | | | White Spruce forest | a | |
| | | | Tussock muskeg tundra | a | |
| | | | Rock field | a | |
| | Campbell-Dolomite Uplands, N.W.T. | 68°20′ N 133°40′ W | Open Black Spruce woodland | o | Ritchie (1977) |
| | | | Black Spruce forest | o | |
| | Inuvik, N.W.T. | 68°23′ N 133°42′ W | *Picea mariana-Vaccinium uliginosum* woodland | r-a | Black and Bliss (1978) |
| B.33 Alpine Forest Tundra | Nahoni (1200 m) and Ogilvie (1350 m) Uplands, N.W.T. | 65°36′ N 136°41′ W 64°18′ N 137°21′ W | Alpine lichen communities | r-o | See and Bliss (1980) |
| MONTANE | | | | | |
| M.5 Douglas-fir and Lodgepole pine | Banff and Jasper National Parks, Alberta (1280-1830 m) | 50°55′ to 53°10′ N | Lodgepole Pine-lichen woodland forest | r | |
| | | 115° to 119° W | Lodgepole Pine forest | r | |
| Alpine tundra | Jasper National Park, Signal Mt. (2180-2260 m) | 52°51′ N 117°59′ W | Dryas rock tundra | r | Hrapko and LaRoi (1978) |
| | | | Heath tundra | r-o | |
| | | | Sedge-wood rush snow bed tundra | r | |
| COASTAL FOREST | | | | | |
| C.3 Northern Pacific Coast | Pacific Rim National Park, Vancouver Island, B.C. | 49°10′ N 125°55′ W | Sphagnum bog | r | Pojar (1974) |
| GREAT LAKES-ST. LAWRENCE FOREST | | | | | |
| L.6 Temiscouata-Restigouche | Bic and Gaspé Peninsula, Quebec | 48° to 49°15′ N 64°15′ to 68° W | Slaty sea ledges and sea cliffs | x | Scoggan (1950) |
| L.12 Rainey River | Southeastern Manitoba | 49°00′ to 49°40′ N 95°10′ to 96°20′ W | Jack Pine forest | o | Mueller-Bombois (1964) |
| | | | Black Spruce-feather moss forest | f | |
| | | | Deciduous forest (Trembling Aspen, Balsam, Poplar) | r | |
| | | | Jack Pine-deciduous forest | r | |
| | | | Tamarack-White Birch forest | r | |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| USA HEMLOCK-WHITE PINE NORTHERN HARDWOODS | | | | | |
| N. Appalachian Highlands | Presidential Range, New Hampshire | 44° 15′ N 71°20′ W | Dwarf shrub heath with sedge & rush | o-f | Bliss (1963) |
| | | | Dwarf shrub heath | o | |
| | | | Diapensia | r | |
| | | | Bog | r | |
| Great Lakes-St. Lawrence | Lake Agassiz peatlands, Minnesota | 48°05′ N 92°45′ W | Mixed swamp forest | r | Heinselman (1970) |
| | | | Cedar string bog and fen | r | |
| | | | Tamarack string bog and fen | r | |
| | | | Black Spruce-feather moss forest | r | |
| | | | Sphagnum-Black Spruce-Leather Leaf bog forest | r | |
| | | | Sphagnum-Leather Leaf-laurel-spruce heath | r | |
| LOW ARCTIC TUNDRA | | | | | |
| New Quebec | Port Burnell, N.E. coast of Ungava Bay, Quebec | 60°25′ N 64°52′ W | Dwarf scrub heath on lowlands | o-d | Polunin (1948) |
| | Wakeham Bay, S. Shore of Hudson Strait, Quebec | 61°36′ N 71°57′ W | Lichen heath on lowlands | a | |
| | | | Herbaceous tussocks in marsh areas | f | |
| | | | Dwarf scrub heath on lowlands | f-a | |
| | | | Dwarf scrub heath, snow patches | f | |
| | Puvirnitug, Quebec | 60°02′ N 77° 15′ W | Communities on shores and dry gravel | x | Bournérias (1971) |
| South Coast of Baffin Island | Lake Harbor | 62°52′ N 69°53′ W | Dwarf scrub heath on lowlands | f | Polunin (1948) |
| | | | Dwarf scrub heath on summits and slopes | o | |
| | | | Birch-willow dwarf scrub | f | |
| | Cape Dorset | 64° 10′ N 76° 30′ W | Herbaceous communities on south facing slopes | f | |
| | | | Dwarf scrub heath on lowlands | f-a | |
| Western Coast of Hudson Bay | Coral Harbor, Southampton Island | 64°08′ N 83° 10′ W | Dwarf scrub heath | f | |
| | Chesterfield Inlet | 63°20′ N 90°42′ W | Dwarf scrub heath | a | |
| | | | Dwarf scrub heath, snow patches | f | |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| LOW ARCTIC TUNDRA (continued) | | | | | |
| Keewatin District | Northern Keewatin, N.W.T. | 64° to 69° N | Sedge meadow | r | Thompson (1980) |
| | | | Willow-sedge meadow | r | |
| | | 91° to 98° W | Orthophyll scrub | r | |
| | | | Lichen-heath plateau | r | |
| | | | Lichen uplands | r | |
| | | | Barrens | r | |
| | Snow Bunting Lake, N.W.T. | 66° 10′ N 94° 25′ W | Low meadow | o | Larsen (1972b) |
| | | | Rock field | f | |
| | | | Scattered lichens on esker summits | f | |
| | Pelly Lake, N.W.T. | 66° 03′ N 101° 03′ W | Wet Cotton Grass meadow | o | |
| | | | Dry lichen heath | a | |
| | | | Dwarf scrub-herb tundra | o | |
| | | | Rock field | a | |
| | Dubawnt Lake N.W.T. | 64° 01′ N 99° 25′ W | Black Spruce forest | o | |
| | | | Tussock muskeg tundra | a | |
| | | | Rock field | a | |
| Mackenzie District Eastern Area | Clinton Colden Lake, N.W.T. | 64° 08′ N 107° 27′ W | Dwarf scrub | a | Larsen (1971a) |
| | | | Tussock muskeg tundra | a | |
| | | | Rock field | a | |
| | Matthews Lake, N.W.T. | 64° 05′ N 111° 15′ W | Marshy hummocks | a | Cody and Chilcott (1955) |
| Mackenzie Delta and Tuktoyaktuk Peninsula | Various sites | 68° 45′ to 69° 55′ N 131° 20′ to 134° 40′ W | Dwarf scrub heath | r-a | Corns (1974) |
| | | | Medium scrub heath | r-a | |
| | | | Dwarf Birch on raised center polygons | r-a | |
| | | | Sedge heath and sedge-Cottongrass heath | r-f | |
| | | | Sedge meadow | r-f | |
| | Various sites | 68° 20′ to 69° 55′ N 131° 20′ to 134° 45′ W | Dwarf scrub heath | f | Hernandez (1973) |
| | | | Cottongrass dwarf birch heath | f | |
| | | 69° N 131° 52′ W | Black Spruce forest-tundra | f | Ritchie (1974) |
| | | | White Spruce-birch forest | f | |
| | | 69° 10′ N 133° 10′ W | Cottongrass-lichen | f | |
| | Tuktoyaktuk | 69° 27′ N 133° W | Dwarf shrub heath | a | Haag (1974) |
| | Tuktoyaktuk | | Dwarf shrub heath | f-a | Wein and Bliss (1973) |
| ALASKA, USA INTERIOR FOREST | | | | | |
| | Eastern Alaska Yukon-Tanana Upland (390 m) | 63° 42′ N 144° 23′ W | Black Spruce forest | a | LaRoi (1967) |

