# STUDIES ON VEGETATIVE AND REPRODUCTIVE GROWTH OF LINGONBERRY, *VACCINIUM VITIS-IDAEA* L.

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

By

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

November 1981

ACKNOWLEDGEMENTS

I would like to thank my advisors, Dr. Cecil Stushnoff and Dr. David Wildung for their constant encouragement, support, and professional advice which sustained me throughout my graduate studies. I also wish to thank my committee members, Dr. Paul Read, Dr. Peter Ascher, Dr. Patrice Morrow, and Dr. John Hall for their help in developing my various research projects and their constructive criticism of my thesis.

I am especially grateful to Professor Philip VanVeldhuizen for statistical advice; to Dr. Bonita Neiland for the loan of equipment and laboratory space; to Dr. Eduard Stadelmann for training on the microscope; and to Shirley Munson for the use of her lab and for her warm friendship and help during my studies. Special thanks to Kobra, Carlos, Joe, Richard, Vicky, Brian, Shuby, and Scott for being very special friends.

Finally, I want to thank Bob, without whose help and understanding, patience, and 314 trips to Smith Lake, this thesis would not have been written.

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## Introduction

The lingonberry, *Vaccinium vitis-idaea* L., is a woody, evergreen shrub of circumpolar distribution whose fruit is harvested from native populations throughout most northern regions of the world. Recently, plans to domesticate the lingonberry have been implemented in Scandinavia and Germany because of unpredictable fruit yields from native populations, labor shortages, and increased pressure from urban development near major native berry populations. In Alaska, efforts to increase the utilization of natural renewable resources and to develop potential uses for vast acreages of marginal lands have led to studies on the biology and cultivation of *V. vitis-idaea*.

A search of the literature on *V. vitis-idaea* revealed a considerable number of investigations most of which were concerned with aspects of native plant ecology. Regional phenology studies, floristic summaries, and ecological frequency and distribution lists in arctic to north-temperate regions commonly include *V. vitis-idaea* since it is an abundant ground cover in a diversity of plant communities. In addition, studies on anatomy, plant nutrition, pollination ecology, physiology, and propagation are reported, but few of these studies have been pursued in great detail. Most of these investigations have been completed in Eurasia, presumably with the subspecies *vitis-idaea*. Very little research involves the subspecies *minus* in North America. Fewer than one dozen papers are concerned specifically with *V. vitis-idaea* cultivation. Consequently, studies elucidating basic growth and

development patterns as well as those relating to cultural practices and environmental manipulation are required in order to produce a successful horticultural fruit crop.

The present study is an investigation into certain aspects of vegetative and reproductive growth of V. vitis-idaea. Three general areas of research have been emphasized: the ecology of native populations, field cultivation practices, and controlled environment experimentation. Studies on the ecology of native populations include vegetative and reproductive phenology, seasonal fruiting characteristics, pollination ecology, and the timing of flower bud differentiation and development. Cultivation experiments emphasize vegetative growth responses to four Alaskan substrates and light intensity modifications. The controlled environment experimentation involves an assessment of the number of hours of chilling temperatures required to resume growth following onset of dormancy. The results of these investigations are summarized in the five papers which follow the literature review.

It is anticipated that these studies will combine with previous research to form a basic assessment of vegetative and reproductive growth of the lingonberry as well as a determination of potential methods for increasing growth through cultivation practices. In addition, these studies will serve as a foundation for future research into the development of controlled field management practices and breeding and selection studies for improved berry production in Alaska.

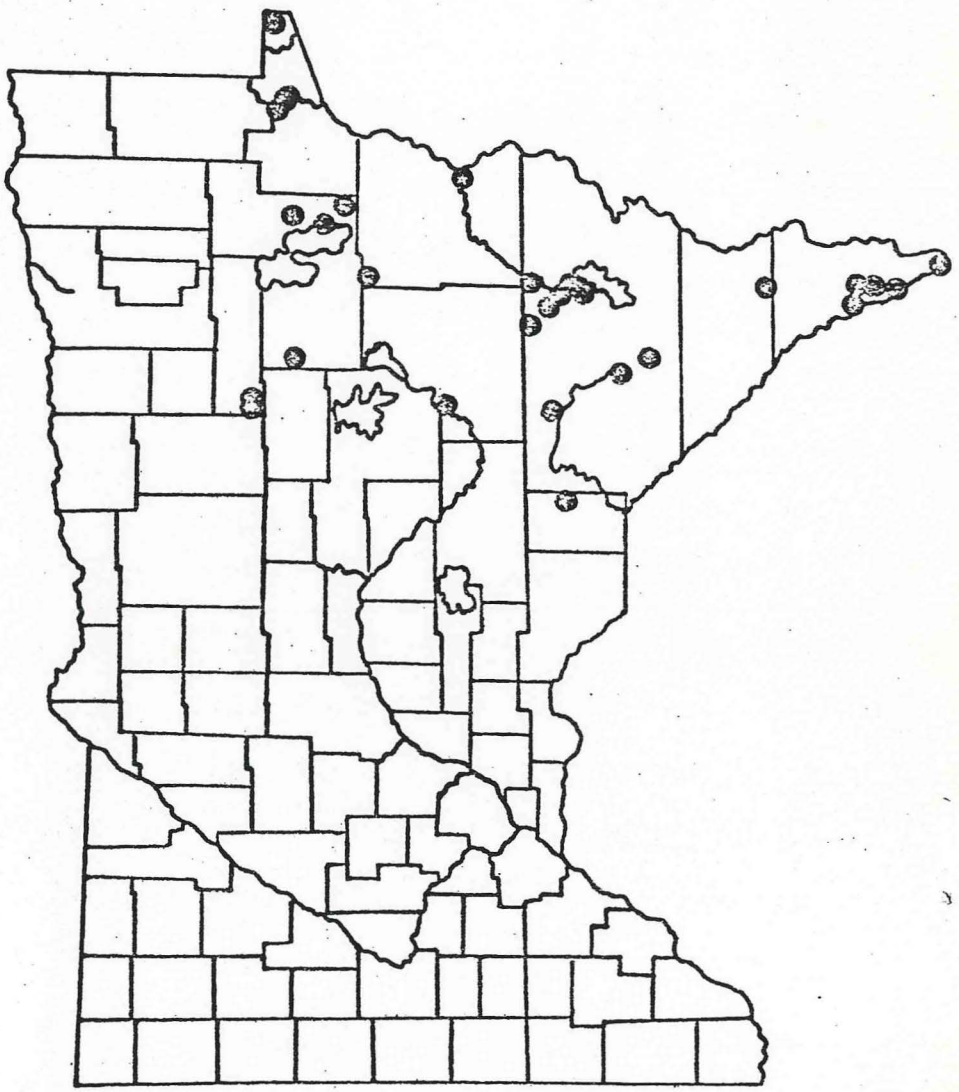
# REVIEW OF THE LITERATURE

## Taxonomy and Distribution

The genus, Vaccinium, one of approximately 70 genera of the family Ericaceae, includes more than 350 species of wide geographic distribution extending from arctic to subtropical regions and at higher elevations in the tropics (Hutchinson 1969). Approximately 25 species occur in North America (Munson 1901, Lawrence 1951). These species have been variously grouped into six (Gray 1867, Munson 1901), eight (Fernald 1970), or ten (Camp 1945) groups or subgenera. Vaccinium vitis-idaea L. belongs to the subgenus Vitis-Idaea (Moench)W. Koch. It is considered the sole member of this group by Camp (1945) and Fernald (1970) but is associated with V. ovatum Pursh and V. crassifolium Andr. in Munson's classification (1901). According to Camp (1945) plants of Vitis-Idaea are characterized by an evergreen life form, flowers in terminal racemes, four locules per ovary, and eight stamens with non-spurred anthers.

V. vitis-idaea is a circumpolar plant which occurs throughout arctic America, extending southward to New England, the Great Lakes Region, and British Columbia (Munson 1901, Chandler and Hyland 1941, Hulten 1968). It is ubiquitous throughout Alaska. In Minnesota it is found only rarely from Cook to Lake of the Woods and Clearwater Counties (Morley 1969) (Fig. 1). It also occurs on the islands of the Bering Sea; from Kamchatka to Japan; in Greenland; from Iceland and northern Europe to the Pyrenees, northern Italy, and the Caucasus; and in Asia from northern Siberia southward to northern China and Korea (Printz 1921, Hulten 1937, 1970, Anon. 1977) (Fig. 2).

Figure 1. The distribution of Vaccinium vitis-idaea L. in Minnesota (Courtesy of G. Ownbey, Curator, University of Minnesota Herbarium).



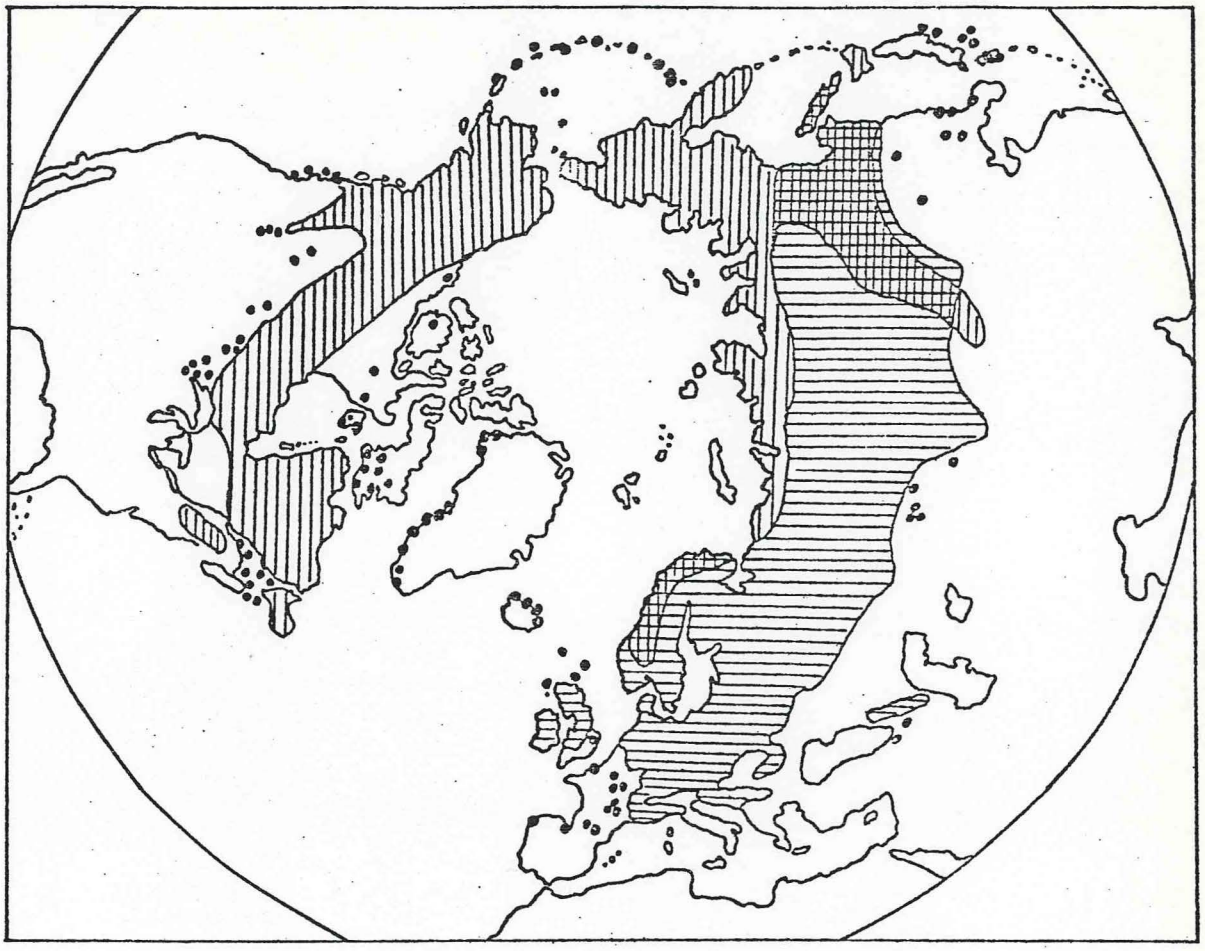
In general, the species is subdivided into two geographical races which Loddiges (1822, 1825) designated as variety minor, a dwarf arctic-montane race, and variety major, a larger lowland race. Subsequently, these races have been given various designations which are listed in Table 1 along with generic and specific synonyms. Most recently, Hulten (1949, 1970) has recognized the two races as subspecies vitis-idaea and minus (Lodd.) Hult.

Two other subdivisions have been reported: the variety pruinosum Takeda, a tall variety with glaucous berries from Sakhalin (Hulten 1970), and the variety ovata Henriksson, a variety with oblong-ovate berries from Sweden and Norway (Henriksson 1923, Jorstad 1962).

The two major races, subspecies minus and vitis-idaea, are distinguished primarily by plant size. Subspecies vitis-idaea is a very coarse plant which often grows to 30 cm in height. Leaf size is substantially larger than the dwarf form, averaging 2.5 cm and 1.0 cm in length and width respectively. In contrast, subspecies minus rarely exceeds 20 cm in height, and leaf size averages 1.0 cm in length and 0.5 cm in width (Hulten 1949, Fernald 1970, Welsh 1974). Other distinguishing characteristics are summarized by Hulten (1949) as follows:

> "Vaccinium vitis-idaea [ssp. vitis-idaea] has leaves with 3-4 nerves usually arranged in pairs, strongly marked and sunk in the tissues of the upper side of the leaf. The sepals are broadly triangular and longer than broad. The

Figure 2. World distribution of Vaccinium vitis-idaea L. (Redrawn from Hulten 1970).



Vaccinium vitis-idaea ssp. vitis-idaea

V. vitis-idaea ssp. minus

filaments are pubescent to the tip and the style exceeds the anthers and protrudes considerably from the corolla.

Subspecies minus on the other hand has leaves which are nerveless or else has 2-3 faintly marked nerves on each side. The sepals are rounded with an apex, very short and broad. The filaments are glabrous in their upper part between the two halves of the anther and the style exceeds the anther by about the length of the tubules and only very slightly protrudes from the corolla."

Hulten (1949) maintains that the only subspecies found in North America is minus. This subspecies also occurs in eastern Asia, along the northern coast of Siberia, and in the mountains of Scandinavia where frequent introgressions occur between it and subspecies vitis-idaea (Hulten 1970) (Fig. 2). Camp (1945) believes that both subspecies occur in North America.

Elevation to approximately 2200 m has little influence on V. vitis-idaea abundance (Smith 1962), but there is a progressive decrease in plant height, leaf size and number, and the number of flower buds per inflorescence with increasing elevation (Alyanskaya 1972). V. vitis-idaea grows to 1200 m in the British Isles (Ritchie 1955b) and in arctic Alaska (Hulten 1970), 1800 m in the Belosica Mountains on the Yugoslav-Greek border (Dimitrovski 1973), 2000 m in the Altai Mountains, Mongolia (Printz 1921), 2500 m in Italy, and 2700 m in the Caucasus (Hulten 1970).

Table 1. Generic, specific, and subspecific synonyms of *Vaccinium vitis-idaea* L.

| Synonym | Source |
|---|---|
| *Vitis-Idaea Vitis-Idaea* Britt. | Britton & Brown 1913 |
| *V-I. Vitis-Idaea* Britt. var. *punctata* Moench. | Rehder 1940 |
| *V-I. punctata* var. *minus* (Lodd.) Moldenke | Moldenke 1956 |
| *Rhodococcum vitis-idaea* (L.) Avr. | Avrorin 1958 |
| *R. minus* (L.) Avr. | Avrorin 1958 |
| *Vaccinium buxifolium* Gillb. | Fernald 1902 |
| *V. punctatum* Lam. | Munson 1901 |
| *V. punctifolium* Stokes | Munson 1901 |
| *V. nemorosum* Salsib. | Munson 1901 |
| *V. vitis-idaea* L. var. *pumilum* Hornem | Fernald 1902 |
| *V. vitis-idaea* L. var. *microphyllum* | Hulten 1937 |
| *V. vitis-idaea* L. var. *minus* Lodd. | Hulten 1949 |
| *V. vitis-idaea* L. ssp. *major* Love | Love 1950 |
| *Folium vitis-idaea* | Racz et al. 1962 |

In Minnesota, *V. vitis-idaea* is known as the lingonberry, but worldwide more than 25 common names have been reported. These names are listed in Table 2.

Habitat

*V. vitis-idaea* produces upright stems which originate from subterranean, horizontal rhizomes. Stems may appear singly, one or two per square meter, as in many *Sphagnum* sp. or tussock-forming bogs or in dense clones several meters in diameter as in some mixed spruce-hardwood or pine forests. Many ecological studies throughout the circumboreal to north-temperate regions include descriptions of *V. vitis-idaea* (eg. Polunin 1940, Yakovlev 1948, Ritchie 1955b, Scoggan 1957, Smith 1962, Tikhomirov 1969, Pojar 1974, Kjelvik and Karenlampi 1975), and all create a picture of a very diverse habitat. For instance, in Alaska the plant grows from very dry roadside slopes with little or no developed organic layer to acid-peat bogs; from mature forests with up to 75 percent shade to fully exposed alpine and arctic tundra slopes. It often occurs in greatest abundance on top of decaying tree stumps in mature forests (Taylor 1932, Drury 1956, Heller 1962, Britton 1966, Fleming 1968, Viereck and Little 1972, Oldemeyer and Seemel 1976, Holloway, unpublished).

Throughout its range *V. vitis-idaea* appears to be most abundant in forest habitats which have moist, acid soils, moderate shade, and a well-developed organic matter layer (Yakovlev 1948, Ritchie 1955b, Hulten 1968, Brown and West 1970).

Table 2. Common names of *Vaccinium vitis-idaea* L.

| Country | Name | Country | Name |
|---|---|---|---|
| United States | lingonberry | USSR | brusnika |
| | moss cranberry | Japan | kokemomo |
| | rock cranberry | France | airelle rouge |
| | lingberry | | Pomme de Terre |
| | lingen or lingon | | Vigne du mont Ida |
| | lin-berry | Germany | preiselberre |
| | red whortleberry | Finland | cowberry |
| | mountain cranberry | | puolukka |
| | alpine cranberry | Sweden | lingon |
| | lowbush cranberry | Norway | tyttebaer |
| | dry ground cranberry | Poland | brusznica |
| | shore cranberry | | |
| | red bilberry | | |
| | foxberry | | |
| | vine of Mount Ida | | |
| Netherlands | whinberry | | |
| Canada | partridgeberry | | |

Vegetative Growth - Morphology and Anatomy

Three to four weeks after germination the seedlings of V. vitis-idaea are 4-5 mm in length with two reddish-green, ovate-oblong herbaceous cotyledons. After three months the seedling consists of a slender vertical shoot, 2-2.5 cm in length bearing alternate, evergreen leaves (Ritchie 1955b, Muller 1978). According to Hall and Beil (1970) a tap root growing vertically in the substrate predominates in the seedling root system, and several rhizomes grow laterally from the crown. In contrast, observations by Ritchie (1955b), Leiser (1968) and Smith (1962) have revealed no tap root but a finely branched, adventitious root system.