TABLE 1. *(continued)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| ALASKA, USA | | | | | |
| INTERIOR FOREST (continued) | | | | | |
| | Eastern Alaska Yukon-Tanana Upland (600 m) | 62°06′ N 145°52′ W | Black Spruce forest | a | |
| | (345 m) | 65°15′ N 146°47′ W | White Spruce-fir forest | r | LaRoi (1967) |
| | (600 m) | 63°33′ N 148°48′ W | White Spruce-fir forest | a | |
| | (705 m) | 61°59′ N 146°53′ W | White Spruce-fir forest | a | |
| | Near Fairbanks | 64°80′ N 148°06′ W | Open Black Spruce forest with feather-moss and lichen | f | Dyrness & Grigal (1979) |
| | | | Closed Black Spruce forest with feather-moss | f | |
| | | | Open Black Spruce woodland with moss and lichen | f-a | |
| | | | White Spruce forest with alder | f-a | |
| | Sites near Fairbanks | 65° N 147° W 65° N 148° W | Black Spruce forest | r-f | |
| | National Moose Range, Kenai Peninsula | 58° to 62° N 150° to 151° W | Mature spruce-deciduous forest | f-d | Oldemeyer and Seemel (1976) |
| | | | Mature deciduous forest (Trembling Aspen, White Birch) | d | |
| | | | Spruce regrowth after 1947 fire | f-d | |
| | | | Birch-spruce regrowth after 1947 fire | f-d | |
| COASTAL FOREST | | | | | |
| | Glacier Bay, S.W. Alaska (5-45 m) | 58°22′ N 135°37′ W | Hemlock-spruce forest | r | Reiners *et al.* (1971) |
| | | | Lodgepole Pine muskeg | r | |
| LOW ARCTIC TUNDRA | | | | | |
| | Upper Firth River Valley, Alaska-Canada | 69° N 141° W | Dwarf scrub-herbaceous communities on centers of frost polygons | x | Drew and Shanks (1965) |
| | | | String fen and bog | x | |
| | | | Sedge meadow | x | |
| | Umiat | 69°22′ N 152°08′ W | Willow scrub | o | |
| | | | Alder scrub | r | |
| | | | Cottongrass-dwarf scrub heath | f | |
| | | | Sedge-dwarf shrub heath | f | |

TABLE 1. *(concluded)*

| Vegetation region* section | Location and elevation (m) | Latitude and longitude | Plant community | Relative abundance of *V. vitis-idaea* var. *minus* | Reference |
|---|---|---|---|---|---|
| LOW ARCTIC TUNDRA (continued) | | | | | |
| | Ogotoruk Valley | 68° 06′ N 165° 46′ W | Cottongrass tussock tundra | o | |
| | Cape Thompson region | 65° 45′ to 69° 00′ N | Wet herbaceous meadows | r | Johnson *et al.* (1966) |
| | | 162° 00′ to 166° 15′ W | Cottongrass tussocks on soilifluctia slopes and with ice-wedge polygons | o | |
| | | | Sedge communities of high center polygons | o | |
| | | | Meadows on dry rocky uplands | r | |

*Vegetation Regions in Canada after Rowe (1972), Alaska after Viereck and Little (1975), and the conterminous United States after Braun (1950). Low arctic climate designation after Bliss (1979).

Jay Peak, Vermont, a sub-alpine site had a leaf surface-to-biomass ratio of 51 ± 9 $cm^2/g$ (Svoboda and Taylor 1979). In Norwegian birch forest, this ratio for *V. vitis-idaea* was 96 $cm^2/g$ dry wt. on 18 June, attained its maximum of 211 $cm^2/g$ dry wt. on 20 July and fell to 121 $cm^2/g$ dry wt. by the end of August (Berg *et al.* 1975). Most of the leaves were held at angles of less than 30° from the horizontal.

*(b) Physiology.* Chlorophyll content of *Vaccinium vitis-idaea* var. *minus* in tundra associations at Tuktoyaktuk (Hutchinson *et al.* 1976) was 11.0 μg/leaf on 15 July 1973, rose to 18.4 μg/leaf by 20 August but dropped to 9.5 μg/leaf by 31 August. Plants contained 2.4 mg/g dry wt. chlorophyll α, 1.3 mg/g dry wt. chlorophyll β and 0.8 mg/g dry wt. carotenes. Total chlorophyll content in plants from a mature forest at Norman Wells was only 1.92 mg/g dry wt. in August.

Field transpiration when measured between 14.10 and 21.10 hr on 14 July 1973 had a mean value of 1.6 ± 0.6 mg $H_2O$/min/g dry wt./leaf. It had risen to 2.4 ± 1.2 mg $H_2O$/min/g dry wt./leaf when measured between 11.50 and 15.50 hr on 24 August (Hutchinson *et al.* 1976). Pigment summaries for plants affected by oil spills indicate an enhancement of pigments in regrowth after summer spills but a reduction in pigments in regrowth after winter oil spills (Hutchinson *et al.* 1976). At Hardangervidda, Norway, in a birch forest, the previous years' *V. vitis-idaea* var. *vitis-idaea* leaves were harvested on 15 and 20 July and 15 August. They yielded an average of 3.37 mg chlorophyll α and β per g dry wet.; 176 mg chlorophyll per g nitrogen; 2.06 mg chlorophyll per 100 $cm^2$ leaf area; the carotenoid ratio was 1.82 and nitrogen content 2.31% (Berg 1975). Data for *V. vitis-idaea* in lichen heath and dry meadow, and for older leaves are also given by Berg (1975).

The distribution of $^{14}C$ photosynthates (Berg *et al.* 1975) indicates that at budbreak, green parts of *V. vitis-idaea* accounted for 22% of the recovered radiocarbon in lichen heath and 39% in birch forest, while below-ground parts contained 55% in the lichen heath, and 35% in the birch forest. Two weeks after budbreak green parts accounted for 37% (lichen heath) and 49% (birch forest) and below ground parts 39% (lichen heath) and 21% (birch forest). At both sampling periods the remainder of $^{14}C$ was found in the non-green above-ground parts.

Hadley and Bliss (1964) studied the energy reserves of several alpine species including *V. vitis-idaea* var. *minus* on Mt. Washington. For this species they found that new shoots produced 5270 ± 24.4 cal/g and a lipid content of 3.12 ± 0.08%, quite similar to old shoots with 5288 ± 25.9 cal/g and a lipid content of 3.86 ± 0.12%. The protein content of new shoots (10.3%) was significantly higher than that of older shoots (8.7%). The calories per gram of rhizomes and roots (4996 ± 17.5) were nearly equal to those of the shoots, but the lipid (1.43 ± 0.08%) and protein (5.3%) contents were significantly below values for the shoots. In a preliminary study Bliss (1962a) had shown that caloric values for the entire plant increased during early July but declined somewhat as the berries matured. Wielgolaski and Kjelvik (1975) give caloric values for *V. vitis-idaea* in

TABLE 2. *Vaccinium vitis-idaea* L. var. *minus* Lodd. and associated species in nine representative plant communities.

| | Coastal barren Bonavista, Newfoundland | Open bog Elma, Manitoba | *Picea mariana* bog Deep L., Manitoba | | *Pinus banksiana* Candle L., Sask. | Tussock muskeg N. Ennadai L., N.W.T. | *Picea glauca* forest St. Elias Mts., Yukon | *Picea mariana-Sphagnum* Fairbanks, Alaska | Rockfields Pelly L., N.W.T. | | *Picea mariana* open forest Inuvik, N.W.T. Stand 12. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | I | II | III | | IV | V | VI | VII | VIII | | IX |
| Lat. | 48° 33′ | 49° 53′ | 50° 53′ | | 53° 50′ | 61° 10′ | 61° 32′ | 64° 80′ | 66° 03′ | | 68° 19′ |
| Long. | 53° 02′ | 95° 54′ | 100° 51′ | | 105° 20′ | 100° 55′ | 140° 30′ | 148° 06′ | 101° 03′ | | 133° 30′ |
| Altitude (m) | 50 | | 650 | | 550–700 | 150 | 1365 | 275–500 | 15–30 | | — |
| Slope (∘) | varied | 0 | 0 | | varied | 0–3 | 1 | 3–9 | varied | | — |
| Aspect | — | — | W | | varied | — | S | SE | — | | — |
| Bare ground % | 1 | — | — | | — | — | 0 | — | — | | — |
| **Shrubs and Herbs** △ | C% | RF% | C% | F% | F% | F% | C* | C% | F% | C% | F% |
| *Vaccinium vitis-idaea* var. *minus* | 20 | 8 | 4 | 69 | 59 | 94 | 4 | 22 | 81 | 22 | 100 |
| *V. angustifolium* | 23 | | | | | 20 | | | | | |
| *Empetrum nigrum* | 15 | | | | | 65 | 5 | | 57 | 1 | 24 |
| *Kalmia angustifolia* | 10 | 6 | | | | | | | | | |
| *Ledum groenlandicum* | 5 | 13 | 32 | 94 | 23 | 2 | | 29 | | 1 | 44 |
| *Potentilla tridentata* | 2 | | | | 6 | | | | | | |
| *Chamaedaphne calyculata* | | 19 | 1 | 1 | | | | | | | |
| *Oxycoccus quadripetalus* | | 10 | | | | | | | | | |
| *Gaultheria hispidula* | | | 4 | 56 | | | | | | | |
| *Corylus cornuta* | | | 6 | 25 | | | | | | | |
| *Carex disperma* | | | 12 | 57 | | | | | | | |
| Gramineae | | | 7 | 57 | | | | | | 1 | 32 |
| *Smilacina trifolia* | | | 12 | 43 | | | | | | | |
| *Rubus pubescens* | | | 6 | 50 | 4 | | | | | | |
| *Carex leptalea* | | | 9 | 50 | | | | | | | |
| *Linnaea borealis* var. *longiflora* | | | 8 | 43 | 66 | | | | | | |
| *Oxycoccus microcarpus* | | | 2 | 38 | | 10 | | + | | | |
| *Galium triflorum* | | | 2 | 33 | | | | | | | |
| *Moneses uniflora* | | | 1 | 29 | | | | | | | |
| *Circaea alpina* | | | 1 | 17 | | | | | | | |
| *Mitella nuda* | | | 1 | 14 | 5 | | | | | | |
| *Vaccinium myrtilloides* | | | | | 49 | | | | | | |
| *Cornus canadensis* | | | | | 49 | | | + | | | |
| *Maianthemum canadense* | | | | | 33 | | | | | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Elymus innovatus* | 33 | | | | | | |
| *Rosa acicularis* | 25 | | | | | | |
| *Equisetum scirpoides* | 22 | | 3 | | | | + |
| *Fragaria virginiana* | 19 | | | | | | |
| *Arctostaphylos uva-ursi* | 18 | | 1 | | | | |
| *Petasites palmatus* | 12 | | | | | | |
| *Pyrola secunda* | 11 | | | | | | |
| *Trientalis borealis* | 11 | | | | | | |
| *Oryzopsis pungens* | 10 | | | | | | |
| *Lathyrus ochroleucus* | 9 | | | | | | |
| *Galium boreale* | 9 | | | | | | |
| *Epilobium angustifolium* | 7 | | | | | | |
| *Viola canadensis* | 7 | | | | | | |
| *Viburnum edule* | 6 | | | | | | |
| *Alnus crispa* | 5 | | | | | | + |
| *Disporum trachycarpum* | 4 | | | | | | |
| *Aralia nudicaulis* | 4 | | | | | | |
| *Pyrola asarifolia* | 4 | | | | | | |
| *Melampyrum lineare* | 4 | | | | | | |
| *Pyrola virens* | 3 | | | | | | |
| *Picea glauca* | | | 5 | | | | |
| *Calamagrostis canadensis* | 3 | | | 20 | | | |
| *Arctostaphylos alpina* | | | | 4 | | | |
| *Ledum palustre* | | 90 | 5 | 4 | 89 | 27 | 100 |
| *Rubus chamaemorus* | | 81 | | 8 | | 1 | 32 |
| *Vaccinium uliginosum* | | 58 | 6 | 5 | 13 | + | 16 |
| *Andromeda polifolia* | | 39 | | | | | |
| *Carex rotundata* | | 95 | | | | | |
| *Eriophorum vaginatum* ssp. *spissum* | | 21 | | 1 | | 17 | 40 |
| *Hierochloë alpina* | | | | | 68 | | |
| *Carex* sp./spp. | | | | | 65 | | |
| *Cassiope tetragona* | | | | | 27 | | |
| *Carex bigelowii* | | | | | 25 | | |
| *Silene acaulis* | | | | | 10 | | |
| *Salix herbacea* | | | | | 9 | | |
| *Salix arctica* | | | | | 6 | | |
| *Arctagrostis latifolia* | | | | | 4 | | |
| *Betula glandulosa* | | 42 | 7 | 5 | | 7 | 64 |
| *Salix phylicifolia* ssp. *planifolia* | | | | 2 | | | + |
| *S. arctophila* | | 53 | | | | | |
| *Potentilla palustris* | | 8 | | | | | |
| *Equisetum sylvaticum* | | | | 8 | | | |
| *Carex chordorrhiza* | | 18 | | | | | |
| *Salix glauca* ssp. *acutifolia* | | | 4 | | | | + |
| *Pedicularis labradorica* | | | 3 | | | | |
| *Saussurea angustifolia* | | | 2 | | | | + |

TABLE 2 (*continued*)