Nearly 80 percent of the total biomass of a mature V. vitis-idaea plant is below ground (Persson 1978). Most of the subterranean biomass consists of rhizomes which branch dichotomously and contain spirally-arranged leaf scales. Roots originating from the axils of the leaf scales and averaging 0.01-0.03 cm in diameter are scattered along the entire length of the rhizome (Ritchie 1955b, Smith 1962). The root-rhizome system extends from the surface to as much as 28 cm below the substrate surface (Karandina 1954, Ritchie 1955b, Smith 1962, Kerekova 1970, Persson 1978). Smith (1962) noted that the maximum rooting depth is a function of the depth of the organic matter layer, but Kerekova (1970) has found no such correlation.

A mucilagenous sheath surrounds the root cap, meristematic region, and elongation zone of V. vitis-idaea. It is present at all

stages of development and may prevent root tip desiccation or increase the effective absorbing area of the root (Leiser 1968). The roots support endotrophic and ectotrophic mycorrhizal fungi which stimulate both root and shoot growth (Warming 1908, Haselwandter 1979). Some of these fungi are interchangeable on V. myrtillus, V. uliginosum, and V. vitis-idaea (Freisleben 1934).

Very few seedlings of V. vitis-idaea are found in native populations (Ritchie 1955b). Most above-ground biomass results from vertical stem production from rhizomes. Approximately 22 percent of the leafy stems are located terminally on the rhizome while 78 percent arise from older, mid-rhizome locations (Smith 1962). Total above-ground biomass has been estimated to be from 1000 to 3000 kg/ha on the Kenai Peninsula, Alaska (Oldemeyer and Seemel 1976). Biomass estimates for selected Fennoscandian ecosystems are listed in Table 3.

In general, stems remain vegetative from three to six years (Torrey 1914, Ritchie 1955b, Fernqvist 1977). Following flowering no more terminal growth occurs and the stem eventually becomes leafless. The approximate life-span of a leaf is from two to four years (Ritchie 1955a, Hadley and Bliss 1964, Kuriganova 1972).

The terete, pubescent stems are covered with a thick cuticle. Stems from plants growing in swampy taiga soils do not have stomates, whereas those growing in the forest-steppe have stomates in the epidermis of the youngest shoots (Yakovlev 1948). The cortex consists of either thin-walled transparent cells or thick-walled cells

Table 3. Biomass estimates for selected Fennoscandian ecosystems (Kjelvik and Karenlampi 1975).

| Ecosystem | Total living above-ground biomass (g dry wt. per $m^2$) |
|---|---|
| Kevo, Finland | |
| Birch forest | 156.6 |
| Moist birch forest | 87.2 |
| High elevation birch forest | 44.9 |
| Low alpine heath | 54.8 |
| Pine forest | 307.7 |
| Alpine lichen heath | 34.3 |
| Hardangervidda, Norway | |
| Birch forest | 27.3 |
| Lichen heath | 34.3 |

containing chlorophyll (Warming 1908). Very young cortex exhibits large intercellular spaces which appear crushed in older tissues. Concurrent with decreasing volume of intercellular spaces is the development of cork tissue (Yakovlev 1948). Spring and winter wood are not distinct (Warming 1908).

The ovate-oblong leaves exhibit a revolute development pattern (Hara 1956). Both upper and lower epidermis are covered with a thick cuticle. The lower epidermis contains stomates and glandular hairs which exude tannins (Warming 1908, Yakovlev 1948, Kaverzneva 1972). The mesophyll consists of several layered palisade cells from 0.11 to 0.20 mm thick and a loose spongy mesophyll, 0.11-0.24 mm thick (Holloway, unpublished). Average leaf thickness ranges from 0.36 to 0.41 mm (Ritchie 1955a, Holloway, unpublished).

Phenology of Vegetative Growth

In Nova Scotia the formation of vegetative buds begins in late June, and buds are fully developed by the time plants become dormant in autumn (Bell and Burchill 1955). Leaf expansion can begin as early as March in the British Isles (Ritchie 1955b), but it generally occurs from mid May to mid June (Hadley and Bliss 1964, Kuriganova 1972, Wielgolaski 1974). Shoot growth proceeds through June, usually ending in mid July (Hadley and Bliss 1964). Roots and rhizomes have two periods of growth, once in early spring and again in autumn (Ritchie 1955b).

## Factors Affecting Vegetative Growth and Development

### Temperature

Ulmer (1937) has reported that non-acclimated plants of *V. vitis-idaea* are killed at -2.5°C and acclimated plants survive to -22°C. Studies by Sakai and Otsuka (1970) reveal that non-acclimated stems of *V. vitis-idaea* from alpine habitats survive without injury to -7°C but are killed at -12°C. If collected in October, stems and leaves survive freezing to -20°C and rhizomes to -10°C. In winter, leaves are hardy to -70°C, stems and buds to -30°C, and rhizomes to -20°C. Similar seasonal trends in freezing resistance are reported for stem and leaf tissue of subarctic Alaska plants by Riedmuller-Scholm (1974). Monthly cold temperature resistance limits for *V. vitis-idaea* are listed in Table 4.

Experiments with artificial hardening show that *V. vitis-idaea* leaves attain maximum hardiness (survive freezing to -70°C) when exposed to 0°C for 10 days followed by -3°C for 7 days. In contrast, leaves held at a mean air temperature of 10°C survive to -10°C, and those exposed to 0°C for 10 days survive to -25°C (Sakai and Otsuka 1970).

In studies of deacclimation, Riedmuller-Scholm (1976) found that *V. vitis-idaea* leaf and stem tissue loses its resistance to -80°C within 5 days of being placed in a growth chamber with a -4°C constant temperature and a photoperiod of 4 hours light. Deacclimation does not appear to be mediated by daylength.

Table 4. The limits of low temperature resistance of V. vitis-idaea leaf and stem tissue collected monthly from a Picea glauca forest near Fairbanks, Alaska (Riedmuller-Scholm 1974).

| Month | Minimum survival temperature (°C) | Month | Minimum survival temperature (°C) |
|---|---|---|---|
| January | -80[z] | July | -6 |
| February | -78 | August | -4 |
| March | -44 | September | -18 |
| April | -6 | October | -26 |
| May | -6 | November | -36 |
| June | -10 | December | -80 |

[z] low temperature limit of experimental freezer

Resistance to high temperatures also reaches a maximum level in mid winter. V. vitia-idaea leaf and stem tissue can survive temperatures as high as 48° to 58°C throughout the year (Riedmuller-Scholm 1974).

Light

V. vitis-idaea grows in habitats where light intensity measurements range from 3.4 percent of photosynthetically active radiation to complete illumination (Krylova and Trembalya 1978). Oldemeyer and Seemel (1976) have found that the percentage cover of V. vitis idaea in mature spruce-hardwood forests is negatively correlated with increasing cover of the tree canopy. In other plant communities, a positive correlation between percent canopy cover and V. vitis-idaea biomass was found. Smith (1962) noted that the greatest abundance of V. vitis-idaea occurs in moderate to heavy shade. In cultivated field experiment Lehmushovi and Hiirsalmi (1973) found that shade (10-25 percent of complete illumination) increased both stem growth and plant height.

Soil and Mineral Nutrients

"V. vitis-idaea grows in extreme nutritional environments characterized by leached soils with low pH, low base saturation, and low lime content. The nutrient turnover is slow and the amount of available nutrients is small" (Ingestad 1973).

Growth and productivity are negatively correlated with increasing soil pH (Ipatov et al. 1977). The pH range within which plants grow in the wild is 2.7-5.5 (Krylova and Trembalya 1978). Development of

plants is favored by acid soils and a substantial decaying organic matter layer (Tear 1972, Stark et al. 1978).

When the total concentration of mineral nutrients is increased the growth rate of V. vitis-idaea is decreased. An increased tissue pH and cation concentration promotes both ammonium toxicity and lime-induced chlorosis which cause poor growth or death of the plant (Ingestad 1976).

Studies by Mueller-Stoll (1947), Marthaler (1939), and Havill et al. (1974) have shown that V. vitis-idaea utilizes sources of nitrogen other than nitrate, while Ingestad (1973) found no difference in growth with either ammonium or nitrate as a nitrogen source.

The quantity of mineral nutrients found in the soil is not a good indicator of the quantity found in plant tissue samples (Ingestad 1973, Firsova and Pavlova 1975). Certain elements including Ca, Mn, Al, Ag, Pb, and B tend to accumulate in tissues even at low soil concentrations (Musaeva 1965, Ingestad 1973). In contrast, Izdebski and Popiolek (1975) showed a positive relationship between soil and tissue P and K. Possible mechanisms for uptake of K by roots have been studied by Jensen and Pettersson (1978).

Oldemeyer and Seemel (1976) observed a dramatic seasonal fluctuation in leaf and stem mineral nutrient concentrations (Table 5). Since V. vitis-idaea is evergreen, a migration from stems and leaves to subterranean storage organs is suspected to occur prior to onset of dormancy. Izdebski and Popiolek (1975) found similar seasonal

Table 5. Mineral concentrations in leaf and stem tissue of Vaccinium vitis-idaea in late summer and mid winter (Oldemeyer and Seemel 1976).

| Element | Concentration (ppm) | | | |
|---|---|---|---|---|
| | August | | February | |
| | Mean | SD | Mean | SD |
| Ca | 4920.0 | 545.3 | 26.7 | 3.2 |
| Mg | 1328.0 | 273.6 | 4.6 | 0.4 |
| K | 438.3 | 288.7 | 29.8 | 5.9 |
| Na | 55.0 | 13.2 | 22.8 | 0.4 |
| Cu | 5.8 | 3.8 | 0.2 | 0.1 |
| Fe | 51.3 | 19.9 | 3.2 | 0.9 |
| Mn | 17.7 | 3.6 | 1.9 | 0.3 |
| Zn | 8.3 | 3.8 | 0.3 | 0.3 |

trends in P and K concentrations. Possible mechanisms for uptake of K by roots of V. vitis-idaea have been studied by Jensen and Pettersson (1978).

Vegetative Propagation

The first experimental fields of V. vitis-idaea in Finland and Sweden were developed from clusters of plants dug from wild populations and transplanted into cultivated fields (Lehmushovi 1975, Fernqvist 1977). In Finland the percent cover on a milled peat substrate increased from 10 to nearly 100 percent within 5 years. Despite this success, division of wild plants has not been recommended because of substantial genetic heterogeneity of the plant material and the introduction of weed species into field plantings (Lehmushovi 1975, Lehmushovi and Sako 1975).

Stem cuttings root easily if propagated in the spring prior to bud break or in early fall (Lehmushovi 1975, Lehmushovi and Sako 1975, Bandzaitene and Butkus 1978). One-year-old shoots root better than younger cuttings, but little difference is evident in rooting percentage among one-, two-, and three-year-old cuttings (Bandzaitene and Butkus 1978). Milled peat is the best rooting medium when compared with sand, humus, or mineral soil. Treatment of cuttings with 6000 ppm indole butyric acid solution increased total rooting percentages by only 7 percent over control plants (Lehmushovi 1975, Lehmushovi and Sako 1975).

The shoot fragment propagation method in which shoots are segmented, scattered over the surface of a rooting medium, and covered with a thin layer of substrate has not been successful with V. vitis-idaea (Lehmushovi 1975).

A significant problem encountered with the use of stem cuttings is the apparent loss of the ability of resulting rooted plants to produce rhizomes. This problem may curtail the use of stem cuttings as a means of vegetative propagation because cultivated field establishment and plant renewal are dependent upon substantial rhizome and leafy branch production (Oster 1974, Lehmushovi and Sako 1975, Lehmushovi 1977b).

Rhizome cuttings, 5 cm in length, root easily under the same timing and substrate conditions reported for stem cuttings (Lehmushovi 1975). On an average, there is one bud per 1.5 cm length of the rhizome (Fernqvist 1977).

Reproductive Growth - Morphology and Anatomy

Following 3-6 years of vegetative growth, flower promordia are initiated in apical buds of V. vitis-idaea. Flowers may appear singly or in racemes of up to 15 florets (Torrey 1914, Hall and Beil 1970). In some productive populations the average number of flowers per stem is five (Torrey 1914, Tear 1972). During any one growing season, from 0 to nearly 50 percent of the total number of stems in a population contains flower buds (Torrey 1914, Hall and Beil 1970, Wielgolaski and Karenlampi 1975). In arctic regions flowers occur

only on plants growing in protected areas, in rock crevices on southern exposures (Wielgolaski and Karenlampi 1975). In general, fruit set averages 30 percent of flower production, but wide fluctuations occur annually. Fruit set ranging from 0 to 70 percent has been reported (Torrey 1914, Hall and Beil 1970, Kolupaeva 1972 a, b, Lehmushovi 1977a).

Flower buds are initiated during the summer preceding anthesis. The stage at which buds enter winter rest varies annually within a single population as well as among population locations. Buds collected in Nova Scotia by Bell and Burchill (1955) exhibited an acropetal development pattern. In the basipetal floret of dormant buds the four placentae are differentiated as mounds of meristematic tissue, and the ovules hardly are perceptible. The female gametophyte and integument are not differentiated. The anthers become inverted early in development, and the four regions of the sporogenous tissue may or may not be differentiated. Palser (1961) observed that the anthers over-winter in the microspore mother cell stage in populations collected in New Hampshire, Alaska, and Northwest Territory.

In the immature anther the apical awns are cellular throughout, but as development proceeds the tissue begins to disintegrate, progressing inward and downward until the pore is connected with the pollen sac (Matthews and Knox 1926, Palser 1961). The pollen grains, in the form of tetrahedral tetrads, are shed at the corolla aperture (Matthews and Knox 1926). A detailed analysis of pollen morphology is provided by Oldfield (1959) and Knuth (1909).

The pendulous, urceolate flowers are 4-6 mm in length and white to pinkish-red in color. Flowers are four-merous, actinomorphic, usually perfect, and epigynous with four locules per ovary and 15-20 ovules per carpel. Knuth (1909) has observed populations with staminate as well as perfect flowers. There are eight (rarely nine) included stamens which open by pores at the ends of long antherine awns. The single style equals or exceeds the length of the corolla at anthesis (Knuth 1909, Matthews and Knox 1926, Wiggins and Thomas 1962, Hulten 1968, Fernald 1970).

The spherical or ovate berries are uniformly burgundy when ripe. In immature fruit only the exocarp is colored, the other parts being white. The yellow, short-beaked seeds have a thick testa, bulky ,protein-rich endosperm, and an elongated embryo consisting chiefly of the radicle in the axis (Winton 1902).

Berries are rich in K, Ca, Mg, and P as well as carotene, $B_1$, $B_2$, folic acid, and C vitamins (Heller and Scott 1962, Anon. 1967, Bandzaitene and Butkus 1975b, Botticher 1977). The primary components of the dry matter of berries are carbohydrates and non-volatile organic acids (Senchuck and Borukh 1976). The fruit also is characterized by a high tannin, benzoic acid, and anthocyanin content (Anon. 1977, Bandzaitene and Butkus 1977) and has a pH of 2.5 (Stark et al. 1978). The most important single component of berry aroma is 2-methyl butyric acid (Anjou and Von Syndow 1967, 1969).

Phenology of Reproductive Growth

Phenological observations throughout a wide range of latitudes and altitudes show that the major flowering season of V. vitis-idaea is from late May through mid July with maximum flowering usually occurring in June (Ritchie 1955b, Hadley and Bliss 1964, Kolupaeva 1972a, Kuriganova 1972, Dimitrovski 1973, Pojar 1974, Bandzaitene and Butkus 1975a, Anon. 1977, Snigrev and Khvesko 1978). Bandzaitene and Butkus (1975a) and Ritchie (1955b) also mention a second, late-summer, flowering season. "Summer flowering is observed from the end of June until the first frost. It is less intensive. Racemes do not form, and solitary blossoms grow out on long (1-2 cm) scapes in the axils of the spring shoots" (Bandzaitene and Butkus 1975a). In the British Isles the second flowering season occurs only at lower elevations (Ritchie 1955b). Fruit ripening occurs from late August through September and in some localities into October (Hadley and Bliss 1964, Kolupaeva 1972a, Kuriganova 1972, Dimitrovski 1973, Anon. 1977, Snigrev and Khvesko 1978).

Cytology and Breeding

The chromosome number of V. vitis-idaea is 2n=24 (Hagerup 1928, Newcomer 1941, Darrow et al. 1944, Schultz 1944, Darlington and Wylie 1955, Rousi 1966, Pojar 1973). No tetraploids have been found, but Ahokas (1971) reported a triploid population with 2n=36 chromosomes from Finland.

*V. x intermedium* Ruthe, a natural hybrid between *V. vitis-idaea* and *V. myrtillus*, was discovered in northern Germany in 1826 (Gourlay and Vevers 1919). This hybrid is confined to ecologically disturbed areas in the vicinity of the parent populations in Sweden, Czechoslovakia, Denmark, Russia, Poland, Germany, and the British Isles. *V. x intermedium* is morphologically distinct from the parents, exhibiting intermediate vegetative and reproductive structures including stem pubescence and shape; leaf thickness, shape, and serration; corolla shape and color; style length; and berry color (Gourlay 1929, Ritchie 1955a, b, Stace 1975). Fruit set rarely occurs, possibly due to the production of a low percentage of viable pollen (Rousi 1966) or to self incompatibility. Any fruit which are produced contain very few seeds (Gourlay 1929). "The hybrid has been re-synthesized only when *V. myrtillus* is used as the female parent, and the progeny appear identical with the natural *V. x intermedium*. Selfed wild *V. x intermedium* produce no seeds, and of the four possible backcrosses only female *V. x intermedium* x male *V. vitis-idaea* is successful" (Stace 1975).