| | Coastal barren Bonavista, Newfoundland | Open bog Elma, Manitoba | *Picea mariana* bog Deep L., Manitoba | | *Pinus banksiana* Candle L., Sask. | Tussock muskeg N. Ennadai L., N.W.T. | *Picea glauca* forest St. Elias Mts., Yukon | *Picea mariana-Sphagnum* Fairbanks, Alaska | Rockfields Pelly L., N.W.T. | *Picea mariana* open forest Inuvik, N.W.T. Stand 12. | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | I | II | III | | IV | V | VI | VII | VIII | IX | |
| Lat. | 48° 33′ | 49° 53′ | 50° 53′ | | 53° 50′ | 61° 10′ | 61° 32′ | 64° 80′ | 66° 03′ | 68° 19′ | |
| Long. | 53° 02′ | 95° 54′ | 100° 51′ | | 105° 20′ | 100° 55′ | 140° 30′ | 148° 06′ | 101° 03′ | 133° 30′ | |
| Altitude (m) | 50 | | 650 | | 550–700 | 150 | 1365 | 275–500 | 15–30 | — | |
| Slope (°) | varied | 0 | 0 | | varied | 0–3 | 1 | 3–9 | varied | — | |
| Aspect | — | — | W | | varied | — | S | SE | — | — | |
| Bare ground % | 1 | — | — | | — | — | 0 | — | — | — | |
| **Shrubs and Herbs** △ | C% | RF% | C% | F% | F% | F% | C* | C% | F% | C% | F% |
| *Pyrola grandiflora* | | | | | | | 2 | | | | |
| **Mosses** | | | | | | | | | | | |
| *Polytrichum juniperinum* | | 15 | | | | | 1 | 4 | | + | 12 |
| *Sphagnum fuscum* | | 14 | 13 | 14 | | | | | | 1 | 8 |
| *Aulacomnium palustre* | | 5 | 2 | 14 | | | | | | | |
| *Pleurozium schreberi* | | | 29 | 57 | | | | 29 | | | |
| *Hylocomium splendens* | | | 9 | 29 | | | 4 | 2 | | | + |
| *Mnium* sp. | | | 2 | 29 | | | | | | | |
| *Ptilium crista-castrensis* | | | 2 | 14 | | | | | | | |
| *Helodium blandowii* | | | 1 | 14 | | | | | | | |
| *Aulacomnium acuminatum* | | | | | | | | | | 2 | 24 |
| *A. turgidum* | | | | | | | | | | 5 | 60 |
| *Dicranum angustum* | | | | | | | | | | 3 | 32 |
| *D. undulatum* | | | | | | | | | | 2 | 12 |
| *D. fuscescens* | | | | | | | 1 | | | 1 | 84 |
| *Sphagnum* spp. | | | | | | | | 48 | | 17 | 40 |
| *Brachythecium* spp. | | | | | | | | | | + | 16 |
| *Eurynchium pulchellum* | | | | | | | | | | | |
| *Rhytidium rugosum* | | | | | | | 3 | | | 1 | 32 |
| *Bryum pseudotriquetrum* | | | | | | | | | | + | 26 |
| *Sphagnum* sp. & *Cladina rangiferina* | 24 | | | | | | | | | | |
| *Hypnum revolutum* | | | | | | | | | | 1 | 24 |
| *Dicranum elongatum* | | | | | | | | | | 2 | 12 |
| *D. muelhlenbeckii* | | | | | | | 2 | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Aulacomnium palustre* | | 2 | | | | |
| *Rhacomitrium* sp. | | | | 15 | | |
| Moss species | 90 | | | 86 | 43 | 96 |
| **Liverwort** | | | | | 6 | 84 |
| **Lichens** | | | | | | |
| Lichen species | 70 | | | 100 | 12 | 80 |
| *Cladonia* spp. | | | 16 | | 2 | 44 |
| *C. arbuscula* | | 3 | | 100 | 12 | 80 |
| *C. amaurocraea* | | 3 | | | | |
| *C. alpestris* | | | | | | |
| *Peltigera polydactyla* | | 3 | | | | |
| *P. aphthosa* | | 2 | + | | + | 12 |
| *P. canina* | | | 4 | | | |
| *Cladina mitis* | | | | | 12 | 84 |
| *C. rangiferina* | | | | | 12 | 40 |
| *Cetraria nivalis* | | 2 | | 22 | 1 | 12 |
| *C. islandica* | | | | 1 | 12 | |
| *C. cucullata* | | | | 22 | 3 | 84 |
| *Stereocaulon tomentosum* | | 4 | | | | |
| *Alectoria nitidula* | | | | 25 | | |
| *A. ochroleucha* | | | | 66 | | |

Additional species not in Table.

III Shay and Shay (1979)
*Ribes glandulosum*
*Andromeda glaucophylla*
*Picea mariana*
*Larix laricina*
*Abies balsamea*
*Drosera rotundifolia*
*Habeneria obtusata*
*Listera cordata*
*Coptis trifolia*
*Rubus acaulis*
*Tomenthypnum nitens*

IV Swan and Six (1966)
*Lycopodium complanatum*
*Geocaulon lividum*
*Schizachne purpurascens*
*Aster ciliolatus*
*Oryzopsis asperifolia*
*Vicia americana*

V Larsen (1965)
*Pedicularis labradorica*
*Pinguicula villosa*
*Carex capillaris*
*C. stans*
*Eriophorum angustifolium*
*Picea mariana*
*Loiseleuria procumbens*

VI Birks (1977)
*Dryas integrifolia*
*Carex concinna*
*Cladonia pyxidata*
*Pohlia nutans*
*Dicranella heteromalla*

VII Dyrness and Grigal (1979)
*Nephroma arcticum*

VIII Larsen (1973)
*Luzula confusa*
*Stellaria longipes*
*Poa* spp.
*Salix brachycarpa* var *niphoclada*

IX Black and Bliss (1978)
*Astragalus alpinus*
*Equisetum arvense*
*Arctagrostis latifolia*
*Ptilidium ciliare*
*Tomenthypnum nitens*
*Drepanocladus* spp.

TABLE 2 *(continued)*

Footnotes for Table

I — Hall (1979); II — Reader and Stewart (1971); III — Shay and Shay (1979); IV — Swan and Dix (1966); V — Larsen (1965); VI — Birks (1977); VII — Dryness and Grigal (1979); IX — Black and Bliss (1978).

Sample size Site: I, 100 points along a 100 m transect;
II, 50 random points;
III, 14–0.25 $m^2$;
IV, 30–0.25 $m^2$;
V, 180–1 $m^2$;
VI, 16 $m^2$ plot;
VII, 48–25 $m^2$ plots;
VIII, 20–1 $m^2$;
IX, 25–0.1 $m^2$.

C% — percent cover; F% — percent frequency; RF% — relative frequency %; C* — cover Domin 1-10 scale; species included have F% $\geqslant$ 3%, C% $\geqslant$ 2%, + cover > 2% for species already listed in another site.

Δ Nomenclature follows Scoggan (1979), original authors slightly modified.

V Nomenclature follows original authors.

Norwegian tundra dry meadow sites as 4895 ± 25 calories per g dry wt. for green material, 4734 ± 32 for non-green material above the roots, 4731 ± 52 for living roots and 4634 ± 83 for dead material.

The light compensation point for this species on Mt. Washington was 200 ftc and the light saturation point 2000 ftc. Following the cessation of terminal shoot growth, respiration decreased with a resulting increase in net photosynthesis (Hadley and Bliss 1964). *Vaccinium vitis-idaea* was one of the species selected for detailed physiological study in Norway. Nygaard (1975) reports the effects of low temperature pretreatment (8-12 hr at +2-3° C and 12-16 hr at +10° C) and high temperature pretreatment (8-12 hr at +15° C and 12-16 hr at +23-25° C) at a relative humidity of 80% using an infrared gas analyzer. The apparent photosynthesis in *V. vitis-idaea* pretreated at high temperatures was higher than when pretreated at low temperatures. For example with high temperature pretreatment apparent photosynthesis at 15° C was 4.2 mg $CO_2$/g/hr and with low temperature pretreatment photosynthesis at 15° C was 2.1 mg $CO_2$/g/hr (see Nygaard 1975, p. 165). Such acclimation effects were smaller in experiments carried out in summer than in fall. The $CO_2$ compensation point as a function of acclimation temperature was 63 ppm at 25° C in low temperature material, 51 ppm at 25° C for high temperature material, and 86 ppm for untreated material.

Skre (1975) reports $CO_2$ exchange data for *V. vitis-idaea* under different experimental conditions and compares his Norwegian data with other studies. The values for apparent photosynthesis of 5-6.7 mg $CO_2$/g/hr are higher than those of Hadley and Bliss (1964) and Scott and Billings (1964) but agree with those of Nygaard (1975).

The composition of stems and leaves of *V. vitis-idaea* var. *minus* was monitored at various seasons on the Kenai Peninsula, Alaska (LeResche and Davis 1973, Oldemeyer and Seemel 1976, Oldemeyer *et al.* 1977). Their data indicate a slight protein peak in summer (Table 3) also shown by Scotter (1965) in northern Saskatchewan. However there was a dramatic decrease from summer to winter in values for Ca, Mg, K, Na, Cu, Fe, Mg, Zn and Mn.

In the test garden at Kentville, Nova Scotia, the levels of various elements found in *V. vitis-idaea* var. *minus* are similar to those given by Gerloff *et al.* (1964) for several other ericaceous species. At Kentville, levels of N and P in current leaves (Table 4) were greatest in June and decreased to September. Calcium in the current growth increased as the season progressed undoubtedly due to the buildup of calcium pectate in the cell walls of the leaf tissue. Similar trends were previously reported for *Vaccinium angustifolium* (Townsend *et al.* 1968). The

TABLE 3. Composition of stems and leaves of *V. vitis-idaea* L. var. *minus* Lodd. from northern Saskatchewan and the Kenai Peninsula, Alaska.

| | Scotter* 1965 July 1960 | Sept. 1960 | Mar. 1961 | LeResche and Davis 1973 3 analyses May 1971 | Oldemeyer and Seemel 1976 3 sites Aug. 1973 | 6 sites Feb. 1974 | Oldemeyer *et al.* 1977 6 sites July 1974 |
|---|---|---|---|---|---|---|---|
| Carbohydrate % | | | | | | | |
| Cell walls | | | | 67 | 33.1 ± 1.26 | 37.7 ± 1.89 | 50.5 |
| Acid detergent fibre | | | | 17.6 | 29.3 ± 1.41 | 31.9 ± 2.00 | 44.6 |
| Lignin | | | | 50.0 | 12.6 ± 1.04 | 13.2 ± 1.62 | 23.8 |
| Protein % | 6.33 | 7.87 | 6.34 | 5.4 | 5.7 ± 0.42 | 5.4 ± 0.30 | 7.6 |
| Minerals ppm | | | | | | | |
| Ca | 4700 | 5500 | 5500 | 6300 | 4920 ± 545.28 | 26.7 ± 3.23 | 699 |
| Mg | - | - | - | 1700 | 1328 ± 273.60 | 4.6 ± 0.41 | 1426 |
| K | - | - | - | 3400 | 438 ± 288.68 | 29.8 ± 5.94 | 3691 |
| Na | - | - | - | 80 | 55 ± 13.23 | 22.8 ± 0.41 | 72 |
| Cu | - | - | - | - | 5.9 ± 3.82 | 0.2 ± 0.03 | 13.8 |
| Fe | - | - | - | - | 51.3 ± 19.86 | 3.2 ± 0.88 | 44 |
| Zn | - | - | - | - | 8.3 ± 3.82 | 0.3 ± 0.32 | 8.6 |
| Mn | - | - | - | - | 17.6 ± 3.62 | 1.9 ± 0.29 | 111.8 |
| P | 1000 | 1600 | 1100 | 900 | - - | - - | - |
| Ether extract % | - | - | - | 2.1 | - - | - - | - |
| Ash % | 2.32 | 2.71 | 2.25 | 2.1 | - - | - - | - |
| Crude fat % | 2.81 | 2.81 | 3.16 | - | - - | - - | - |
| fibre % | 15.63 | 20.37 | 17.70 | - | - - | - - | - |

*Northern Saskatchewan, leaves only were analysed.

TABLE 4. Nutrient levels in *Vaccinium vitis-idaea* L. var. *minus* Lodd leaves from the test garden at Kentville, Nova Scotia

| Leaf cohort | Date | % composition on dry wt. basis N | P | K | Mg | Ca |
|---|---|---|---|---|---|---|
| pyg[1] | 2 June 79 | 0.87[2] | 0.060 | 0.27 | 0.12 | 0.61 |
| c | 2 June 79 | 1.43 | 0.145 | 0.58 | 0.12 | 0.29 |
| pyg | 5 July 79 | 0.81 | 0.067 | 0.42 | 0.13 | 0.55 |
| c | 5 July 79 | 0.92 | 0.103 | 0.59 | 0.14 | 0.39 |
| pyg | 2 Aug 79 | 0.70 | 0.060 | 0.32 | 0.16 | 0.52 |
| c | 2 Aug 79 | 0.85 | 0.095 | 0.38 | 0.13 | 0.41 |
| pyg | 5 Sept 79 | 0.76 | 0.072 | 0.43 | 0.15 | 0.61 |
| c | 5 Sept 79 | 0.87 | 0.093 | 0.48 | 0.15 | 0.50 |

1. pyg = preceding year's growth, c = current growth.
2. samples dried at 70°C and analysed by standard procedures (A.O.A.C. 1970).

decline of N content in the previous year's leaves during the early summer suggests that senescence has commenced. Levels of N, P and K were higher in the current leaves than the preceding year's at all dates, whereas with Ca, the preceding year's leaves had the higher values. For Mg, values were more or less equal for the two years at the various sampling dates. The unfertilized soil producing the leaves sampled (Table 4) was a well drained Berwick sandy loam with a pH of 4.6 (Cann *et al.* 1965).

Analysis of mineral content of *V. vitis-idaea* in IBP tundra sites in Norway and Finland is given in Wielgolaski *et al.* (1975). In general the data are similar to the Kentville analyses.

Stark *et al.* (1979) have shown that ripe fruit has a high tannin content (721 mg/100 g fresh weight), high anthocyanin content (127 mg/100 g), low pH (2.5) and a total sugar content of 6.6%. Hoffman *et al.* (1967) found the ascorbic acid of *V. vitis-idaea* var. *minus* on 15 September was 22.5 mg/100 g and the $\beta$-carotene on 23 September 1964 was 0.79 $\mu$g/g of berries.

*(c) Phenology.* Bell and Burchill (1955) found that *V. vitis-idaea* var. *minus* overwintered with ovule development barely evident and sporogenous tissue present in some flowers. According to these authors it was the 12th ericaceous species to bloom in Nova Scotia, from mid-June to early July. A major difference between *V. vitis-idaea* var. *minus* and its European counterpart var. *vitis-idaea* is the fact that the latter had two flowering periods per season (Ritchie 1955). On 15 May 1979 vegetative growth measured 1 cm on plants in the transplant garden at Kentville (lat. 45°04'N) and full bloom occurred on 25 May. This was an unusually early season, approximately two weeks early. With plants further north the date is later, blooming in the Yukon about mid-July. The first flowering of this species at Sheep Mountain, southwest Yukon, (lat. 61°21'N) occurred about 1 July and continued for nearly a week; it was the 48th of 60 species to flower (Hoefs 1979). On Mt. Washington (lat. 44° 17'N), Hadley and Bliss (1964) reported that vegetative growth started 18 June, plants were in flower on 2 July, and bore young fruits by 25 July. Ritchie (1955) states that root growth occurs in both early spring and fall in *V. vitis-idaea* var. *vitis-idaea.* Old leaves of var. *minus* were starting to drop in August of the second year in Nova Scotia. Svoboda and Taylor (1979) indicated that leaves persist for 3 years. *Vaccinium vitis-idaea* shoots began to grow from 23-30 June in a Norwegian alpine heath 200-300 m above tree line (Wielgolaski and Karenlampi 1975), the time of snowmelt being a very important feature that varies from year to year. Growth in Finland begins about 20 days after snowmelt (Kjelvik and Karenlampi 1975) and lasts about 40 days. There is a shorter period between snowmelt and budbreak in Norway and length growth ends about 25 July in Norwegian birch forest and lichen heath. The delay in budbreak may be a form of protection for plants growing on exposed sites with thin, early melting snow cover (Wielgolaski and Karenlampi 1975). In Norwegian alpine lichen heath, shoot growth of *V. vitis-idaea* was 7 mm in 1971 and almost the same in the warmer summer of 1972. It grew about 10 mm in a dry alpine meadow in both years, while in subalpine birch forest it grew 39 mm in 1971 and 42 mm in 1973, appearing to be strongly dependent on moisture (Wielgolaski and Karenlampi 1975). Maximum shoot length was attained in early July in the subalpine birch forest, and toward the end of July in the alpine lichen heath. *Vaccinium vitis-idaea* in the birch forest had a higher fertility (3.2%) than in lichen heath sites (0.6%) and dry meadow (0%).