Artificial hybrids have been produced by crossing *V. vitis-idaea* with *V. macrocarpon* Ait. (Schultz 1944, Christ 1977, Liebster 1977), *V. ovatum* Pursh (Schultz 1944), and *V. microcarpum* (Turcz, et. Rupr.) Schmalh. (Ahokas 1979). In all instances the hybrids have been infertile. As a result of his hybridization studies, Schultz (1944) concluded that *V. vitis-idaea* is a morphologically and cytologically intermediate species between the blueberries, subgenus *Cyanococcus*, and cranberries, subgenus *Oxycoccus*.

## Factors Affecting Reproductive Growth and Development

### Pollination

A positive correlation exists between seed number and berry weight in V. vitis-idaea (Canada Dept. of Agric. 1970). Each additional seed increases berry weight by 9.1 mg. Consequently, adequate pollination will contribute to increased fruit size and yield.

The stigma and anthers develop simultaneously, and pollen is liberated primarily during early anthesis (Knuth 1909, Haslerud 1974). Germinating pollen is found on the stigmas of recently opened flowers, but cleistogamy is not apparent (Haslerud 1974). Fertilization generally occurs five days after pollination (Fernqvist 1977).

Copious quantities of nectar are produced from a disc at the base of the style. Pollination is often effected by insects harvesting the nectar (Lovell 1948, Ritchie 1955a, Pojar 1974). Bumblebees, syrphid flies, and thrips are frequent visitors throughout the flowering season (Knuth 1909, Hagerup 1954, Ritchie 1955a, b, Haslerud 1974). Entomogamy is considered by some authors to be essential for fruit production (Ritchie 1955a, Fernqvist 1977, Lehmushovi 1977a). The wide fluctuations in fruiting percentages noted annually may be due in part to insufficient numbers of insect pollinators (Lehmushovi 1977a).

Hagerup (1954) and Torrey (1914) consider anemogamy to be important in V. vitis-idaea. Damp, calm weather during the flowering season severely reduces berry yields by making pollen transport difficult or impossible (Torrey 1914). Autogamy also is possible and

and is considered by Haslerud (1974), Tikhmenev (1979), and Hagerup (1954) to be the primary mode of pollination in V. vitis-idaea. "Entomogamy is most often accidental or optional and serves only to supplement autogamy in natural populations" (Tikhmenev 1979).

Cross pollination results in significantly greater fruit set and larger berry size than self pollination (Hall and Beil 1970, Pojar 1974, Fernqvist 1977), although pollination between two separate clones in the wild occurs less frequently than within the same clone (Lehmushovi 1977a).

Temperature

Frost during the flowering season, along with rain, and severe drought can cause substantial losses of buds, flowers, and immature fruit amounting to 30-60 percent of the total plant productivity (Lehmushovi 1977a). A temperature of -1.5°C can kill 55 percent of the flowers, and -3.5°C can prevent development of an equally large percentage of fruit (Tear 1972). Temperature also influences the timing of reproductive phenophases. The stages most affected are spring growth initiation, bud swelling, and anthesis (Ritchie 1955b, Bandzaitene and Butkus 1975a). Low temperatures also may inhibit flower bud initiation as well as subsequent development (Wielgolaski 1974).

Light

Plants growing in habitats with light intensities between 10 and 25 percent of complete illumination exhibit fewer flowers and fruit

than plants growing in full sunlight (Lehmushovi and Hiirsalmi 1973, Lehmushovi 1977a, b). Berry size increases with decreasing light intensities (Lehmushovi and Hiirsalmi 1973). Ascorbic acid, glycosides, and tannin accumulate in greater quantities in berries grown in full sunlight (Gozin 1972).

Seed Germination

Seeds of V. vitis-idaea germinate within three weeks when grown between 20° and 25°C (Fernqvist 1977). Seeds fresh from the berry exhibit a conditional dormancy at temperatures below 15°C and above 30°C (Bandzaitene and Butkus 1973, Densmore 1974). The capacity to germinate at 25°C is reduced by drying the seeds for 30 days either in air or in a desiccator with $CaCl_2$. The dormancy induced by drying can be broken by one month of stratification at 2-3°C (Densmore 1974). In most instances, seeds stratified between 0° and 5°C or under natural winter temperatures for up to 5 months exhibit germination percentages and rates equal to or better than non-stratified dry seeds (Nichols 1934, Ritchie 1955b, Babb 1959, Densmore 1974, Lehmushovi 1975). Stratified seeds do not germinate as well as seeds fresh from the berry (Hall and Beil 1970, Densmore 1974).

Seeds germinate as well (Densmore 1974) or slightly better (Bandzaitene and Butkus 1973) in the light as in continuous darkness. Germination does not occur in seeds treated with 0.1 N $H_2SO_4$ for 5 minutes (Hall and Beil 1970).

Milled peat or an equal mixture of peat and sand provides the best substrate for seed germination. Sterilized filter paper, humus, unsterilized peat-sand mixture, sand, mineral soil, and heath soils are not as effective (Ritchie 1955b, Lehmushovi 1975, Fernqvist 1977).

## Cultivation of *Vaccinium vitis-idaea*

### Current Economic Status

*V. vitis-idaea* is an important fruit crop in many northern regions of the world. The major exporting countries in Europe are Sweden, Finland, and the Soviet Union, and the primary importer is Germany (Anon. 1957, Liebster 1975, 1976, 1977, Botticher 1977) (Table 6). Sweden also exports fruit to the United States, but most of this is processed rather than fresh fruit. The major source of fresh fruit in the United States is Canada (Table 7).

*V. vitis idaea* is harvested on the east coast of Newfoundland primarily on the Avalon and Bonavista Peninsulas (Hall 1978b). Production in Newfoundland for 1977 was 111,535 kg (Stark et al. 1978). This was 42,465 kg less than the 1969 production (Hall and Beil 1970). Price paid to pickers in 1977 ranged from $0.22 to $0.27 per kg (Stark et al. 1978). Approximately one-third of the crop is retained in Newfoundland for local consumption while the remainder is exported to Europe and the United States. Exports for 1976 were 37,825 kg (Hall and Beil 1970).

In 1914 berry harvesting in Newfoundland was a family enterprise with an average daily yield by hand-picking of 113.6 kg.

Table 6. European exports and imports of *Vaccinium vitis-idaea* L. (Statistical Office of the European Communities 1977, 1978, 1979).

| Country | *Vaccinium vitis-idaea* - Fresh Fruit | | | | | |
|---|---|---|---|---|---|---|
| | Amount Exported (1000 kg) | | | Amount Imported (1000 kg) | | |
| | 1977 | 1978 | 1979 | 1977 | 1978 | 1979 |
| Germany | 305 | 197 | 127 | 3473 | 1974 | 1594 |
| France | 6 | 66 | 10 | 134 | 55 | 5 |
| Italy | 3 | 5 | 7 | 28 | 15 | 28 |
| Netherlands | 99 | 84 | 50 | 185 | 151 | 99 |
| Belgium | 116 | 103 | 166 | 236 | 227 | 93 |
| United Kingdom | 4 | 47 | - | 200 | 204 | 235 |
| Ireland | 1 | 19 | - | 5 | - | 1 |
| Denmark | - | 1 | - | 168 | 110 | 89 |
| Sweden[z] | 971 | 898 | 738 | - | - | - |
| Finland[z] | 2232 | 926 | 306 | - | - | - |
| Soviet Union[z] | 493 | 146 | 463 | - | - | - |
| Norway[z] | 74 | - | - | - | - | - |

[z] Data represents exports to the other European countries listed, not world exports.

Table 7. Total imports of Vaccinium vitis-idaea L. fresh and preserved products into the United States (Foreign Agriculture Service 1980).

| Year | Total Imports (kg) | Source |
|---|---|---|
| 1945 | 447,695 | Canada<br>Finland |
| 1955 | 33,133 | Sweden |
| 1957 | 136,033 | |
| 1972 | 33,133 | |
| 1975 | 6,615 | Canada<br>Norway<br>Sweden |
| 1976 | 20,830 | |
| 1977 | 2,153 | |
| 1978 | 2,136 | Canada<br>Switzerland |
| 1979 | 1,438 | New Zealand[z] |

[z] Correspondence with J. C. Todd, Ministry of Agriculture and Fisheries, Levin Horticultural Research Centre, Levin, New Zealand, has revealed a possible discrepancy in this information. Todd is not aware of any grower or exporter of lingonberries in New Zealand.

Following a cleaning process by winnowing, the berries were packed in water in 90-liter barrels (Torrey 1914). Currently, most of the crop is still hand harvested, but in some regions a small hand rake is used (Hall 1978b). The fruit is cleaned, frozen, and exported to the United States in plastic-lined cardboard cartons.

In Nova Scotia, berries are harvested from the highlands along the sea coast. Production in Nova Scotia in 1969 did not exceed 4500 kg (Hall and Beil 1970).

Commercial harvest of V. vitis-idaea in Alaska averages less than 5000 kg annually. Three establishments, Alaska Wild Berry Products in Homer, Raven Pond Jellies in Talkeetna, and Sourdough Trading Post in Anchorage produce processed products which are sold locally, chiefly to tourists. Fresh berries are sold sporadically at farmer's markets, but currently none are exported. The fruit for processing is hand harvested from wild populations throughout Alaska, but primarily from populations on the Kenai Peninsula. Processors advertise for fruit in local newspapers beginning in late August and pay pickers from $0.78 to $1.00 per kg (Eden 1979, Richardson 1979).

In the early 1920's berries from Alaska were shipped to Seattle for $0.56 per kg, but prices were not competitive with fruit from Europe which sold in Seattle for $0.18 per kg (Moore 1958). Subsequent attempts to market fresh berries outside Alaska also have proven to be uneconomical (Marsh 1966).

Products such as sauce, preserves, candy, jelly, syrup, and pickles are processed and marketed in Japan (Iwagaki et al. 1977), throughout Europe (Anon. 1957, Liebster 1975, 1976, 1977), and in Alaska (Eden 1979, Richardson 1979, Urion 1979). In Siberia berries have been fermented and distilled with barley or rye or combined with honey to produce a wine (Munson 1901). Combinations of berries with dairy products such as yogurt have not been accepted by European consumers (Muller 1977), but lingonberry ice cream in Alaska has been successfully test marketed (Pillsbury 1958).

The leaves and stems of V. vitis-idaea are used as a source of pharmaceutical arbutin. In Rumania arbutin is manufactured by the Herbapol Company under the name Idalbina and is used to cure human intestinal disorders (Racz et al. 1962).

In the United States the plant is known commercially as an ornamental ground cover rather than a fruit crop (Rehder 1940, Wyman 1956, Hay and Synge 1974). Plants are propagated from seed or division of wild plants. No selections have been made for plant improvement.

History of Cultivation Research

V. vitis-idaea was cultivated first in 1789 (Rehder 1940) but only recently intensive efforts have been initiated to develop a high-quality horticultural fruit crop. Previously, all fruit was collected from wild populations, but urban encroachment and changes in logging practices in major fruit harvesting regions, lack of

sufficient labor force to harvest the fruit, uncontrollable fruit quality, and fluctuations in annual yields have stimulated research into methods of cultivation and plant improvement (Anon. 1957, Lehmushovi and Sako 1975, Botticher 1977).

The first cultivation experiments in Finland began in 1968 at the Institute of Horticulture in Piikkio (Lehmushovi and Hiirsalmi 1973, Liebster 1975). These experiments showed that plants growing in cultivated fields could yield nearly five times those growing in the wild (Liebster 1975). Research was intensified in 1971 by Aaro Lehmushovi, Heimo Hiirsalmi and Jaakko Sako, and permanent plantings were established to determine the economic feasibility of V. vitis-idaea cultivation in Finland (Liebster 1975).

Concurrent with the Finnish trials, research was begun in Sweden by Jaan Tear and the Novia Food Corporation (formerly AB Bjare Industries). Initial research emphasized the study of wild plant ecology and reproductive potential (Tear 1972). The first cultivated field plantings were developed in 1971 on a farm near Ottarp and consisted of approximately 5 ha of plants (200,000 plants per ha) transplanted from wild populations. Other field plantings have since been developed including those initiated by Ingevald Fernqvist at the Horticultural Research Station in Alnarp (Fernqvist 1977).

Research with V. vitis-idaea in Alaska was begun in 1965 by Arvo Kallio at the Agricultural Experiment Station, Fairbanks. Initial experiments involved fertilization of wild populations to determine if fruit yield and vegetative growth could be improved. The experiments

were terminated in 1967, and research was not resumed until the present study was initiated in 1977.

In Canada, most work with V. vitis-idaea has occurred at the Agriculture Canada Research Station in Kentville, Nova Scotia and the Department of Forestry and Agriculture in St. Johns, Newfoundland (Torrey 1914, Hall 1978a, b, Stark et al. 1978). Superior clones collected from wild populations by I. V. Hall (1978a) were established in test gardens at Kentville in 1977 to evaluate their potential for commercial production.

Work in Germany was begun by G. Liebster (1975, 1976) at the Technical University of Munich in Weihenstephan in 1973. Cultivation methods for both V. vitis-idaea and V. macrocarpon were studied to determine the economic potential of each as a cultivated horticultural fruit crop in Germany.

## Cultivation Experiments

### Substrates

In Finland, milled peat provides a better substrate than sand or a 1:1 mixture of sand and peat for growth and fruit production in cultivated fields. Growth is poorest on a sand substrate (Hiirsalmi and Lehmushovi 1972, Lehmushovi and Hiirsalmi 1973, Lehmushovi 1977b). Trials in Sweden have shown that the best substrate is sandy, acidic (pH 5-6) soil with at least a 2 percent organic matter content (Fernqvist 1977). Trials in Finland have shown that mulching increases fruit yields both in cultivated fields and in wild stands.

In a comparison of sand, milled peat, gravel, and straw mulches, and unmulched mineral soil, sand promoted the greatest fruit yields in cultivated fields (Lehmushovi and Sako 1975, Lehmushovi 1977a). In wild stands plants mulched with milled peat produced a greater berry yield and size than those mulched with sawdust, bark humus, tree bark, sand, or straw (Lehmushovi 1977b).

Irrigation

Observations on cultivated fields in Sweden show that irrigation, particularly in May and June, is necessary for plant establishment and good vegetative growth (Fernqvist 1977).

Fertilizers

Because of the relatively low mineral nutrient requirements of V. vitis-idaea, Ingestad (1973) recommended that fertilization be frequent using small quantities of fertilizer over an extended period of time. In order to verify this recommendation, Fernqvist (1977) applied six treatments of ammonium nitrate and ammonium sulfate (1:1) fertilizer in concentrations from 1.5 to 12.0 g of N per $m^2$ to cultivated fields. He found that shoot growth, yield, and berry weight decreased with increasing nitrogen. In earlier trials using pot cultures Oster (1974) found that 5-10 g of N per $m^2$ positively influenced V. vitis-idaea growth only on nutrient deficient sandy soils. In conclusion, Fernqvist (1977) stated that mineral nutrition of cultivated V. vitis-idaea may be a growth limiting factor on very poor soils, but fertilizer needs, in general, are very small.

On cultivated fields in Finland, application of a 11-11-22 fertilizer at 10 kg per are increased fruit yield but decreased berry size (Lehmushovi and Hiirsalmi 1973). The increase in shoot growth caused by fertilization is very slight (Lehmushovi 1977b). Fruit yield in wild populations is improved substantially with fertilization (Lehmushovi 1977a). However, if these populations contain appreciable quantities of grasses and broad-leaved herbs, V. vitis-idaea often disappears from the area due to competition with the other plants which also benefit from fertilization (Kallio 1965, Lehmushovi 1977a).

Weed Control

Fernqvist (1977) recommends an autumn application of terbacil, glyphosate, MCPA, or dichlobenil, or a spring application of Venzar, simazine, linuron, or terbacil for weed control in V. vitis-idaea plantings. Venzar, linuron, and simazine provide selective control against annual weeds, while MCPA and dichlobenil are effective against perennial weeds. Lehmushovi (1977b) reports effective control of grasses with maleic hydrazide. Terbacil and atrazine also provide good weed control, but amitrole causes plant injury.

Insect, Disease, and Animal Pests

Insects

The most destructive insect pest found in wild populations of V. vitis-idaea is a small fruitworm observed in Newfoundland (Torrey 1914, Wood 1979) and by the author in Alaska. Larvae collected from

Newfoundland populations "... are about 7-9 mm in length, pinkish-brown in color and emerge from the berry in late September...the larva spins a loose web in the late fall and apparently does not pupate until the following spring. Tentative identification keys the larva to the family Olethreutidae, possibly to the genus Epinotia Hubner. Another attempt keyed it to Grapholitha sp. also of the family Olethreutidae" (Wood 1979).

An unknown insect attacks the flowers prior to anthesis by cutting a small hole at the base of the corolla and destroying the pistil and stamens. Its occurrence is rare in Newfoundland (Torrey 1914) and Alaska (Holloway, unpublished).

The gall mite, Phyllocoptes vitis-idaea Roiv. (Roivanen 1949) and several microlepidoptera (Michaelis 1963) have been observed on the leaves of V. vitis-idaea, but in most instances damage in wild stands is not extensive. The insects found on V. vitis-idaea in the British Isles are summarized by Ritchie (1955b).

Diseases

Pathogenic microorganisms associated with V. vitis-idaea are summarized by several authors (Torrey 1914, Kujala 1950, Ritchie 1955b, Eglitis et al. 1966, Gjaerum and Langnes 1969, Ericksson 1970, Gourley 1979a, b). Exobasidium vaccinii (Fckl.) Wor. is common in wild populations of V. vitis-idaea in Alaska (Eglitis et al. 1966), particularly during wet growing seasons. Although it is found on V. angustifolium and V. macrocarpon plants growing in Newfoundland,

it has not been reported on V. vitis-idaea in that region (Gourley 1979a). Exobasidium vaccinii also is found on wild plants growing in Sweden, but it has not been a problem in cultivated fields (Fernqvist 1977).

Two leaf-spot fungi, Lophodermium hypophyllum (Dearn. et. House) Sear and L. melaleucum (Fr. et. Fr.) DeNot. are common in wild populations in Alaska and Newfoundland respectively (Eglitis et al. 1966, Gourley 1979a). An unknown fungus causing leaf-spot and abscission causes severe damage in cultivated fields in Sweden (Fernqvist 1977). Repeated applications of Benomyl are effective in reducing its occurrence. Another leaf-spot disease, Mycosphaerella stemmatea, is reported from Sweden, but it causes minor damage in cultivated fields (Fernqvist 1977).