## 7. *Reproduction*

*(a) Floral biology. Vaccinium vitis-idaea* is slightly protandrous, that is, the anthers ripen and release their pollen before the stigma of the same flower is receptive but is partially self-compatible. It produces both odors

and nectar (Pojar 1974). In Newfoundland cross pollination is by bees and butterflies (Torrey 1914), while in southern B.C. it is pollinated by bumble bees and bee flies (Pojar 1974). Warming (1908) lists four bumble bees: *Bombus balteatus, B. consobrinus, B. lapponicus* and *B. jonellus* as the chief pollinators in Greenland. Torrey (1914) states that under field conditions in southeastern Newfoundland flowers remain open for about a week and that under favorable conditions, 30% of the pollinated flowers set fruit. Flowers that were cross-pollinated between clones set fruit more readily than selfed flowers (Hall and Beil 1970). A significant positive correlation (r = 0.466) was found between seed number and berry weight (Hall and Butler 1971). Two nectar samples from 50 blossoms collected on 26 May 1979 yielded 1.0 and 1.6% soluble solids.

*(b) Seed production and dispersal.* Seventy-five berries collected on Tancook Island, Nova Scotia in October 1978 were stored at 1° C until 21 March 1979, when their mean weight was 0.403 ± 0.098 g and the mean number of seeds was 15.2 ± 7.4. In contrast, an average of 6.7 seeds per berry was reported for var. *vitis-idaea* in Britain where seed set and berry production followed pollination by 2-4 weeks (Ritchie 1955).

Data from a stand of *V. vitis-idaea* var. *minus* on Tancook Island, Nova Scotia, show that the weight of sterile shoots was not significantly greater than that of fruiting shoots (without berries) and the weight of berries exceeded 1000 kg/ha. The weight of 25 immature berries (0.15 ± 0.01 g) taken on 25 July 1979 from the same locality was considerably less (berries will increase in weight by at least one-third in final month of growth) than that of mature berries reported above. Veijalainen (1976) reports the average yield of *V. vitis-idaea* in a good uncultivated site in Finland to be 500 kg/ha and the maximum yield in cultivation to be 8150 kg/ha. The yield from a fertilized forest was 3000 kg/ha.

Seeds are dispersed in the droppings of many birds and mammals, such as *Dendragapus obscurus* (Grouse), *Calachites canadensis* (Spruce Grouse), *Piranga erythromelas* (Scarlet Tanager), *Sialia sialis* (Eastern Bluebird), *Hylocichla* spp. (Thrushes), and other songbirds, as well as *Ursus americanus* (Black Bear), *Tamias striatus* (Eastern Chipmunk), *Peromyscus leucopus* (White-footed Mouse) and other mammals (Martin *et al.* 1961).

*(c) Seed viability and germination.* Seeds were collected from 13 sites in eastern Newfoundland on 13 and 14 September 1977 and held in a refrigerator at 1° C until 20 December when germination tests began. Seeds placed on the surface of a peat-vermiculite medium under 16 h light at 26° C and 8 h dark at 24° C had 87% germination after 59 days. The highest rate of germination was in seeds extracted from fresh, mature berries and a steady decline occurred with less than 10% germinating by 12 to 16 months. Johnson (1975) studied buried seeds in a subarctic lichen woodland east of Great Slave Lake, and reported that 65% of the sample cores contained seed of *Vaccinium vitis-idaea* and *V. uliginosum*. *Vaccinium vitis-idaea* counts showed 3.3 seeds/1000 cc of which 0.7 seeds/1000 cc were fertile at Porter Lake (180 years post-fire), and 4.8 seeds/1000 cc with zero fertility as Selwyn Lake (98 years post-fire). In Britain, Ritchie (1955) reports a lower percentage seed germination for freshly harvested seeds but an increased rate for cold-treated seeds.

*(d) Vegetative reproduction.* Examination of ericaceous communities in the Atlantic Provinces and Quebec suggests that lateral growth is by rhizome proliferation of ramets from the original seed-established clones (Hall and Beil 1970). Harper and White (1974) report a similar situation in *V. myrtillus*. Large old clonal plants may eventually break up by frost action, fire, burrowing, etc. into separate clones which, in turn, produce their own vegetative shoots and rhizomes. Pojar (1974) reports vegetative reproduction by creeping stems, and Johnson and Rowe (1977) indicate that this is an efficient means of vegetative reproduction in subarctic habitats.

Eighty-two percent of the stem cuttings from 14 Newfoundland clones produced roots, when held under intermittent mist, from 15 September 1977 to 7 December 1977. Studies in Finland on propagation have shown that rooting of stem cuttings is best in the spring (89%). Milled peat (85%) is superior to humus (55%) as a rooting medium; indole butyric acid at 6000 ppm gave a slight increase in rooting (90%), and pieces of rhizome behaved similarly to stem cuttings (Lehmushovi 1975). Rooting success was 83% for the controls.

## 8. *Population Structure and Dynamics*

*(a) Dispersion patterns. Vaccinium vitis-idaea* is generally dispersed contagiously, the creeping stems forming patches, but it may form mats (Hrapko and LaRoi 1978) described as loose, in moist mossy situations, or dense in dry, rocky sites (Viereck and Little 1972).

*(b) Age distribution.* In Sweden, Teär (1972) found that the age of plants in a woodland varied from one to nine years with the average being four. His method of determining age was based on counting the number of annual rings at the base of the aboveground stem as previously shown for *V. myrtillus* by Flower-Ellis (1971) and for *V. angustifolium — V. myrtilloides* by Hall (1957). Harper (1977) points out that shrubs are difficult for

population biology studies as the aboveground parts may be of a different age than the underground system. After any major disturbance such as a forest fire, habitat becomes available for colonisation but seedlings are subject to severe inter- and intraspecific competition from annuals in the first year, perennials (mostly sedges, grasses, legumes and composites ) from years two to five and later by shrubs and trees (Torrey 1914) (see also Table 2). Once established *V. vitis-idaea* var. *minus* will persist indefinitely unless shaded out by conifers. Within 25 years after fire its frequency becomes relatively stable (Johnson and Rowe 1977).

*(c) Size distribution.* Ten plants which had been previously grown in 10 cm clay pots were set out in the transplant garden at Kentville in 1970. In 1979 they had an average maximum crown diameter of 70 cm. In this experiment plants grew free from competition, but under normal field conditions crown diameter would probably have been less.