Three other diseases, Sclerotinia sp., which causes mummy berries; an unknown organism which causes stem canker; and another which causes stunted growth and sterility, have been observed frequently in cultivated fields in Sweden (Fernqvist 1977). One other disorder known as club shoot disease has been described on V. vitis-idaea and V. pennsylvanicum in Newfoundland. Bright pink club shoots are produced from basal buds in a witches' broom-type growth pattern. Stem length is nearly double that of healthy stems (Torrey 1914).

Gourley (1979a) studied the fruit rot pathogens isolated from both healthy and diseased berries collected from wild stands in Newfoundland. These isolated microorganisms are listed in Table 8.

Table 8. Microorganisms and their occurrence from surface sterilized healthy and diseased fruit of lingonberry, Vaccinium vitis-idaea L. on two artificial media (Gourley 1979a).

| Microorganisms | Frequency (%) | | | |
|---|---|---|---|---|
| | Healthy | | Diseased | |
| | PDA[z] | 2%M[y] | PDA | 2%M |
| Alternaria sp. | 31 | 13 | 2 | |
| Aureobasidium pullulans | 31 | 13 | 12 | 16 |
| Bacterium sp. | | 13 | 2 | 4 |
| Botrytis cinerea | | | 2 | |
| Coniochaeta sp. | | 13 | 2 | 14 |
| Curvularia clavata | 6 | | | |
| Epicoccum nigrum | 6 | | | |
| Fusicoccum putrefaciens | 19 | 13 | 2 | 4 |
| Gelatinospora tetrasperma | | | 5 | 2 |
| Geotrichum candidum | | | | 2 |
| Hamigera striata | | 6 | | |
| Mortierella ramanniana var. ramanniana | | | 4 | |
| Penicillium clavariforme | | 13 | 4 | |
| Penicillium thomii | | | 11 | 10 |
| Penicillium spp. | 6 | 6 | 2 | 4 |
| Phialophora sp. | | | 2 | |
| Pleospora herbarum | | 13 | | |
| Sporonema oxycocci | | 19 | 7 | 6 |
| Stagnospora sp. | | | 2 | |
| Sterile | 38 | 13 | 37 | 37 |
| Verticillium sp. | | | | 2 |
| Other | 19 | 25 | 25 | 10 |
| Number of fruit | 16 | 16 | 57 | 51 |

[z] Potato Dextrose Agar

[y] 2 percent Malt

Three of the fungi isolated from V. vitis-idaea also cause fruit rot in V. macrocarpon. One of these fungi, Sporonema oxycocci Shear, is the principal cause of storage rot in V. macrocarpon in Nova Scotia (Gourley 1979 a).

Animals

V. vitis-idaea is an important food plant for wildlife. The foliage and berries compose part of the diet of willow grouse (Pulliainen and Salo 1973), rock ptarmigan (Pulliainen 1970, Bossert 1976), arctic hare (Pulliainen 1972), black bear (Halter 1972), and caribou and moose (Oldemeyer and Seemel 1976). Few problems are encountered at wild sites where most berries currently are harvested, but with cultivation, an easily accessible food supply may help to create a problem that could reduce berry yields substantially.

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# SEASONAL PATTERNS OF REPRODUCTIVE AND VEGETATIVE GROWTH IN FOUR ALASKAN POPULATIONS OF LINGONBERRIES


## Abstract

A study of seasonal growth sequences was made on four populations of lingonberries growing near Fairbanks, Alaska. Reproductive bud growth began in mid May, with full bloom occurring one month later. Full bloom lasted 19-27 days. Fruit ripening occurred 78-84 days after full bloom. The greatest increase in berry size occurred from late June to mid July. The timing of phenophase development was similar among the four populations. Correlations between seed number and berry weight were highly significant ($r = +.44 - +.51$) in three populations. For each additional seed, berry weight was increased by 4.2 - 7.2 mg.

Floral primordia first appeared in buds collected in late June. By September ovules were present in the proximal florets, but the integument and female gametophyte were not differentiated. The anthers were inverted, but the apical awn and pore were not present. Sporogenous tissue was not differentiated. Rare exceptions to this pattern were noted.

Seasonal losses of flowers or fruit ranged from 36 to 94 percent. Hail damage accounted for some of these losses. Others may be related to a lack of insect pollinators. Fruit set and size were significantly lower in plants caged to exclude insects than in open-pollinated plants.


## Introduction

Ecological and floristic surveys throughout arctic to north-temp-

erate regions often include the lingonberry, Vaccinium vitis-idaea L., since it is an abundant sub-shrub in a diversity of plant communities (Hulten 1970). Few studies deal specifically with the lingonberry. Consequently, little is known about the seasonal growth and development patterns of this plant. Research on plant communities in British Columbia by Pojar (1974) includes descriptions of the reproductive biology and pollination ecology of lingonberries. Similar studies were reported by Ritchie (1955a,b) in the British Isles. Phenological studies, particularly in the Soviet Union, have outlined the seasonality of certain vegetative and reproductive events in the growth cycle of lingonberries (Torrey 1914, Hadley and Bliss 1964, Kuriganova 1972, Dimitrovski 1973, Wielgolaski 1974, Bandzaitene and Butkus 1975, Snigrev and Khvesko 1978). No comparable studies have been reported for lingonberry populations in Alaska.

The purpose of this research was to detail sequences of growth and development of four Alaskan populations of lingonberries and attempt a more inclusive summary of events transpiring during the growing season. Emphasis was placed on reproductive biology with additional studies on pollination ecology and vegetative growth.

## Materials and Methods

Phenology. Observations on the seasonality of reproductive and vegetative growth were made on four populations of lingonberries located near Fairbanks, Alaska. The Chena I and Chena II sites comprised two separate populations of lingonberries, 10 m apart, located approximately 0.5 km west of the Chena River near the Chena Pump Road.

The third lowland site was located on the southeastern edge of Smith Lake near the University of Alaska. The single upland site was located at 1.6 km Gilmore Trail. Specific site characteristics are listed in Table 1.

One plot, 4 $m^2$, was selected at random from each population. Fifty vegetative and 50 reproductive stems were selected by stratified random sampling within each plot. Seven reproductive phenophases were identified and observations on their seasonal progression were made every three days throughout the growing season. The phenophases were defined as follows:

1. Tight bud- no visible bud growth;
2. Loose Bud- buds beginning to expand, individual florets barely perceptible, corolla apex dark red;
3. Pink bud- racemes elongated, individual florets distinct with corolla expanded but not open, corolla pink or white;
4. Full bloom- corolla fully expanded, stigma protruding from corolla aperture;
5. Petal fall- loss of corolla;
6. Green fruit- visible enlargement of ovary, exocarp green or red;
7. Ripe fruit- exocarp color, burgundy.

Throughout the growing season data were collected on the number of flowers and/or fruit per stem. The diameter of the proximal fruit was measured with calipers. Following the 1978 growing season, 90 ripe berries taken at random from each site were individually weighed, and

the number of seeds per berry counted. The relationship between seed number and berry weight was analyzed using the correlation coefficient and regression analysis.

The seasonality of vegetative growth was observed by measuring the length of the terminal bud growth on each of the 50 vegetative stems per plot. Measurements were made with calipers from the base of the bud scale scar to the base of the youngest emerging leaf or to the base of the newly-formed apical bud. The number of new leaves per shoot was recorded on August 31.

Taylor minimum-maximum thermometers were placed at plant level at each site, and daily air temperatures were recorded during the growing season. Observations were made throughout the 1978, 1979, and 1980 growing seasons. The random selection of vegetative and reproductive stems was repeated at the beginning of each season. Because the observations were begun during the pink bud stage of development in 1978, data are incomplete for that season.

Flower bud differentiation. At the Chena I site, ten terminal buds were collected twice weekly during the growing season to determine the timing of reproductive bud differentiation and floral development. Buds were immediately fixed in Carnoy's Solution and stored at $1^{o}C$ for two months. Buds were dehydrated in Sass' Tertiary Butyl Alcohol Series, embedded in paraffin, sectioned with a microtome to 9 or 11 micron thickness, and stained with safranin and fast green (Sass 1940, Berlyn and Miksche 1976).

Insect pollination study. At the Gilmore Trail site in 1979 and the Chena I site in 1979 and 1980, portions of a population of lingon-

berries were enclosed in insect exclusion cages to study the effects of insect pollination on fruit set and development. An area 200x130 cm in size was randomly selected from a single, uniform population of lingonberries. This plot was subdivided into six, 60x60 cm treatment sections with 10 cm separating adjacent treatments. Twenty stems selected at random within each section comprised the treatment unit. Wooden frames, 60x60x30 cm in length, width, and height respectively, were covered with mosquito netting and were randomly placed on half of the treatment units. The cages were placed over the lingonberries immediately prior to anthesis and were removed upon completion of petal fall. Control plots were not covered with frames or netting. The experiment consisted of two treatments (caged and open-pollinated) and three replicates in a completely randomized design with subsampling. Different populations in the same locality comprised the experimental unit at the Chena I site in 1979 and 1980.

During the 1979 growing season, Taylor minimum-maximum thermometers were randomly placed at plant level in both treatments, and daily air temperatures were recorded until the cages were removed at petal fall. Light intensity was measured at plant level in both treatments with a LI-COR Model LI-185 Quantum/Radiometer/Photometer.

The number of flowers per stem was counted prior to anthesis. Ripe fruit were counted and weighed with the number of seeds per berry counted, and the fruit diameter measured with calipers. In 1979, fruit were harvested at both sites on September 1, while the 1980 harvest occurred on August 28. Data were analyzed with the analysis of variance and Duncan's New Multiple Range Test at the 1 and 5 per-

cent levels.

Results and Discussion

Phenology. Visible reproductive bud growth was first evident at all sites during mid May. The seasonal progression was uniform across sites and years through the loose bud stage (Table 2). Fully elongated racemes with unopened corollas, characteristic of the pink bud stage, were present at all sites during the first week of June. Maximum full bloom occurred approximately six weeks after snow melt and four weeks after visible growth began. The timing of maximum full bloom differed by no more than 9 days at all sites during the three seasons. Full bloom lasted from 19 to 27 days; the duration being slightly longer at the Smith Lake and Gilmore Trail sites. There was considerable overlap among pink bud, full bloom, and petal fall phenophases. Visible ovary enlargement was observed in the oldest fruit at the base of the raceme, while the youngest florets at the raceme apex were just beginning anthesis. The major flowering period ended in early July. Additional flowering was observed at the Chena I and Chena II sites in mid to late August, but its occurrence was sporadic. No fruit resulted from this late-summer flowering.

Fruit ripening occurred from 78 to 84 days after full bloom (Table 2). Fruit color was green, and berries that were exposed to direct sunlight, particularly at the Smith Lake site, were red on upper surfaces during July and early August. The exocarp became progressively more red, and in late August berries at all sites were uniformly bright red. During ripening, the red color darkened to burgundy. Ripening occurred within a two-week period, generally beginning on September 1.

Measurable increases in the diameter of the proximal fruit were recorded while the younger florets were still in the pink bud stage of development. Corolla and stamen abscission occurred simultaneously, followed in 2-5 days by pistil abscission. The calyx remained permanently attached to the fruit. A rapid increase in berry diameter occurred from petal fall to mid July (Figure 1). The increase in size during this stage was greater than in any other period of fruit maturation. By mid July, fruit at all sites had attained at least 50 percent of their total diameter. Ninety percent of the fruit diameter had been attained by early August, approximately one month prior to fruit ripening (Table 3). Mature fruit at the Chena I site were slightly larger than those at the other three sites (Table 3). Fruit at all sites were smaller in 1978 than in 1979 and 1980.

Phenophase development occurred 3-6 days later at the Gilmore Trail site than at Chena I, II, and Smith Lake (Table 2). This delay may be related to the slightly cooler maximum air temperatures at the Gilmore Trail site (Table 4). The maximum development of each phenophase also occurred later in 1978 than during 1979 and 1980. This delay also may be related to cooler, early-season air temperatures; however more than three seasons of data will be necessary to determine specific correlations between phenophase seasonality and air temperature.

Our observations are similar to those by other researchers who have shown that the major flowering season of lingonberries growing throughout a wide range of latitudes and altitudes extends from late May through early July with maximum flowering in June. Fruit ripening occurs in early September (Ritchie 1955b, Hadley and Bliss 1964, Kolu-

paeva 1972, Kuriganova 1972, Dimitrovski 1973, Pojar 1974, Bandzaitene and Butkus 1975, Anonymous 1977, Snigrev and Khvesko 1978). One exception is the observations in Newfoundland by Torrey (1914) who recorded flowering in July and fruit ripening in October. Bandzaitene and Butkus (1975) and Ritchie (1955b) also mention a second, late-summer flowering season. This flowering season is less intense and does not result in ripe fruit (Bandzaitene and Butkus 1975).

Plants at the Chena II site averaged slightly greater numbers of flowers per stem than plants at the other three sites (Table 3). The Smith Lake population had the lowest number of flowers per stem. Despite these differences all sites had very few ripe fruit at the end of the growing season. Seasonal losses of flowers or fruit began during the pink bud stage of development and proceeded rapidly during June and July (Figure 2). The greatest proportion of losses occurred prior to July 31 at all sites. Losses ranged from 36 percent at the Chena I site in 1979 to 94 percent at the Gilmore Trail and Smith Lake sites in 1979 and 1980 respectively. With the exception of the Chena I site in 1979, losses of greater than 50 percent were recorded at all sites during the three years of observation.

Total losses of flowers or fruit were slightly lower for each year at the Chena I site than at all other sites. Losses were not uniform across sites for each growing season. For instance, in 1979 a loss of 36 percent was recorded at the Chena I site. During that same year, a loss of 94 percent was recorded at the Gilmore Trail site. At the Chena II site, the highest loss occurred during the 1978 season, while at Smith Lake the highest loss occurred during the 1980 season.

Similar results have been reported in other regions by Torrey (1914), Hall and Beil (1970), Kolupaeva (1972), and Lehmushovi (1977). Losses of fruiting potential have been attributed to low fruit set possibly caused by inadequate pollination (Fernqvist 1977), self pollination (Hall and Beil 1970, Fernqvist 1977), and cold temperatures, rain, or drought during anthesis (Tear 1972). The only direct cause we observed for the loss of flowers and immature fruit was hail damage. Hail storms on June 15, 1978 at the Chena I site and on July 4, 1979 at the Gilmore Trail site contributed to immediate losses of up to 40 and 35 percent respectively. Possibly because of greater tree cover, losses at the Chena II site in 1978 were lower than at Chena I. At the Gilmore Trail site, a considerable number of immature fruit were scarred by hail, and premature abscission was common. This damage may have been the major cause of the 94 percent loss of fruiting potential during the 1979 season.

Correlation between seed number and berry weight. Seed number and berry weight were highly correlated in three of the four lingonberry populations (Table 5). For each additional seed, berry weight was in creased by 7.2 mg in the Chena II population, 6.8 mg in the Gilmore Trail population, and 4.2 mg in the Smith Lake population. These data are similar to a Canadian study which found that each additional seed increased the weight of the berry by 9.1 mg (Canada Dept. of Agric. 1970). Although, in general, the largest berries had the most seeds, this relationship did not hold for the Chena I population. Berries from the Chena I site had an average seed count per berry that was more than double the counts at the other three sites. The maximum

seed count and berry weight also were greater for the Chena I population. Pooling data from all four populations resulted in a highly significant (P = .01) correlation coefficient of +.52 between seed number and berry weight. These data suggest that for most natural populations of lingonberries, large berry size will result from fertilization of the maximum number of ovules. Promotion of adequate pollination probably will be important. However, it should be possible, through breeding and selection, to develop lingonberries with good fruit size and fewer seeds. This attribute may be advantageous in years of poor pollination intensity.

Flower bud differentiation. The first flower primordia were observed on buds collected on June 20, 1978, June 22, 1979, and June 26, 1980. Prior to these dates, all buds had meristems which were small, rounded mounds in the axils of the cataphylls. In late June the meristem apices became flattened, and sepals, petals, stamens, and carpel appeared rapidly (Figure 3a,b). The growth sequence was similar to that described for the cranberry by Roberts and Struckmeyer (1943), and for the blueberry by Bell and Burchill (1955a),Aalders and Hall (1964), Stushnoff and Palser (1969), and Gough and Shutak (1978). Stems which had differentiated flower buds during the previous growing season were in the late full bloom and petal fall phenophases when new primordia were differentiated (Table 2). Growth on non-flowering stems had climaxed, and the rate of stem elongation was beginning to decrease (Figure 4).

The timing of flower differentiation was variable among stems. Less than half of the buds collected had developed floral structures on

the dates given above, but by the first week of July, all of the sample buds showed some stages of floral development. Differences also occurred within a raceme. Development was acropetal (Figure 3c). The third floret from the base was approximately 8-10 days later in development than the proximal floret.

In mid July, sepals, petals, stamens, and carpel were present in all of the proximal florets (Figure 3d). The pistil was one-third to one-half its final length at the end of the growing season. The four placentae were visible as mounds of darkly-staining meristematic tissue, and the anthers had begun to invert. By the end of July, ovules were present as barely perceptible mounds on the placentae. The anthers continued to elongate in both acropetal and basipetal directions, and separate lobes became evident. Externally, the flower buds were at least 1.0 mm in width and obovate in shape. The oblong-ovate vegetative buds averaged less than 0.5 mm in width.

In mid August, ovules were present on all of the proximal florets (Figure 3e). The anthers continued to elongate, but the apical awn and pore were not evident. In 90 percent of the flower buds, development of the proximal floret proceeded nor further through the end of September. Younger florets continued to develop, but only the lower two or three florets reached the stage of the oldest floret. Externally, in mid August, the entire flower bud had enlarged to an average width of 2.0 mm. Vegetative buds were less than 1.0 mm in width. The entire reproductive bud also began to bend so that by mid September, the bud was nearly perpendicular to the stem.

In general, the stage at which reproductive buds entered winter

rest was similar to that described for lingonberries by Bell and Burchill (1955b). Ovules were present in the proximal florets, but the female gametophyte and integument were not differentiated. Palser (1961) found that the anthers normally over-winter in the microspore mother cell stage, while Bell and Burchill (1955b) observed that the sporogenous tissue may or may not be differentiated. In our study, the sporogenous tissue was not differentiated.

With the exception of two buds collected on August 18, 1979 and August 10, 1978, all flower buds exhibited the above development pattern. The two exceptions had fully-developed pollen tetrads in mature anthers (Figure 3f). These flower buds may be related to the late-summer flowering mentioned earlier. Because the entire developmental sequence was not observed, it is not known whether these buds were initiated during the current or previous growing seasons.