*(d) Growth and turnover rates.* Observations in the field in Nova Scotia and Newfoundland revealed that seedlings showed high rates of survival and new crops of seedlings are produced in favorable years. Once established, plants spread by slender creeping stems rooting at nodes (Viereck and Little 1972). Fresh weight of *V. vitis-idaea* var. *minus* from Tancook Island, Nova Scotia, was 253.5 ± 69.5 g/m$^2$ for sterile shoots, 207.5 ± 43.7 g/m$^2$ for fruiting shoots and 112.5 ± 19.8 g/m$^2$ for fruit (unpublished data). Stewart and Reader (1972) reported 845 ± 8% terminal growing points per m$^2$, and 740 ± 7 rooted shoots per m$^2$ with a mean weight of 15 mg per rooted stem. Leaves contributed 27.8 g/m$^2$ (53%), flowers and fruits 13.8 g/m$^2$ (26%), new stems 8.5 g/$^2$, (16%), old stems 3.6 g/m$^2$ (5%) to the 52.7 g/m$^2$ net primary production in aerial components in a S.E. Manitoba bog. Ericoides, *Ledum groenlandicum* (Labrador-tea), *Chamaedophne calyculata* (Leather-leaf), *Kalmia polifolia* (Bog-laurel), *Oxycoccus quadripetalus* (Small cranberry) and *Vaccinium vitis-idaea* var. *minus*) had net aerial primary production of 298.2 g/m$^2$, their total annual subsurface production was 1461.1 g/m$^2$ with 1234.6 g/m$^2$ remaining after 1 year's decomposition (Stewart and Reader 1972).Thirty nine percent of the *V. vitis-idaea* leaves decomposed after 1 year in the bog. In contrast in an Alaskan site Shaver and Chapin III (1980) reported total aboveground biomass in a tussock tundra community to be 59 g/m$^2$ with above ground productivity being 16 g/m$^2$/yr. Leaves accounted for 35.4 ± 8.8 g/m$^2$., stems 18.3 ± 3.3 g/m$^2$, and 2.4 ± 0.1 g/m$^2$ occurred in the unstructured organic layer (Shaver and Cuttler 1979). *Vaccinium vitis-idaea* var. *minus* accounted for 22% of the average 2 year production. The mean annual aerial production at four sites near Inuvik, Alaska (Wein and Bliss 1973a) was 6.1 g/m$^2$ with new leaf growth appearing in mid-July. Productivity in the Kenai peninsula, Alaska, ranged from 1000-3000 kg/ha (Oldemeyer and Seemel 1976). Data for productivity in various Fennoscandian communities is given in Kjelvik and Karenlampi (1975). Leaves persist for at least 3 years.

*(e) Successional role.* Seeds can germinate on bare ground if conditions are favorable, but *V. vitis-idaea* var. *minus* is not generally a pioneer species, although it grows on the summits of the highest rockfields at Pelly Lake, N.W.T. with *Rhododendron lapponicum* (Lapland Rosebay), *Hierochloë alpina* (Holy Grass), *Alectoria ochroleuca* (Lichen) and *A. nitidula* (Larsen 1972b). It invades the nearby tundra bog gravel communities dominated by *Alectoria ochroleuca, A. nitidula, Hierochloë alpina* and *Luzula confusa* (Woodrush). It also invades senescent *Eriophorum vaginatum* (Cotton-grass) tussocks in communities dominated by the *Eriophorum* and areas of frost activity after the pioneers (Larsen 1972b). It combines the *Empetrum nigrum* and a lichen mat to form a seral community leading towards White Spruce (Ritchie 1959). Mueller-Dombois (1964) reports it in successionally advanced Jack Pine stands with 2-5 cm humus and rotten wood on the ground.

In the far north *V. vitis-idaea* var. *minus* assumes a climax role (Cody 1954a) whereas in the barrens of Newfoundland it acts as a seral species before being displaced by *Picea mariana* (Black Spruce) and *Abies balsamea* (Balsam Fir).

### 9. *Interaction with Other Species*

*(a) Competition.* Since light intensities below 2152 lux are limiting (Hadley and Bliss 1964), *Picea glauca* (White Spruce), *P. mariana,* and *Abies balsamea* must be considered serious competitors for light. Similarly *Kalmia angustifolia* (Sheep-laurel), *Ledum groenlandicum* and *Potentilla tridentata* (Three-toothed Cinquefoil) and other species occupying the same habitat, compete for water, nutrients, etc. (Table 2).

Of some 15 species responsible for net primary productivity of bog vegetation in southeastern Manitoba *V. vitis-idaea* var. *minus* with 7.8% relative cover is sixth in importance. Furthermore, it ranked third in total annual above-ground net production being exceeded only by *Chamaedaphne calyculata* and *Ledum groenlandicum:* respective values were 52.7, 106.1 and 68.1 g/m$^2$ (Reader and Stewart 1971). In the Mackenzie Delta between Dempster (64° N 138° W elevation 1200 m) and Umiat (69° N 151° W), sites north of the tree line and dominated by *Eriophorum vaginatum* ssp. *spissum* had 12-31% of their cover provided by *Ledum decumbens, V. vitis-idaea, V. uliginosum* and *Betula nana* spp. *exilis. Eriophorum vaginatum, L. palustre* and *V. vitis-idaea* contributed 78-81% of the annual production (Wein and Bliss 1974).

*(b) Symbiosis.* Warming (1908) stated that *V. vitis-idaea* has both endotrophic and ectotrophic mycorrhiza associations. Ritchie (1955) cites additional European work which was carried out on *V. vitis-idaea* var. *vitis-idaea.*

*(c) Predation and parasitism.* Macoun (1884) stated that the fruit of *V. vitis-idaea* var. *minus* was invaluable as a source of food to birds migrating north in spring. Foliage of the species is eaten by a number of mammals such as *Alces alces* (Moose), *Lepus americanus* (Snowshoe Hare), *Rangifer tarandus groenlandicus* (Barren-ground Caribou), and *Ursus americanus* (Black Bear). In Alaska, Cushwa and Coady (1976) found that *Alces alces* ate large quantities of this evergreen during the winter on the Kenai Peninsula but inland, deep snow prevented consumption. In digestion trials Oldemeyer and Seemel (1976) report *in vitro* dry matter disappearance in August of this species as 50.7%. The composition of stems and leaves showed carbohydrates of cell walls to be 33.1%, acid-detergent fiber 29.3%, lignin 12.6% and protein 5.7%. In February the dry matter was lower (41.8%) carbohydrates were greater and protein about the same at 5.4%.

There is a suggestion by Kelsall (1968) that the green leaves of *V. vitis-idaea* as well as those of *Ledum groenlandicum, L. decumbens* and *Arctostaphylos uva-ursi* (Common Bearberry) may supply some special ingredient in the winter diet of *Rangifer tarandus.* In his quantitative analysis of stomach contents of caribou in northwestern Saskatchewan and District of Mackenzie he showed that *Vaccinium uliginosum* and *V. vitis-idaea* account for 3.8% of summer 21.5% of winter foods. Leaves of *V. vitis-idaea* consisted of 5.76% protein, 3.13% fat and 20.20% crude fibre. Scotter (1965) pointed out that the nutritive value of lichens was lower than that of a shrub group consisting of *Arctostaphylos uva-ursi, Ledum groenlandicum* and *Vaccinium vitis-idaea.* The group average for protein was 7.38% crude fat 3.98% and crude fibre 18.25% dry matter basis. Porsild (1962) states that species of *Vulpes* (foxes), *Lagopus* (ptarmigan), *Corvus* (ravens), *Larus* (sea gulls) and Anatidae (geese) feed on *Vaccinium* spp. fruit.

In Newfoundland, *Lepus americanus* feeds heavily on the shoots in winter and *Ursus americanus* eats this species in spring when snow has melted from the barrens but persists in the adjoining forests; *U. americanus* and *Vulpes vulpes* (Red Fox) consume quantities of the fruit in late fall and this constitutes a large proportion of their diet.

The fruit, in Newfoundland, is occasionally infested with *Grapholitha* sp. (Olethreutidae) whose larval stage generally leaves the fruit by the second week of September before fruit harvest (Hall 1978).

The major fungal diseases listed by Conners (1967) are: Red leaf — caused by *Exobasidium vaccinii,* Witches'-broom — *Pucciniastrum goeppertianum,* and leaf rust — *Pucciniastrum vaccinii.* Conners states that *E. vaccinii* occurs on *V. vitis-idaea* var. *minus* in Alaska, and Savile (1959) cites several infested specimens from British Columbia and Quebec.

*(d) Toxicity and allelophathy.* None Known.

## 10. *Evolution and Migration*

Camp (1945) placed this species in a section by itself and offered no explanation for its origin. The North American plants are consistently smaller than those in Europe (Fernald 1950). Camp (1945), however, reported that both dwarf and robust types were present in the east as well as west of this continent. Hultén (1949) states that only spp. *minus* is found in North America.

Frost and Ising (1968) used thin layer chromatography of phenolic compounds in studying *V. myrtillus, V. vitis-idaea* and the hybrid between them (*V. intermedium*). Differences in the chromatograms of the bilberries from Breanäs in southern Sweden and Värmdön near Stockholm were considerable. Between the hybrids from the localities, differences were also noted in the phenolic compounds, identified only as to position.

## 11. *Response Behavior*

*(a) Fire.* This is an important factor within the botanical range of *V. vitis-idaea* var. *minus.* In fire-prone ecosystems survival is related to the amount of moisture in the soil, the season of the year and depth of rhizome layer. In arctic *Eriophorum* tussock communities Wein and Bliss (1973a) report *V. vitis-idaea* ssp. *minus* and *E. vaginatum* ssp. *spissum* (Hare's Tail) had not recovered fully from fires after two growing seasons. The nutrient levels in leaves of *V. uliginosum* ssp. *alpinum* were higher from burned areas than unburned sites.

*Vaccinium vitis-idaea* var. *minus* appears within the first six years after fire rapidly attaining its maximum and maintaining a frequency of between 70 and 100% in a range of Black Spruce-lichen, Jack Pine-lichen, and White Spruce-birch communities of all ages up to 280 years (Johnson and Rowe 1977). Black and Bliss (1978) report similar findings in *Picea mariana-Vaccinium uliginosum* forests where fire does not change plant succession as dominant vascular plants soon resprouted and achieved preburn prominence. After eight years *V. vitis-idaea* var. *minus* had a frequency of 56% and cover of 8% rising to a maximum frequency (100%) and cover (55%) at 144 years. It was the only species to increase in cover and frequency in stands aged 120-200 years, and to maintain relatively high cover values in communities 200-300 years old. It attained a cover of 15% 130 years after fire on drumlins of sand and gravel near Great Slave Lake with *Stereocaulon paschale* (22%) and *Cladonia stellaris* (17%) (Maikawa and Kershaw 1976). It dominates both burned and unburned sites in the Kenai Peninsula, Alaska (Oldemeyer *et al.* 1977).

In Eastern Canada the rhizomes of *V. vitis-idaea* var. *minus* are much finer and generally closer to the surface of the soil than those of *V. angustifolium* which can withstand regular burning (Hall *et al.* 1979). Fire, therefore, weakens the plants and reduces the proportion of *V. vitis-idaea* in mixed stands. Re-colonisation is possible by regrowth from dormant buds on stems and rhizome pieces which escape lethal temperatures.

*(b) Grazing and harvesting.* Small mammals such as Snowshoe Hares clip the ends of stems, destroy apical buds and cause increased branching, while Moose remove entire clusters of stems in a single mouthful. Sheep will only graze *V. vitis-idaea* when more palatable species are wanting (Ritchie 1955).

*(c) Flooding.* The normal habitats of this species are not subject to flooding. In peatlands, it occurs on the tops of hummocks which are drier than depressions (Larsen 1972b).

*(d) Drought.* Prolonged dry spells seriously reduce vegetative growth and decrease fruit size. In the drier part of its range the vigor and frequency of shoots is less.

*(e) Herbicides.* 2,4-D causes browning of stems and leaves, leaf drop, and at high concentrations (1.3 to 1.8 L per 450 L of $H_2O$) death of the plant. Relaled *Vaccinium* spp. are classified as susceptible to 2,4-D; 2,4,5-T; and intermediate to ammonium sulfamate (Ontario Weed Committee 1980).

*(f) Chemical changes:* oil spills. *Vaccinium vitis-idaea* var. *minus* with a frequency of 64% in a cottongrass community, and 42% in a dwarf-shrub community was sprayed with Norman Wells crude oil in July 1973 (Freedman and Hutchinson 1976). Its leaves lost their chlorophyll slowly, the dead leaves remained on plants for up to two seasons and regrowth leaves showed gigantism. A summer spill had greater effect than one in February when plants were covered by 40 cm snow because devolatisation and partial detoxification of the oil occurred before it contacted plant tissue. A year after the summer spill *V. vitis-idaea* had a frequency of 21% in the cottongrass community and 17% in the dwarf shrub community. The authors suggest that a high degree of recovery might be produced after 10 to 15 years, but species diversity would be reduced with bryophytes and lichens eliminated (Freedman and Hutchinson 1976). In mature *Picea mariana* forest, *V. vitis-idaea* had a cover of 48% and frequency of 98% prior to crude oil spills. Summer spills reduced cover to zero, while low and high intensity winter spills reduced cover to 12% and 6%, respectively. Regrowth shoots lost water more rapidly than controls, apparently due to their thinner cuticle (Hutchinson *et al.* 1976). At Tuktoyaktuk, in the cottongrass winter spill site (Hutchinson and Hellebust 1978), recovery provided up to 78% cover in the second year; 58% of this was *Eriophorum*, with *V. vitis-idaea, Calamagrostis canadensis* (Blue-joint), *Ledum groenlandicum* and *Rubus chamaemorus* (Bake-apple) providing the remainder. Hutchinson and Hellebust (1978) give flowering success and other details for *V. vitis-idaea* in cotton grass, mature forest and dwarf shrub communities after crude oil spills.

*(g) Frost.* Opened flowers had a 50% mortality at −1.5° C and the corresponding temperature for unripe berries and flower buds was −3.1 to −3.5° C (Teär 1972). In Japan hardening at 0° C for 10 days enhances freezing resistance in *V. vitis-idaea,* it was maximal after hardening at −3° C for 10 days when resistance to −70° C was induced (Sakai and Otsuka 1970).

## 12. *Relationship to Man*

Fruit of *Vaccinium vitis-idaea* var. *vitis-idaea* has been an important ingredient in the diet of most Scandinavians for centuries and harvested with small comb-sieves by hand in open woodlands. The flavor of raw berries of var. *minus* is very tart, but Porsild (1974) and Ryan (1978) claim that the flavor is improved by slight frost. Porsild (1937) states that this species is a most valuable antiscorbutic due to its high vitamin C content. Hedrick (1919) states, "This is the wi-sa-gu-mina of the Crees and the cranberry most plentiful and most used throughout Rupert's Land". In Alaska, the Inuit names are 'keepmingyuk' (Shismaref north to Noatak), 'keepmik' (Seward

Peninsula) and 'toomalgleet' (Lower Kuskokwim) and the Indian name is 'nutlut' (Heller 1953). Heller states that the berries can be mixed with rose hips to make an excellent jam. Biermann (1975) has written a brief description of the plant and suggested the economic importance of the fruit among people of Scandinavian origin in Minnesota and Wisconsin.

The berries make excellent jams, jellies, and preserves. In favorable years up to 100 tonnes are exported from Newfoundland to Scandinavian countries for human food products.

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