Insect pollination study. Fruit set differed significantly between caged and open-pollinated treatments in all three experiments (Table 6). At the Chena I site during 1979 and 1980, fruit set in the open-pollinated treatment averaged nearly 40 percent, whereas caged plants had less than 10 percent fruit set. Results were similar at the Gilmore Trail site, although the overall set was considerably lower. Treatments also differed in berry size as measured by berry diameter and fresh weight. Plants that were open-pollinated produced significantly larger fruit with greater number of seeds per berry than plants that were caged.

This experiment has shown that lingonberries are entomophilous. These data agree with observations by Ritchie (1955a), Fernqvist (1977),

and Lehmushovi (1977) who consider entomogamy essential for fruit production. Our results do not support the research of Haslerud (1974), Tikhmenev (1979), and Hagerup (1954) who believe that autogamy is the primary mode of pollination in lingonberries. Hagerup (1954) and Tikhmenev (1979) stated that entomogamy is accidental and only serves to supplement autogamy in natural populations. Hagerup (1954) and Torrey (1914) also consider anemogamy to be important in lingonberries, attributing low fruit set to damp, calm weather during anthesis.

In our study, the importance of anemogamy probably is minor. Both lingonberry populations were located in forest communities and were sheltered from wind. The only visible movement of racemes during anthesis was caused by the contact of bumblebees and honeybees. In addition, lingonberry pollen is released as a tetrad and is heavy and sticky (Oldfield 1959). These conditions do not favor anemogamy. Perhaps in more open communities, such as those studies by Hagerup (1954) in arctic North America, anemogamy may be of greater importance.

The fruit set which occurred in caged plants probably is the result of autogamy. The difference in fruit size between treatments may be related to self versus cross pollination. Hall and Beil (1970) and Fernqvist (1977) found that cross pollination resulted in greater fruit set and larger berry size than self pollination. In addition, differences in fruit size may be related to differences in seed number per berry. We showed earlier that, at least in some populations, fruit size is related to the number of seeds per berry. Plants in the open-pollinated treatment at the Chena I site had significantly greater

numbers of seeds per berry than plants in the caged treatment.

The effect of air temperature and light intensity differences between caged and open-pollinated treatments on fruit set and size was considered minimal. Air temperatures did not differ by more than $1^{o}C$ between treatments during the time when the cages were in place. Because of uneven cover by trees and shrubs, the light intensity within the treatment area was variable, ranging from 10 to 60 percent of complete illumination. Although the average percent shade was increased by 5 percent in the caged treatments, the amount of shade was within the range of variability encountered in the open-pollinated treatments.

Vegetative growth. Measurable growth of terminal vegetative buds began during the first week of June, approximately four weeks after snow melt (Figure 4). Growth in length was rapid during June. By July 1, the growth rate had decreased perceptibly at all sites. Fifty percent of the total stem growth occurred by the second week of June at the Chena II and Gilmore Trail sites; by the third week at the Chena I site; and by the fourth week at the Smith Lake site (Table 7). Growth was most rapid at the Gilmore Trail site. The number of days from 50 to 90 percent total stem growth was 9 and 18 respectively for the 1980 and 1979 growing seasons. At all other sites, as many as 68 days elapsed between 50 and 90 percent stem growth, but there was considerable variation from year to year. In 1980, at the Chena II and Smith Lake sites, 8 days were recorded between 50 and 90 percent stem growth, while in 1979, 63 days elapsed between these same percentages. Growth at the Chena I site was more uniform for each year, having from 56 to 68 days between 50 and 90 percent total stem growth.

Final stem length was greater at the Gilmore Trail site than at

the other three sites (Figure 4). These differences may be related to the percent shade at each site (Table 1). Earlier studies (Holloway and Dinkel, unpublished) revealed a highly significant correlation ($r = +.98$) between plant height and shade in native Alaskan populations of lingonberries.

Leaf expansion began during the last week of May and the first week of June. Approximately one month later, all new leaves had expanded and a new terminal vegetative bud was present. The number of leaves produced on terminal vegetative stems was uniform across sites and years. Averages differed by fewer than three leaves at all sites during the three growing seasons. Within each site, differences were less than one leaf per stem (Table 7).

The sequences of stem elongation and leaf expansion were similar to those reported by Hadley and Bliss (1964), Kuriganova (1972), and Wielgolaski (1974). One exception to this general pattern of vegetative growth was reported for lingonberries growing in the British Isles (Ritchie 1955b) where leaf expansion can begin as early as March.

Conclusion. The growing season for lingonberries extended from mid May to early September. Major growth sequences including anthesis, floral primordia differentiation, and maximum vegetative stem elongation occurred in June. The timing of phenophase development was similar among sites, although events appeared to be a few days later at the upland, Gilmore Trail site. One common factor among sites was the substantial loss of fruiting potential during the growing season. Some losses were related to hail damage, but a significant

proportion probably were related to a lack of insect pollinators during anthesis. Both fruit set and size were influenced by insect pollination.

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Table 1. Characteristics of four lingonberry sites located near Fairbanks, Alaska.

| Site | Forest type[z] | Elevation (m) | Slope (%) | Aspect | Shade (%) | Soil type[y] |
|---|---|---|---|---|---|---|
| Chena I | Bottomland spruce-hardwood forest. Evergreen forest with cylindrical crowns. White spruce-black spruce-feathermoss. | 128 | 2 | SE | 35 | Salchaket very fine sandy loam |
| Chena II | same as Chena I | 128 | 2 | SE | 45 | Salchaket very fine sandy loam |
| Gilmore Trail | Upland spruce-hardwood forest. Deciduous forests and woodlands. Aspen type. | 413 | 20 | S | 75 | Fairbanks silt loam moderately deep, 20-30% slope |
| Smith Lake | Lowland spruce-hardwood forest. Evergreen needle woodland with narrow cylindrical-conical crowns. | 149 | 3 | NW | 10 | Goldstream silt loam, 0-3% slope |

[z]From Nieland and Viereck 1977.

[y]From Rieger et al. 1963.

Table 2. Phenophase development of four lingonberry populations located near Fairbanks, Alaska.

| Site | Year | Date of maximum phenophase development | | | | | Number of days | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Loose bud | Pink bud | Full bloom | Petal fall | Ripe fruit | Full bloom | Full bloom to ripe fruit | Ripe fruit |
| Chena I | 1978 | -[z] | 6-15 | 6-18 | 7-3 | 9-7 | - | 81 | 10 |
| | 1979 | 5-22 | 6-3 | 6-12 | 6-30 | 9-1 | 22 | 81 | 8 |
| | 1980 | 5-25 | 6-9 | 6-15 | 6-21 | 9-1 | 19 | 78 | 9 |
| Chena II | 1978 | - | 6-15 | 6-15 | 7-3 | 9-7 | - | 84 | 9 |
| | 1979 | 5-22 | 6-3 | 6-12 | 6-30 | 9-1 | 23 | 81 | 9 |
| | 1980 | 5-25 | 6-6 | 6-12 | 6-18 | 9-4 | 22 | 84 | 7 |
| Gilmore Trail | 1978 | - | 6-18 | 6-21 | 7-9 | 9-13 | - | 84 | 10 |
| | 1979 | 5-28 | 6-6 | 6-18 | 7-3 | 9-7 | 24 | 81 | 9 |
| | 1980 | 5-28 | 6-9 | 6-18 | 6-27 | 9-7 | 25 | 81 | 10 |
| Smith Lake | 1978 | - | 6-15 | 6-18 | 7-3 | 9-10 | - | 84 | 12 |
| | 1979 | 5-25 | 6-3 | 6-12 | 6-30 | 9-1 | 27 | 81 | 9 |
| | 1980 | 5-25 | 6-6 | 6-15 | 6-18 | 9-1 | 26 | 78 | 8 |

[z]Data not available.

Figure 1. Seasonal patterns of cumulative growth in fruit diameter of four Alaskan populations of lingonberries.

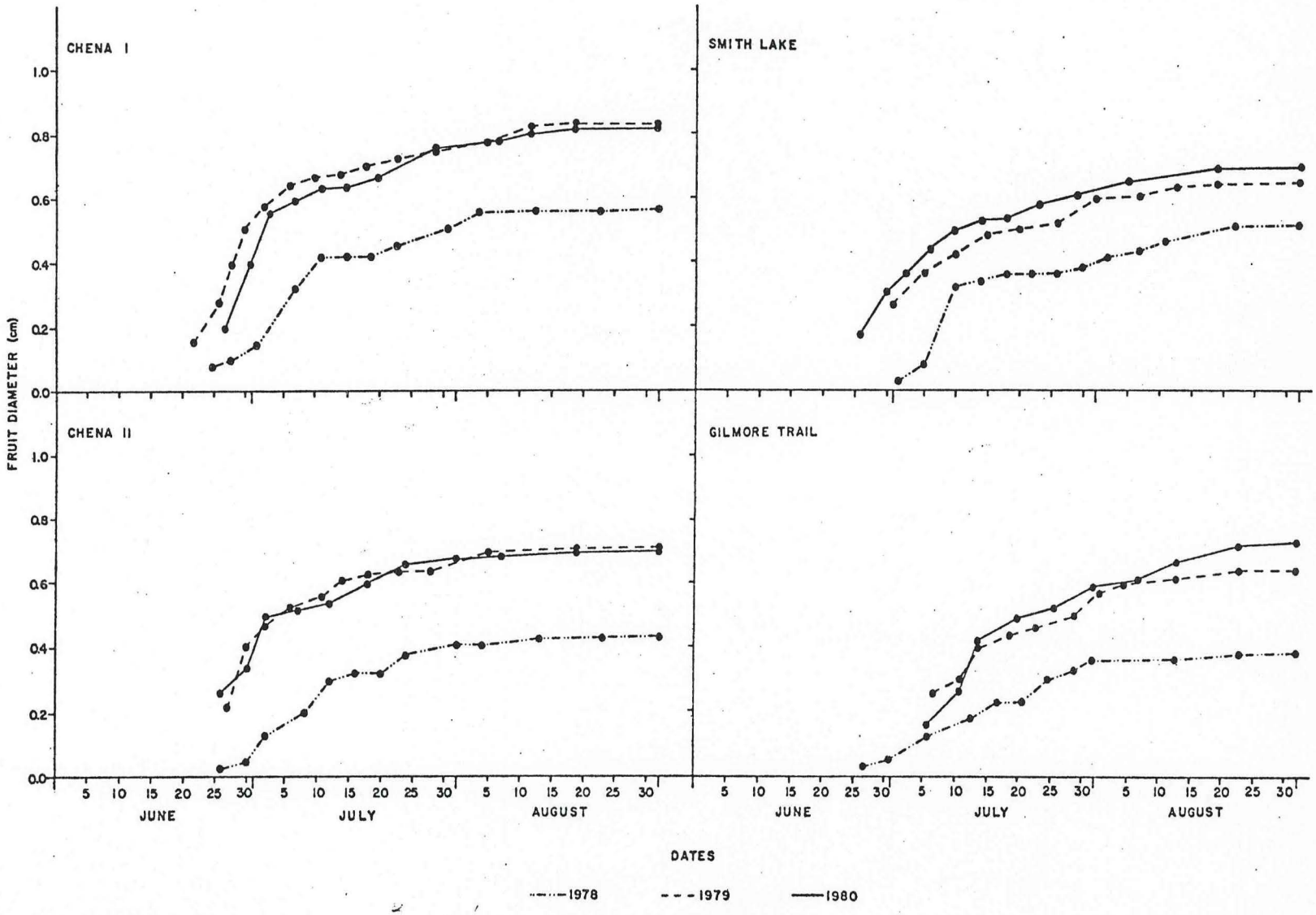

CHENA I
SMITH LAKE
CHENA II
GILMORE TRAIL
FRUIT DIAMETER (cm)
0.0
0.2
0.4
0.6
0.8
1.0
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUGUST
DATES
1978
1979
1980

Table 3. Flowering and fruit characteristics of four Alaskan populations of lingonberries.

| Site | Year | Average number per stem | | Average ripe berry diameter (cm) | Date of percent total fruit diameter | |
|---|---|---|---|---|---|---|
| | | Flowers | Ripe fruit | | 50 | 90 |
| Chena I | 1978 | 5.2 ± 2.7 | 1.8 ± 1.1 | 0.56 ± 0.13 | 7-5 | 7-31 |
| | 1979 | 6.1 ± 2.0 | 3.9 ± 2.1 | 0.84 ± 0.09 | 6-28 | 8-1 |
| | 1980 | 5.3 ± 4.0 | 1.9 ± 1.2 | 0.83 ± 0.01 | 7-1 | 7-28 |
| Chena II | 1978 | 8.3 ± 5.6 | 1.7 ± 0.8 | 0.43 ± 0.13 | 7-9 | 7-26 |
| | 1979 | 7.4 ± 3.3 | 2.6 ± 1.6 | 0.71 ± 0.07 | 6-29 | 7-23 |
| | 1980 | 6.8 ± 6.0 | 2.1 ± 2.0 | 0.70 ± 0.01 | 6-30 | 7-20 |
| Gilmore Trail | 1978 | 5.4 ± 2.0 | 1.5 ± 0.8 | 0.36 ± 0.10 | 7-13 | 7-29 |
| | 1979 | 5.9 ± 1.9 | 0.4 ± 0.2 | 0.64 ± 0.06 | 7-12 | 8-2 |
| | 1980 | 4.7 ± 4.0 | 0.7 ± 0.9 | 0.73 ± 0.01 | 7-13 | 8-12 |
| Smith Lake | 1978 | 3.4 ± 1.5 | 1.0 ± 0.6 | 0.51 ± 0.10 | 7-9 | 8-11 |
| | 1979 | 4.3 ± 1.6 | 1.0 ± 0.9 | 0.69 ± 0.10 | 7-2 | 7-31 |
| | 1980 | 3.2 ± 2.2 | 0.2 ± 0.1 | 0.64 ± 0.01 | 7-4 | 7-31 |

Table 4. Average monthly air temperatures at four lingonberry sites located near Fairbanks, Alaska.

| Site | Year | Average maximum temperature (°C) | | | | | Average minimum temperature (°C) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | May | June | July | August | September | May | June | July | August | September |
| Chena I | 1978 | -[z] | 19.4 | 26.1 | 22.5 | 13.9 | - | 5.0 | 8.2 | 5.7 | 0.8 |
| | 1979 | 22.8 | 23.7 | 25.0 | 22.9 | 13.0 | 0.7 | 7.4 | 8.0 | 5.9 | 0.9 |
| | 1980 | 20.4 | 23.6 | 24.1 | 18.5 | 8.9 | 2.2 | 5.7 | 7.9 | 5.4 | 0.4 |
| Chena II | 1978 | - | 19.5 | 25.0 | 21.0 | 14.1 | - | 6.4 | 9.8 | 6.9 | 1.3 |
| | 1979 | 22.5 | 21.8 | 22.9 | 22.4 | 14.6 | 1.5 | 7.5 | 9.7 | 8.5 | 1.0 |
| | 1980 | 20.1 | 23.5 | 23.2 | 20.1 | 9.1 | 2.0 | 5.9 | 8.0 | 4.4 | -1.4 |
| Gilmore Trail | 1978 | - | 14.7 | 20.0 | 18.5 | 10.6 | - | 7.3 | 10.9 | 9.9 | 6.3 |
| | 1979 | 19.9 | 17.5 | 19.3 | 19.7 | 11.1 | 4.2 | 8.3 | 14.6 | 11.1 | 4.3 |
| | 1980 | 18.2 | 19.6 | 22.2 | 19.4 | 9.6 | 3.9 | 7.5 | 9.4 | 5.8 | 1.4 |
| Smith Lake | 1978 | - | 19.9 | 28.7 | 26.0 | 16.6 | - | 3.8 | 6.5 | 6.3 | -1.0 |
| | 1979 | 25.8 | 25.8 | 27.1 | 26.4 | 15.9 | -2.6 | 4.4 | 6.7 | 5.3 | -2.0 |
| | 1980 | 23.9 | 25.6 | 26.4 | 22.1 | 11.6 | -0.8 | 2.2 | 5.2 | 1.1 | -2.2 |

[z]Data not available.

Figure 2. Seasonal cumulative losses of flowers or fruit in four populations of lingonberries during the 1978 through 1980 growing seasons.

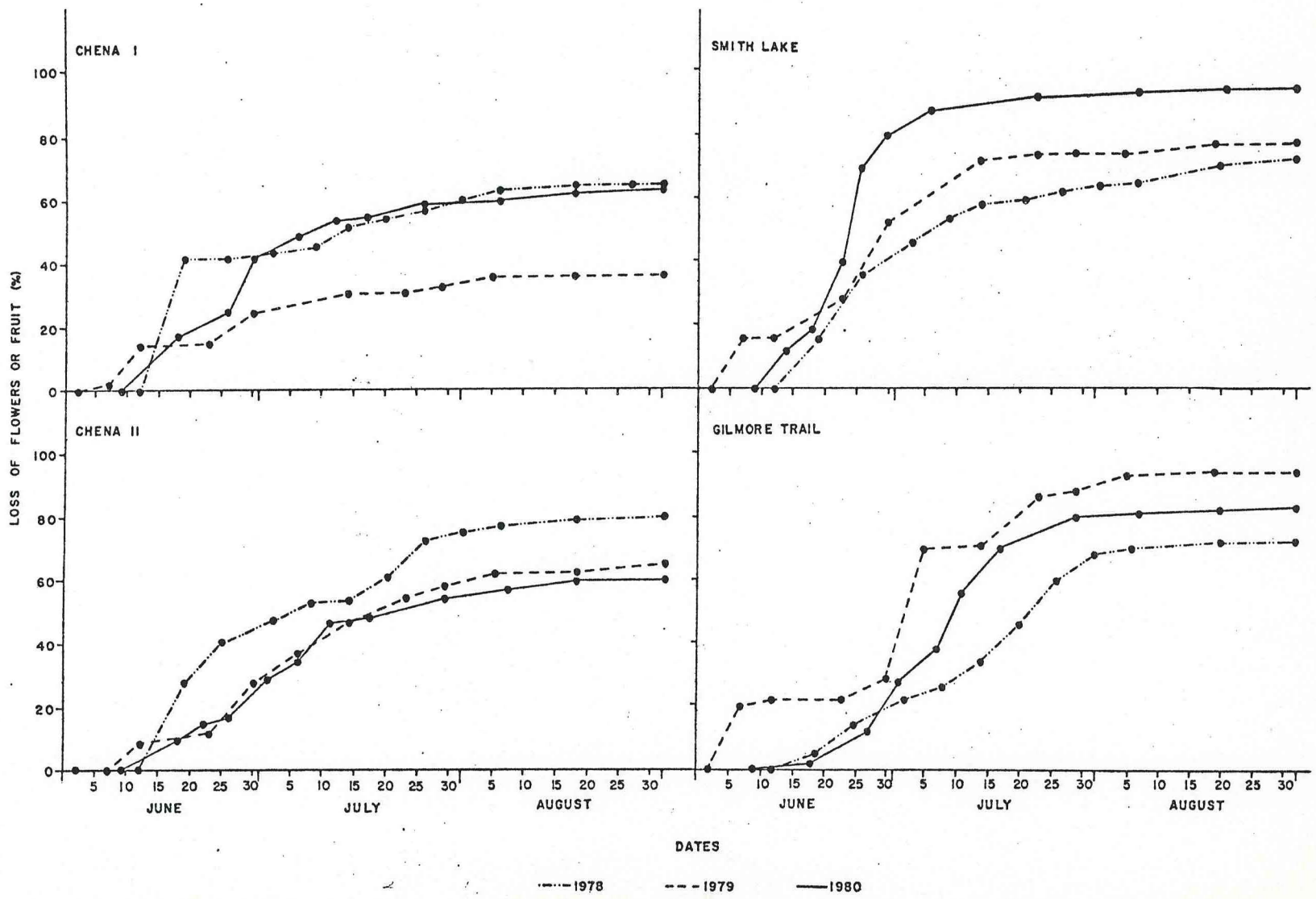

CHENA I
SMITH LAKE
CHENA II
GILMORE TRAIL
LOSS OF FLOWERS OR FRUIT (%)
0
20
40
60
80
100
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUGUST
DATES
1978
1979
1980

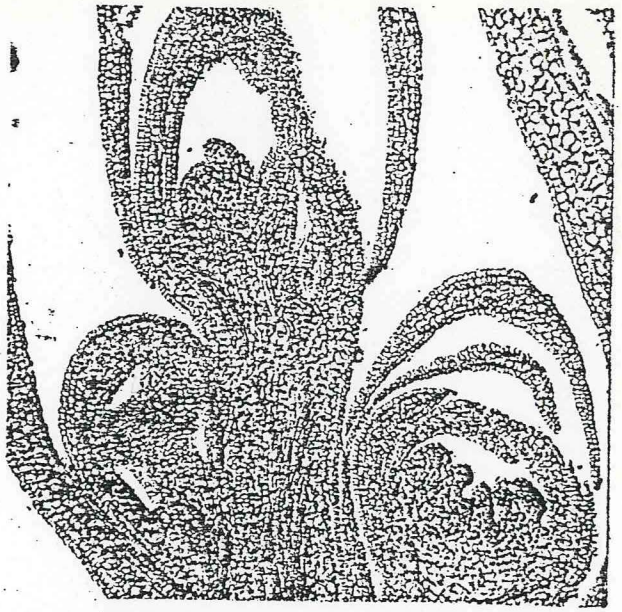
Table 5. Relationship between seed number and berry weight of lingonberries growing near Fairbanks, Alaska.

| Site | Percentage of berries in each weight (g) class | | | | | Number of seeds per berry | | | Correlation coefficient |
|---|---|---|---|---|---|---|---|---|---|
| | 0.00-0.09 | 0.10-0.19 | 0.20-0.29 | 0.30-0.39 | 0.40-0.49 | Max. | Min. | Mean | |
| Chena I | 0.0 | 11.2 | 52.2 | 30.0 | 6.6 | 43 | 0 | 20.6 | +.05 |
| Chena II | 13.3 | 57.9 | 13.3 | 12.2 | 3.3 | 28 | 1 | 9.3 | +.51** |
| Gilmore Trail | 15.5 | 56.7 | 27.8 | 0.0 | 0.0 | 27 | 1 | 7.5 | +.51** |
| Smith Lake | 3.3 | 43.3 | 43.3 | 10.1 | 0.0 | 26 | 0 | 8.8 | +.44** |

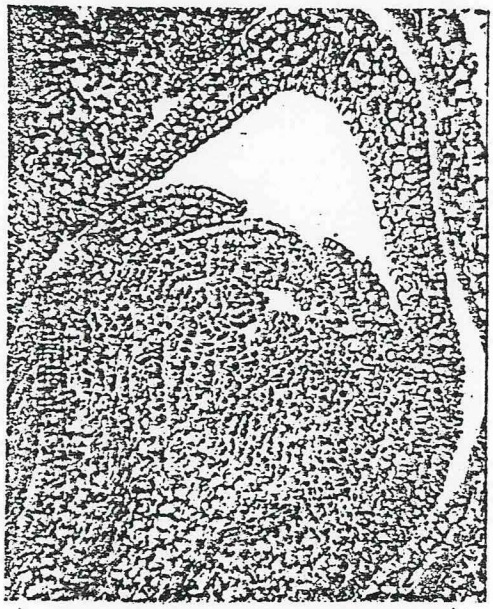
** Data significant at the .01 level.

Figure 3. Flower bud differentiation in lingonberries a) early stage of flower bud development with sepal and petal primordia present; b) early stage of flower bud development with sepals, petals, and stamens visible and the beginning of carpel development; c) acropetal development sequence; d) beginning of anther inversion; e) development stage of the proximal floret at the end of the growing season; f) mature anther with pollen tetrads.

a



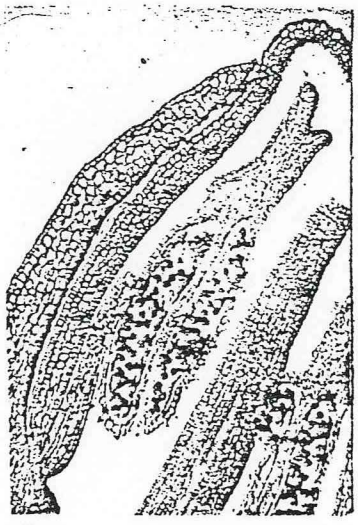
c



b

e

d



f

Table 6. Effects of insect pollination on fruit set and development in lingonberries.

| Site | Year | Treatment | Average number per stem | | Average berry diameter (cm) | Average berry weight (g) | Number of seeds per berry | Percent fruit set |
|---|---|---|---|---|---|---|---|---|
| | | | Flowers | Fruit | | | | |
| Chena I | 1979 | Open-pollinated | 5.7 | 2.2** | 0.80** | 0.27** | 12.7** | 39.6** |
| | | Caged | 5.1 | 0.1 | 0.52 | 0.16 | 5.2 | 0.6 |
| Chena I | 1980 | Open-pollinated | 5.2 | 2.0** | 0.89** | 0.27* | 14.7** | 38.3** |
| | | Caged | 5.3 | 0.5 | 0.69 | 0.19 | 6.9 | 8.9 |
| Gilmore Trail | 1979 | Open-pollinated | 5.3 | 0.4** | 0.39 | 0.13 | 8.9 | 9.4** |
| | | Caged | 4.9 | 0.0 | -[z] | - | - | 0.0 |

**Means significantly different at the 1 percent level.

*Means significantly different at the 5 percent level.

[z]Data not available.

Figure 4. Seasonal patterns of cumulative vegetative shoot growth in four Alaskan populations of lingonberries.

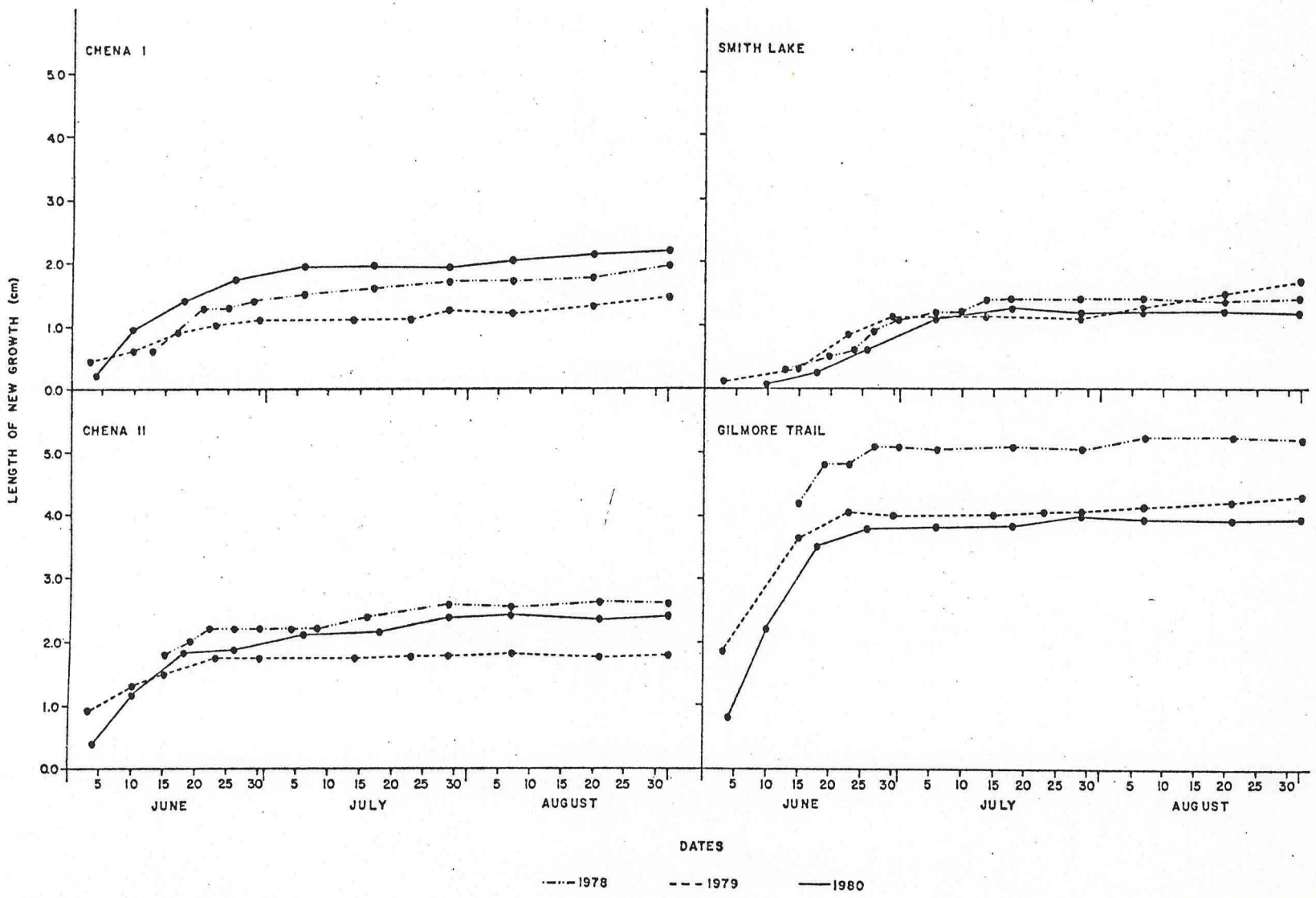

CHENA I
SMITH LAKE
CHENA II
GILMORE TRAIL
LENGTH OF NEW GROWTH (cm)
0.0
1.0
2.0
3.0
4.0
5.0
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUGUST
DATES
1978
1979
1980

Table 7. Stem growth and leaf production in four populations of lingonberries.

| Site | Year | Date of percent total stem growth | | Average number of leaves per new terminal growth |
|---|---|---|---|---|
| | | 50 | 90 | |
| Chena I | 1978 | 6-17 | 8-20 | 8.8 ± 2.3 |
| | 1979 | 6-13 | 8-20 | 9.5 ± 2.0 |
| | 1980 | 6-12 | 8-7 | 9.2 ± 3.8 |
| Chena II | 1978 | -[z] | 7-16 | 7.8 ± 2.0 |
| | 1979 | 6-5 | 8-7 | 8.2 ± 1.8 |
| | 1980 | 6-10 | 7-18 | 7.7 ± 2.9 |
| Gilmore Trail | 1978 | - | 6-18 | 9.7 ± 1.9 |
| | 1979 | 6-5 | 6-23 | 9.6 ± 2.0 |
| | 1980 | 6-9 | 6-18 | 9.0 ± 2.7 |
| Smith Lake | 1978 | 6-25 | 7-11 | 7.8 ± 1.8 |
| | 1979 | 6-23 | 8-25 | 8.0 ± 2.3 |
| | 1980 | 6-27 | 7-5 | 7.2 ± 3.5 |

[z]Data not available.

# THE EFFECTS OF GIBBERELLIC ACID ON FRUITING OF LINGONBERRIES

## Abstract

A single application of 50, 100, or 500 ppm gibberellic acid (GA) during 75 percent full bloom induced seedless fruit development in lingonberries growing in their native habitat in Alaska. Fruit set was increased significantly by the 500 ppm GA treatment in the absence of insect pollination. Fruit set was not increased by GA in open-pollinated plants. Berry weight and diameter were not affected by GA treatments.

## Introduction

Lingonberries, Vaccinium vitis-idaea, are harvested commercially from their native habitat in Alaska, Canada, and throughout Eurasia. Low fruit set caused by inadequate pollination (Fernqvist 1977, Holloway 1981), self pollination (Fernqvist 1977, Hall and Beil 1970), and cold temperatures during anthesis (Lehmushovi 1977) contributes to substantial reductions in annual marketable yields. Fruit set ranging from 0 to 70 percent of blossom production has been reported (Torrey 1914, Hall and Beil 1970, Kolupaeva 1972, Holloway 1981).

Fruit set has been increased in a diversity of crops even under conditions of unfavorable weather and inadequate pollination by exogenous applications of gibberellic acid (GA)(Crane 1964, Nitsch 1970). Included in this group are Vaccinium ashei (Mainland et al. 1980), V. angustifolium (Barker and Collins 1965), V. corymbosum (Mainland and Eck 1966, 1968b, c, 1969a, b, Hooks and Kenworthy 1971),

and V. macrocarpon (Devlin and Demoranville 1967, Mainland and Eck 1968a). In addition to increased fruit set, GA treatments have been found to decrease fruit size in V. macrocarpon (Devlin and Demoranville 1967, Mainland and Eck 1968a) and V. ashei (Mainland et al. 1980). In V. corymbosum the effect of GA on fruit size has been variable (Mainland and Eck 1968b, c, 1969b, Hooks and Kenworthy 1971). No experiments studying the responses of GA applications on V. vitis-idaea have been reported. The purpose of this study was to elucidate the effects of GA on fruit set and fruit development in lingonberries.

## Materials and Methods

In 1979, four blocks, 30x210 cm in size were selected at random from a single, uniform population of lingonberries growing in a black spruce-birch forest near Fairbanks, Alaska. Each block was subdivided into four 30x30 cm treatment sections with 30 cm separating adjacent treatments. Thirty reproductive stems selected at random comprised each treatment unit. Aqueous solutions of GA (Pro-Gibb[z]) at 50, 100, or 500 ppm with 0.05 percent Tween 20 as a wetting agent were applied with a hand sprayer until run-off at an approximate rate of 80 ml per $m^2$. Control plots were sprayed with a similar volume of water. The single application occurred on June 10 at 75 percent full bloom. The experiment consisted of a randomized complete block design with subsampling.

[z]Abbott Laboratories, North Chicago, Illinois.

The 1980 experiment contained four randomized blocks and eight treatments per block. A different population of lingonberries in the same locality comprised the experimental unit. GA was applied at the same rates as in 1979. The 30 stems in each treatment section either remained uncovered or were enclosed in individual glassine envelopes to prevent insect pollination. Stems were covered on May 28 prior to anthesis. The envelopes were removed for spray application on June 9 at 75 percent full bloom, immediately replaced, then permanently removed on June 26 following completion of petal fall.

In both 1979 and 1980, the number of flowers per stem was counted immediately prior to spray applications. Ripe fruit were counted, weighed, and the diameter measured with calipers. Seed counts per berry and the percent seedless fruit set were recorded. In 1979 fruit were harvested on August 28, 30, and September 1. Due to an extremely early snow fall on September 2, 1980, fruit were harvested once on September 5. Data were analyzed using the analysis of variance and Duncan's New Multiple Range Test at the 5 percent level.

## Results and Discussion

Fruit set percentages were not influenced significantly by GA treatments in the 1979 experiment (Table 1). The open-pollinated plants set between 50 and 60 percent of the blossoms in all treatment groups. In 1980, similar results were observed for open-pollinated plants, although the overall set was lower. Plants which were covered and treated with 0, 50, or 100 ppm GA exhibited significantly lower fruit set percentages than the open-pollinated treatments.

Covered plants treated with 500 ppm GA did not differ significantly in fruiting percentages from the GA-treated, open-pollinated plants. Average berry weight and diameter were not affected by GA treatments in either 1979 or 1980 (Table 1).

The number of seeds averaged less than one per berry in all GA-treated, covered plants in 1980 (Table 2). These counts differed significantly from the open-pollinated plants which had seed counts ranging from 3.5 to 4.7 per berry. Within the covered or open-pollinated groups the GA treatments did not differ significantly from each other in the number of seeds per berry. Results with open-pollinated, GA-treated plants were similar in both 1979 and 1980 experiments.

In 1980, seedless fruit comprised 97.4 percent of the total fruit set in the 500 ppm GA-treated, covered plants (Table 2). The covered plants treated with 50, 100, or 500 ppm GA differed significantly in the amount of seedless fruit set when compared with the covered plants treated with 0 ppm GA and all open-pollinated plants. Open-pollinated plants in both 1979 and 1980 experiments produced similar amounts of seedless fruit regardless of GA levels.

This experiment showed that GA induced seedless fruit development in lingonberries, but fruit set was increased only in the absence of pollination. Concentrations of GA greater than 500 ppm may be necessary to increase fruit set under natural conditions, although experiments with related Vaccinium species have shown that concentrations as low as 5 ppm (Mainland and Eck 1969a) have

increased fruit set. In 1980, the 500 ppm GA treatment clearly increased fruit set percentages in the covered plants. The reason for the lack of a similar increase in open-pollinated plants is unknown. Fruit size, as measured by weight and diameter, was not affected by GA treatments.

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Table 1. Percent fruit set, berry weight, and berry diameter of GA-treated lingonberries.

| Treatment GA(ppm) | | Percent fruit set | | Average berry weight (mg) | | Average berry diameter (cm) | |
|---|---|---|---|---|---|---|---|
| | | 1979 | 1980 | 1979 | 1980 | 1979 | 1980 |
| Covered | 0 | -[y] | 1.4a | - | 93.3a | - | 0.60a |
| | 50 | - | 2.6a | - | 105.0a | - | 0.65a |
| | 100 | - | 7.7a | - | 70.0a | - | 0.59a |
| | 500 | - | 41.4b | - | 88.3a | - | 0.60a |
| Open-pollinated | 0 | 52.7a[z] | 39.3b | 162.5a | 121.9a | 0.69a | 0.65a |
| | 50 | 55.4a | 32.5b | 158.6a | 121.1a | 0.70a | 0.65a |
| | 100 | 50.7a | 35.7b | 142.8a | 105.1a | 0.66a | 0.66a |
| | 500 | 58.6a | 33.9b | 160.6a | 118.5a | 0.68a | 0.62a |

[z]Mean separation within each column by Duncan's New Multiple Range Test, 5% level.

[y]Data not available.

Table 2. Number of seeds per berry and percent seedless fruit set in GA-treated lingonberries.

| Treatment | GA(ppm) | Average number of seeds per berry | | Percent seedless fruit set | |
|---|---|---|---|---|---|
| | | 1979 | 1980 | 1979 | 1980 |
| Covered | 0 | -[y] | 0.3a | - | 0.0a |
| | 50 | - | 0.7a | - | 66.7b |
| | 100 | - | 0.2a | - | 83.4bc |
| | 500 | - | 0.1a | - | 97.4c |
| Open-pollinated | 0 | 6.7a[z] | 4.2b | 10.7a | 0.0a |
| | 50 | 5.8a | 3.8b | 16.3a | 21.6a |
| | 100 | 6.6a | 4.7b | 18.7a | 19.4a |
| | 500 | 6.4a | 3.5b | 15.9a | 22.3a |

[z]Mean separation within each column by Duncan's New Multiple Range Test, 5% level.

[y]Data not available.

# THE EFFECTS OF LIGHT INTENSITY ON VEGETATIVE GROWTH OF LINGONBERRIES

## Abstract

Lingonberries were grown in Fairbanks, Alaska for up to three growing seasons in containers under four treatments: 0, 44, 56, and 73 percent shade provided by various thicknesses of polypropylene shade cloth. Following three growing seasons plants in the 0 percent shade treatment produced the greatest number of stems and dry weight per plant. Leaf size and number of leaves per stem did not differ among shade treatments. Leafy rhizome branches were longer under 73 percent shade than under higher light intensities. Rhizomes were longer under 0 percent shade than under lower light intensities. The results indicate that for maximum growth and dry matter accumulation lingonberries should be grown in full sunlight.

## Introduction

The lingonberry, Vaccinium vitis-idaea L., is a woody, evergreen shrub of circumpolar distribution whose fruit is harvested from native populations throughout most northern regions of the world. Recently, plans to domesticate the lingonberry have been implemented in Finland (Lehmushovi and Hiirsalmi 1973, Lehmushovi and Sako 1975, Lehmushovi 1977a, b), Sweden (Fernqvist 1977), Germany (Liebster 1975), and Alaska (Holloway 1981). The continued success of these efforts requires investigations which determine optimum growing conditions for maximum growth and plant establishment in cultivation.

Light intensity is one factor which greatly affects plant growth and development. Lingonberries grow in habitats with light intensities measuring from 3.4 percent of photosynthetically active radiation to complete illumination (Krylova and Trembalya 1978). Oldemeyer and Seemel (1976) have found that the percentage cover of lingonberries in mature spruce-hardwood forests is negatively correlated with increasing cover of the tree canopy. In other plant communities a positive correlation between percent canopy cover and lingonberry biomass was found. Smith (1962) noted that the greatest abundance of lingonberries occurred in moderate to heavy shade. In cultivated field experiments, Lehmushovi and Hiirsalmi (1973) found that shade increased both stem number and plant height. The purpose of this study was to clarify the relationship between light intensity and vegetative growth in lingonberries under controlled field conditions.

## Materials and Methods

A clone of lingonberry, Vaccinium vitis-idaea L. ssp. minus (Lodd.) Hult., was divided into plants consisting of a single rhizome measuring between 10 and 11 cm in length; a single, leafy, vegetative rhizome branch (the main stem), from 6 to 7 cm in length; and an undetermined amount of adventitious roots on the rhizome. Five plants were grown in a 15x15x15 cm plywood container lined with clear polyethylene that was perforated at the base to allow water drainage. The substrate was unsterilized, coarsely ground Sphagnum sp. peat from Fairbanks, Alaska. Containers were buried in the ground to within 2 cm of the top and mulched with additional peat. Polypropylene shade cloth of

various thicknesses was stretched across wooden frames to cover the containers. Each frame measured 100x60x50 cm in length, width, and height respectively. The shade cloth enclosed the top and all sides of the frame to within 10 cm of the ground to allow air movement and reduce air temperature differences among treatments. Light intensity was measured at plant level beneath the frames with a LI-COR Model LI-185 Quantum/Radio-meter/Photometer. Treatments consisted of 0, 44, 56, and 73 percent shade. The control plots (0 percent shade) were not enclosed in frames or shade cloth.

Taylor minimum-maximum thermometers and Irrometers were placed randomly within treatment groups, and daily air temperature and substrate moisture levels were recorded. Treatments were irrigated to maintain substrate moisture levels of less than 20 centibars.

The experiment was a randomized complete block design with five plants per treatment and five replicate blocks, each containing the four shade treatments. The experiment was repeated with plants being maintained under each treatment for one, two, or three growing seasons. In those experiments continuing for more than one season, the shade frames were removed at the time of the first snowfall in autumn and replaced upon snow melt in spring. All experiments occurred during the 1978 through 1980 growing seasons near Fairbanks, Alaska.

Plants were harvested during the first week of September. Data included the number of leaves per stem and stem length of the main stem, lateral branches, and leafy rhizome branches. Counts also

included the number of lateral branches, leafy rhizome branches, and new rhizomes per plant. Leaf length and width measurements were combined into a length-width ratio to give an estimate of leaf size for the main stem, lateral branches, and leafy rhizome branches. All length measurements were made with calipers.

All plant parts within each treatment were divided into four groups: vertical stems, leaves, rhizomes, and roots. Each group was dried separately in a forced-draft oven at 60°C for 24 hours after which dry weight measurements were recorded. Data were analyzed with the analysis of variance and Duncan's New Multiple Range Test at the 5 percent level.

Results

Plants grown for one season under the shade treatments exhibited little vegetative growth as revealed by the number of new plant components generated (Table 1). The number of lateral branches per main stem and the number of leafy rhizome branches averaged less than one per plant for all shade treatments. More new rhizomes per plant were produced than any of the other types of stems. Within each leafy stem type similar numbers of leaves per stem were recorded regardless of shade treatments. Neither stem length (Table 2) nor leaf size (Table 3) differed significantly among shade treatments. Leaves and rhizomes comprised the greatest proportion of dry weight (Table 4). Dry weight for leaves, vertical stems, rhizomes and roots did not differ significantly among shade treatments after the first growing season.

Plants maintained for two growing seasons exhibited significant differences in production of leafy rhizome branches and new rhizomes (Table 1). In both instances, plants grown in the 0 percent shade treatment had significantly greater numbers per plant when compared to plants grown in the 44, 56, and 73 percent shade treatments. Like plants maintained for one season, plants grown for two seasons did not differ in the number of leaves per stem (Table 1), stem length (Table 2), or leaf size (Table 3). In addition, plant dry weight did not differ among shade treatments (Table 4).

Following three seasons of growth, plants differed significantly in the production of lateral branches, leafy rhizome branches, and new rhizomes (Table 1). Within all three groups, plants grown in the 0 percent shade treatment had significantly greater numbers per plant than plants grown in all other shade treatments. Similar numbers of leaves per stem were recorded for the main stem, lateral branches, and leafy rhizome branches regardless of shade treatment.

The average length of the main stem and lateral branches did not differ among shade treatments (Table 2). Leafy rhizome branches were significantly longer in plants grown under 73 percent shade than in plants grown under greater light intensities. In contrast, the length of new rhizomes was significantly greater in plants grown in the 0 percent shade treatment than those grown under lower light intensities. Similar leaf size measurements were recorded for each stem type under all shade treatments (Table 3).

The dry weight of leaves, vertical stems, rhizomes and roots was significantly greater in the 0 percent shade-treated plants when compared to the same plant part in the other three shade treatments (Table 4).

Discussion

This experiment showed that total vegetative growth of lingonberries is greater in full sunlight than under 44,56, or 73 percent shade. These results are contrary to the observation by Smith (1962) that lingonberries predominate in natural environments with moderate to heavy shade. Perhaps shade is not as important in defining lingonberry habitat as other factors such as substrate, moisture and nutrient availability, and plant competition. This view seems possible considering the very wide range of light intensities under which lingonberries have been found to grow (Krylova and Trembalya 1978).

The results also do not agree with the cultivated field experiment of Lehmushovi and Hiirsalmi (1973) who found that shade increases vegetative growth. One possible explanation for this discrepancy might be ecotypic differences between Alaskan and Finnish populations of lingonberries. Based upon morphologic characteristics, four taxonomic subdivisions of the species Vaccinium vitis-idaea L. have been identified (Henriksson 1923, Hulten 1949, 1970), but the full extent of species variability is unknown. Considering the extensive range of the lingonberry, from arctic to north-temperate regions throughout the Northern Hemisphere, and its habitat diversity, ecotypic variation, including variation in response to light intensity, seems possible.

Another possible explanation for the discrepancy between ex-

periments is differences in water stress among treatments in the Finnish experiments. There may have been greater water stress in tissues of plants growing in full sunlight than of those growing in shade, resulting in an increase in growth in shade. This condition is difficult to verify in the Finnish experiment since neither air temperature nor substrate moisture measurements were recorded among shade treatments. In our study, substrates were maintained under equal moisture conditions, and air temperatures did not differ by more than $2^{o}C$ among treatments. The effects of water stress were considered minimal.

Both our study and the experiment by Lehmushovi and Hiirsalmi (1973) indicate an increase in plant height with shade. We recorded an increase in stem length of the leafy rhizome branches only at the lowest light intensity after three growing seasons.

Results of this study have implications for site selection and modification for lingonberry cultivation. In modification of native populations to promote maximum vegetative growth, cover by shrubs and trees should be eliminated and weed growth minimized. Furthermore, it should be possible to grow lingonberries in full sunlight in cultivated fields without provisions for shading to enhance plant establishment.

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Table 1. Average number of stems and leaves per plant of lingonberries grown under 0, 44, 56, and 73 percent shade.

| Percent Shade | Average Number Per Plant | | | | | |
|---|---|---|---|---|---|---|
| | Leaves per main stem | Lateral branches | Leaves per Lateral branch | Leafy rhizome branches | Leaves per leafy rhizome branch | New rhizomes |
| One Season | | | | | | |
| 0 | 16.4a[z] | 0.4a | 4.0a | 0.1a | 3.6a | 2.5a |
| 44 | 15.7a | 0.4a | 3.5a | 0.1a | 3.0a | 1.5a |
| 56 | 18.5a | 0.2a | 4.3a | 0.1a | 2.5a | 2.3a |
| 73 | 15.6a | 0.3a | 4.0a | 0.2a | 2.7a | 1.6a |
| Two Seasons | | | | | | |
| 0 | 18.9a | 2.2a | 5.7a | 3.2a | 5.3a | 3.6a |
| 44 | 14.6a | 1.4a | 5.5a | 1.6b | 4.0a | 1.8b |
| 56 | 17.1a | 1.3a | 5.7a | 1.1b | 3.7a | 1.8b |
| 73 | 15.5a | 1.2a | 4.8a | 0.9b | 4.1a | 1.9b |
| Three Seasons | | | | | | |
| 0 | 18.7a | 4.7a | 8.8a | 12.7a | 6.6a | 13.4a |
| 44 | 18.2a | 2.2b | 7.5a | 6.8b | 4.3a | 7.9b |
| 56 | 16.4a | 2.8b | 7.6a | 4.8b | 5.8a | 4.2b |
| 73 | 19.1a | 2.8b | 8.7a | 5.0b | 4.7a | 5.3b |

[z] Mean separation within each column for each season by Duncan's New Multiple Range Test, 5% level.

Table 2. Average stem length of lingonberries grown under 0, 44, 56, and 73 percent shade.

| Percent Shade | Average Length (cm) | | | |
|---|---|---|---|---|
| | Main Stem | Lateral Branches | Leafy Rhizome Branches | New Rhizomes |
| **One Season** | | | | |
| 0 | 6.50a[z] | 1.40a | 1.93a | 2.04a |
| 44 | 6.67a | 1.00a | 2.58a | 1.93a |
| 56 | 6.35a | 0.87a | 2.07a | 1.85a |
| 73 | 6.35a | 0.84a | 1.99a | 2.25a |
| **Two Seasons** | | | | |
| 0 | 7.13a | 1.02a | 3.42a | 5.03a |
| 44 | 6.60a | 1.36a | 3.79a | 6.25a |
| 56 | 6.82a | 1.44a | 3.74a | 7.75a |
| 73 | 6.40a | 1.84a | 3.62a | 5.44a |
| **Three Seasons** | | | | |
| 0 | 6.64a | 2.15a | 3.94b | 11.25a |
| 44 | 7.42a | 2.92a | 3.61b | 6.06b |
| 56 | 7.31a | 2.98a | 3.18b | 7.55b |
| 73 | 8.07a | 3.41a | 5.84a | 7.93b |

[z] Mean separation within each column for each season by Duncan's New Multiple Range Test, 5% level.

Table 3. Average leaf size of lingonberries grown under 0, 44, 56, and 73 percent shade.

| Percent Shade | Leaf Length-width Ratio | | |
|---|---|---|---|
| | Main Stem | Lateral Branches | Leafy Rhizome Branches |
| One Season | | | |
| 0 | 1.54 N.S.[z] | 1.45 N.S. | 1.00 N.S. |
| 44 | 1.51 | 1.36 | 1.02 |
| 56 | 1.55 | 1.33 | 1.05 |
| 73 | 1.57 | 1.49 | 1.29 |
| Two Seasons | | | |
| 0 | 1.56 N.S. | 1.45 N.S. | 1.32 N.S. |
| 44 | 1.59 | 1.54 | 1.24 |
| 56 | 1.46 | 1.46 | 1.23 |
| 73 | 1.65 | 1.46 | 1.35 |
| Three Seasons | | | |
| 0 | 1.75 N.S. | 1.81 N.S. | 1.47 N.S. |
| 44 | 1.71 | 1.50 | 1.56 |
| 56 | 1.64 | 1.67 | 1.53 |
| 73 | 1.65 | 1.63 | 1.27 |

[z] Means within each column for each season do not differ significantly at the 5% level.

Table 4. Average dry weight of leaves, vertical stems, rhizomes, and roots of lingonberries grown under 0, 44, 56, and 73 percent shade.

| Percent Shade | Dry weight (mg) Vertical Stems | Leaves | Rhizomes | Roots |
|---|---|---|---|---|
| One Season | | | | |
| 0 | 41.9a[z] | 103.1a | 121.5a | 9.6a |
| 44 | 37.2a | 100.7a | 81.7a | 9.0a |
| 56 | 34.5a | 109.6a | 168.5a | 7.5a |
| 73 | 39.0a | 88.8a | 96.4a | 5.4a |
| Two Seasons | | | | |
| 0 | 88.0a | 121.0a | 161.5a | 22.8a |
| 44 | 76.6a | 153.5a | 165.7a | 22.1a |
| 56 | 64.3a | 154.2a | 162.2a | 14.7a |
| 73 | 57.8a | 72.1a | 154.1a | 8.2a |
| Three Seasons | | | | |
| 0 | 191.5a | 474.3a | 309.6a | 53.4a |
| 44 | 92.8b | 223.2b | 142.7b | 21.1b |
| 56 | 103.0b | 241.8b | 170.5b | 16.4b |
| 73 | 108.8b | 266.6b | 165.4b | 17.1b |

[z] Mean separation within each column for each season by Duncan's New Multiple Range Test, 5% level.

# VEGETATIVE GROWTH OF LINGONBERRIES ON FOUR ALASKAN SUBSTRATES

## Abstract

Vegetative growth of lingonberries was observed on plants growing in four unsterilized, native-Alaskan substrates: coarsely-ground Lemeta peat, Fairbanks silt loam soil, a mixture of peat and silt loam soil, and washed Chena very fine sandy loam soil. Following three growing seasons, plants in the peat treatment showed the greatest increase in vegetative growth as revealed by the number of new stems produced, stem length, and dry weight per plant. Leaf size did not differ among substrate treatments. The leaves on plants grown in the peat substrate remained green throughout the entire experiment. The leaves of plants in all other treatments showed varying degrees of chlorosis followed by reddening and necrosis. Differences in concentration of N, P, K, Mn, Fe, Zn, and Al in whole-plant tissue samples were recorded. The results indicate that for maximum growth and dry matter accumulation, lingonberries should be grown in a peat substrate.

## Introduction

The lingonberry, *Vaccinium vitis-idaea* L., is a woody, evergreen shrub whose distribution extends from arctic to north-temperate regions in Eurasia and North America. Throughout this range, the lingonberry is most abundant in forest habitats which are characterized by leached soils with low base saturation, low lime content, and a low level of available nutrients (Ingestad 1973). Vegetative growth and fruit productivity are favored by acid soils (pH 5-6) (Ipatov et al.

1977, Tear 1972) and a substantial decaying organic matter layer (Tear 1972, Stark et al. 1978). Few studies have been reported which determine the optimum substrate environment for lingonberries in cultivation. Experiments in Finland have shown that milled peat (pH 4.4) provides a better substrate than sandy soils (pH 6.4) or a mixture of equal volumes of sand and peat (pH 5.0). Vegetative growth is poorest on sandy soils (Lehmushovi and Sako 1975). A Swedish study has shown that the best substrates for lingonberry cultivation are sandy, acidic (pH 5-6) soils with at least a 2 percent organic matter content (Fernqvist 1977). Similar studies using substrates from Alaska have not been reported. The purpose of this experiment was to study the differences in plant nutrition and development of lingonberries growing on four Alaskan substrates in order to determine the optimum substrate environment for maximum vegetative growth.

Materials and Methods

A clone of lingonberry, Vaccinium vitis-idaea L. ssp. minus (Lodd.) Hult. was divided into plants consisting of a single rhizome, 10-11 cm in length; a single, leafy, vegetative rhizome branch (the main stem), 6-7 cm in length; and an undetermined amount of adventitious roots on the rhizome. Five plants were grown in a 15x15x15 cm plywood container lined with clear polyethylene that was perforated at the base to allow water drainage. Containers were buried in the ground to within 2 cm of the top. Treatments consisted of equal volumes of four unsterilized, native-Alaska substrates: coarsely

ground Lemeta peat (Peat); Fairbanks silt loam soil (soil); a mixture of equal volumes of peat and silt loam soil (soil-peat); and washed Chena very fine sandy loam soil (sand) (Rieger et al. 1963). Irrometers were placed within each substrate, and treatments were irrigated with rain water to maintain substrate moisture levels below 20 centibars. Daily substrate temperatures were recorded at a depth of 7 cm with a Taylor Bi-Therm soil temperature probe.

Samples of each substrate were frozen for chemical analysis[z] which included percent ($NO_3$ + $NO_2$)-N by KCl leaching (Black et al. 1965) and colorimetric analysis on a Technicon Autoanalyzer II; Bray-1 phosphate (Black et al. 1965); ppm of K, Ca, and Mg by $NH_4OAc$ leaching and Inductively Coupled Plasma-Atomic Emission Spectroscopy (ICP) (Dahlquist and Knoll 1978); ppm of Fe, Cu, Zn, and Mn by DTPA-TEA extraction(Lindsay and Norwell 1978) and ICP; Al by KCl extraction and ICP; and organic matter by colorimetric method after wet oxidation with $H_2SO_4$ sulfuric acid dichromate (Black et al. 1965).

The experiment was a randomized complete block design with five plants per treatment and four replicates. The experiment was repeated with plants being maintained within each treatment for one, two, or three growing seasons. All experiments occurred in the field during the 1978 through 1980 growing seasons near Fairbanks, Alaska.

Plants were harvested during the second week of September. Data collected at harvest included the number of leaves per stem and stem

[z]Tissue and soil analyses were conducted by the Research Analytical Laboratory, Department of Soil Science, University of Minnesota.

length of the main stem, lateral branches, and leafy rhizome branches. Counts also included the number of lateral branches, leafy rhizome branches, and new rhizomes per plant. Leaf length and width measurements were combined into a length-width ratio to give an estimate of leaf size for the main stem, lateral branches, and leafy rhizome branches. All length measurements were made with calipers.

All plant parts within each treatment were divided into four groups: leaves, vertical stems, rhizomes, and roots. Each group was washed in deionized, distilled water and dried in a forced-draft oven at 60°C for 24 hours after which dry weight measurement were recorded. The groups were recombined for whole-plant tissue analysis. Samples were ground, dry ashed, and analyzed for percent N by the Kjeldahl method, and for ppm of P, K, Ca, Mg, Al, Fe, Mn, Zn, Cu, and B by ICP. All data were statistically analyzed using the analysis of variance and Duncan's New Multiple Range Test at the 5 percent level.

Results

Very little growth was observed on plants maintained for one growing season. The number of lateral branches, leafy rhizome branches, and new rhizomes averaged less than one per plant regardless of substrate treatment (Table 1). Plants in each treatment also did not differ in stem length (Table 2), leaf size (Table 3), or dry weight (Table 4). The tissue analyses revealed no significant differences among treatments in the concentration of elements in the whole-plant samples (Table 5). Differences among substrates in the concentration of elements are listed in Table 6.

Plants maintained for two growing seasons showed significant differences in the number of new rhizomes and leafy rhizome branches per plant (Table 1). In both instances, plants grown in peat produced more than twice the number of stems per plant than plants grown in soil, soil-peat, or sand. The leafy rhizome branches and new rhizomes also were significantly longer in plants grown in peat than in all other treatments (Table 2). No differences among treatments were observed in the number of leaves per stem of the main stem, leafy rhizome branches, and lateral branches (Table 1); the number and length of lateral branches (Tables 1 and 2); leaf size (Table 3); and dry weight (Table 4).

The leaves on all stems of plants grown in peat remained bright green throughout the second growing season. Plants grown in soil-peat had green leaves on the main stem and lateral branches, but leaves of the leafy rhizome branches were pale green with reddish margins. New leaf growth on plants grown in sand was uniformly chlorotic with reddish margins. Older leaves on the main stem were a uniform dull red color. Plants grown in soil had bright red leaves at the base of the main stem. Leaves became progressively greener toward the stem apex. All new growth was pale green, tinged with red.

The tissue analyses revealed significant differences in the concentration of Al and Fe in the whole-plant samples (Table 5). In both instances, plants grown in soil contained the greatest amount of these elements. The concentration of tissue N was higher in plants grown in peat than in all other treatments. Treatments

did not differ in the concentration of all other elements.

Plants grown for three seasons differed significantly in the number of lateral branches, leafy rhizome branches, and new rhizomes per plant (Table 1). With all three stem types, plants grown in peat had significantly greater numbers per plant than plants grown in the other three substrate treatments. The number of leaves on the main stem and leafy rhizome branches did not differ among treatments. Plants grown in peat had a significantly greater number of leaves on lateral branches than plants grown in soil and sand. The leafy rhizome branches and new rhizomes were significantly longer in plants grown in peat than in all other treatments (Table 2). Leaf size did not differ among substrate treatments (Table 3).

Leaves and rhizomes comprised the greatest proportion of plant dry weight (Table 4). The dry weight of vertical stems, leaves, and rhizomes was significantly greater in the peat treatment than in sand, soil, and soil-peat treatments. Greater amounts of roots occurred in the peat and sand treatments than in soil and soil-peat treatments.

Leaves on plants in the peat substrate remained green throughout the third growing season. All new leaves on plants grown in soil-peat were uniformly chlorotic with reddish margins. Older leaves on the main stem were pale green, becoming increasingly more red as the season progressed. Plants in soil and sand had similar color patterns as plants grown in the same substrates for two seasons. The reddening of the older leaves on the main stem generally was followed by necrosis.

Significant differences were observed in seven of the eleven elements studied by tissue analysis (Table 5). Plants grown in peat had greater concentrations of tissue P, K, and Mn than plants grown in the other three treatments. The quantity of tissue N was highest in the peat and soil treatments. Plants grown in soil and soil-peat had significantly greater quantities of tissue Al and Fe amounting to more than double the concentration found in plants grown in peat and sand. The concentration of tissue Zn was highest in peat and soil-peat treatments. The tissue concentrations of Ca, Mg, Cu, and B did not differ among treatments.

Discussion

This experiment has shown that vegetative growth of lingonberries is best in a peat substrate. Growth is poorest on sand and soil. These results are similar to those reported by Lehmushovi and Sako (1975) who found that milled peat was a better substrate than sand or a mixture of sand and peat. Both of these studies differ from the results reported by Fernqvist (1977) who stated that sandy soils were best for lingonberry growth in cultivation. The discrepancy in these experiments may be explained by differences in chemical and physical properties of the substrates at each experimental location or to plant variability. All three studies reveal the importance of two substrate components: pH and organic matter content.

In their native habitat, lingonberries have been found to grow on substrates having a pH range of 2.7 to 5.5 (Krylova and Trembalya

1978). The optimum range for vegetative growth and productivity is pH 5-6 (Ipatov et al. 1977, Fernqvist 1977). In our study, both the soil and sand substrates have pH values which are greater than the optimum range, while the peat substrate is slightly lower than optimum (Table 6). The soil-peat substrate on which lingonberries grow poorly is within this range. These results indicate that the optimum pH range may be lower than that previously reported, and/or that other substrate components in addition to pH probably influence lingonberry growth. Considerable variability also may exist in lingonberries for tolerance to different pH levels. Brown and Draper (1980) reported such variability in blueberry species and concluded that through breeding, blueberries might be grown on soils with a wider pH range. Comparisons among several populations will be necessary to verify this variability in lingonberries.

The substrate organic matter content seems to promote vegetative growth in lingonberries. In their native habitat, lingonberries often are found in greatest abundance on top of decaying tree stumps and old ant hills (Tear 1972). In forest communities, most of the roots and rhizomes of lingonberries occur in the organic litter horizon (Ritchie 1955, Persson 1978). Smith (1962) noted that the maximum rooting depth is a function of the depth of the organic matter layer, but Kerekova (1970) found no such correlation. The organic matter content also may influence the quantity of mycorrhizal fungi infecting the roots (Haselwandter 1979). Mycorrhizas have been shown to enhance

the efficiency of nitrogen absorption (Stribley and Read 1975) and improve vegetative growth and vigor of several ericaceous plants including lingonberries (Warming 1908, Haselwandter 1979).

Cultivation experiments substantiate the necessity for organic matter in the substrate. Our study and the research by Lehmushovi and Sako (1975) show that substrates composed primarily of organic matter increase vegetative growth. Optimum growth on sandy soils in Sweden requires at least a 2 percent organic matter content (Fernqvist 1977). In our study, the organic matter content of the sand and soil substrates may have been too low for optimum growth (Table 6). Although the soil-peat substrate has an organic matter content which is higher than the minimum reported by Fernqvist (1977), growth still was poor.

Marginal soils having a low organic matter content produce symptoms of Fe chlorosis in blueberries. This nutrient disorder is characterized by interveinal chlorosis of the younger leaves followed by uniform leaf and stem chlorosis and stunted growth (Ballinger 1966). Chlorosis occurred on the youngest leaves of lingonberries grown in sand, soil, and soil-peat, but the characteristic interveinal chlorosis pattern was not evident.

The concentration of Fe in tissue samples is not indicative of the amount of available Fe in the plant. Plants showing Fe chlorosis symptoms often may be higher in the total concentration of tissue Fe than healthy plants (Mengel and Kirkby 1979). DeKock et al. (1960)

believe that a better measure of the amount of available Fe in tissue samples is the P/Fe ratio. High P/Fe ratios indicate a greater quantity of the unavailable form of Fe and are usually associated with iron chlorotic tissues (Mengel and Kirkby 1979). We calculated the following P/Fe ratios for the four treatments following three growing seasons: peat, 3.34; soil-peat, 0.50; soil, 0.23; and sand, 0.76. These data, along with the leaf color symptoms, indicate that Fe deficiency probably is not a factor in this experiment. The differences in tissue Fe concentrations may be related to the quantity of Fe in each substrate since plants having the highest levels of total Fe after two and three growing seasons (Table 5) are associated with substrates having very high Fe concentrations (Table 6).

Concentrations of tissue Al differ significantly among substrate treatments after two and three growing seasons (Table 5). Like Fe, the Al concentration probably is related to the availability of Al in each substrate and to substrate pH (Table 6). Toxic levels of Al occur on acid soils especially where the pH is below 5.5 (Mengel and Kirkby 1979). Since reduced vegetative growth occurred on substrates with a pH of 5.4 and greater, Al toxicity probably did not occur in this experiment. In addition, the symptoms of Al toxicity (dark green leaves, stem purpling, low P concentrations) did not occur. Similar Al concentrations to those reported in our study were recorded by Firsova and Pavlova (1975) for stem and leaf tissue of lingonberries growing in their natural habitat.

The predominant color change noted in this experiment was a progressive chlorosis from younger to older leaves and a reddening of the older leaves on plants in the sand and soil treatments after two growing seasons and to a lesser extent in the soil-peat treatment after three growing seasons. Leaf chlorosis and reddening have been associated with N deficiency in blueberries (Ballinger 1966) and cranberries (Somogyi et al 1962, Torio and Eck 1969). Following two growing seasons, lingonberries in the peat treatment had significantly greater tissue concentrations of N than plants in the other three treatments, indicating a possible deficiency of available N in the soil, soil-peat, and sand treatments. During the third growing season, the tissue N levels were similar for the soil and peat treatments even though plants growing on soil were chlorotic and red while plants on the peat substrate remained green. This discrepancy may be explained by the form of N in each substrate. Nitrate ($NO_3$-N) usually is considered to be the major source of inorganic N for plants, but the rate of nitrification in acid soils below pH 5.5 is very low. Consequently, $NO_3$-N is not considered to be a significant source of N in acid soils (Havill et al. 1974). The use of ammonium ($NH_4$-N) as the major source of N has been demonstrated in blueberries (Cain 1952, Townsend 1966), cranberries (Greidanus et al. 1972), and lingonberries (Mueller-Stoll 1947, Marthaler 1939, Havill et al. 1974). Greidanus et al. (1972) found that cranberries grown with high levels of $NO_3$-N showed deficiency symptoms and poor growth with tissue concentrations of 1.34 percent. In contrast, where $NH_4$-N was the only

source, deficiency symptoms did not occur until tissue concentrations were 0.72-0.91 percent. A similar circumstance in lingonberries might explain why deficiency symptoms occurred in the soil treatment and not in the peat treatment even though the tissue N levels were the same. The soil substrate contained a considerably greater amount of $NO_3$-N than the peat substrate (Table 6).

Lingonberries grown on both the soil and sand treatments showed chlorotic and red growth, although the manifestation of these symptoms was different for each substrate. Perhaps the plants grown on the sand substrate truly are deficient in N because of substrate deficiency, while the reddening and chlorosis in the soil treatment is related to the form and not quantity of N. Since deficiency levels of N and other elements have not been established, and plant color variations in relation to these deficiencies have not been identified in lingonberries, further experimentation will be necessary in order to clarify these observations.

The higher amounts of Mn and Zn recorded in plants grown on the peat substrate do not correlate well with the concentrations of these elements in each substrate (Tables 5 and 6). The higher levels found in the peat-treated plants may be related to a greater solubility of these elements at low substrate pH levels (Mengel and Kirkby 1979).

Two other substrate components, temperature and moisture content, probably are not significant factors in this experiment. Substrate temperature did not differ by more than $1^{o}C$ among the treatments for

each growing season (Table 6). Because of frequent rainfall, irrometer readings rarely reached the 20 centibar limit, and supplemental hand irrigation was unnecessary during most of the experiment. Substrates remained moist, but well-drained.

In conclusion, maximum vegetative growth and optimum plant nutrition occurred in plants grown on a peat substrate. High pH and low organic matter content probably prevent optimum growth on sand, soil, and soil-peat. In addition, leaf chlorosis and reddening reveal nutritional disorders possibly relating to the source or quantity of N as a factor in reducing vegetative growth on soil, soil-peat, and sand. These data determine not only the optimum substrate, but also the location of future experiments with the lingonberry cultivation. Agricultural soils, as exemplified by the silt loam soil, and sandy alluvial soils probably are not appropriate. Incorporation of peat into the agricultural soils improved growth only slightly. Greater quantities of organic matter may be necessary to allow cultivation of lingonberries on agricultural soils, but this procedure may be uneconomical.

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Table 1. Average number of stems and leaves per plant of lingonberries grown in peat, soil, soil-peat, and sand substrates.

| Substrate | Average Number per Plant | | | | | |
|---|---|---|---|---|---|---|
| | Leaves per main stem | Lateral branches | Leaves per lateral branch | Leafy rhizome branches | Leaves per leafy rhizome branch | New rhizomes |
| One Season | | | | | | |
| Sand | 15.38a[z] | 0.31a | 2.33a | 0.00a | -[y] | 0.56a |
| Soil | 15.66a | 0.13a | 3.00a | 0.06a | 0.00 | 0.69a |
| Soil-Peat | 16.97a | 0.19a | 2.33a | 0.06a | 0.00 | 0.50a |
| Peat | 15.98a | 0.44a | 2.83a | 0.06a | 0.00 | 0.81a |
| Two Seasons | | | | | | |
| Sand | 15.38a | 0.06a | 3.00a | 0.00b | - | 0.25b |
| Soil | 17.94a | 0.06a | 4.00a | 0.31b | 2.38a | 0.50b |
| Soil-Peat | 16.77a | 0.31a | 6.67a | 0.81b | 2.64a | 0.38b |
| Peat | 16.23a | 0.94a | 4.00a | 2.25a | 3.65a | 1.13a |
| Three Seasons | | | | | | |
| Sand | 19.25a | 0.19b | 3.00b | 0.06b | 4.00a | 0.88b |
| Soil | 16.52a | 0.38b | 2.33b | 0.63b | 4.57a | 0.31b |
| Soil-Peat | 18.50a | 0.75b | 5.66ab | 0.94b | 3.17a | 1.56a |
| Peat | 18.08a | 2.06a | 8.15a | 4.19a | 4.45a | 4.13a |

[z]Mean separation within each column for each year by Duncan's New Multiple Range Test, 5% level.

[y]Data not available

Table 2. Average stem length of lingonberries grown in peat, soil, soil-peat, and sand substrates.

| Substrate | Average Length (cm) | | | |
|---|---|---|---|---|
| | Main Stem | Lateral Branches | Leafy Rhizome Branches | New Rhizomes |
| One Season | | | | |
| Sand | 7.29a[z] | 0.65a | -[y] | 1.71a |
| Soil | 7.18a | 0.68a | 1.43a | 1.84a |
| Soil-Peat | 7.41a | 0.62a | 1.63a | 1.77a |
| Peat | 8.09a | 0.97a | 2.25a | 2.11a |
| Two Seasons | | | | |
| Sand | 7.31a | 1.40a | - | 1.68b |
| Soil | 7.29a | 1.00a | 1.49b | 1.37b |
| Soil-Peat | 7.65a | 1.35a | 1.94b | 1.54b |
| Peat | 7.26a | 1.20a | 3.50a | 4.06a |
| Three Seasons | | | | |
| Sand | 7.00a | 1.58a | 1.22b | 1.38b |
| Soil | 6.67a | 1.38a | 2.18b | 1.32b |
| Soil-Peat | 6.95a | 1.32a | 1.49b | 1.65b |
| Peat | 7.28a | 1.92a | 3.98a | 4.42a |

[z]Mean separation wtihin each column for each year by Duncan's New Multiple Range Test, 5% level.

[y]Data not available.

Table 3. Leaf size of lingonberries grown in peat, soil, soil-peat and sand substrates.

| Substrate | Leaf Length-width Ratio | | |
|---|---|---|---|
| | Main Stem | Lateral Branches | Leafy Rhizome Branches |
| One Season | | | |
| Sand | 1.54 N.S.[z] | 1.52 N.S. | -[y] |
| Soil | 1.49 | 1.56 | - |
| Soil-Peat | 1.57 | 1.45 | - |
| Peat | 1.56 | 1.47 | - |
| Two Seasons | | | |
| Sand | 1.60 N.S. | 1.55 N.S. | - |
| Soil | 1.55 | 1.59 | 1.35 N.S. |
| Soil-Peat | 1.59 | 1.57 | 1.55 |
| Peat | 1.62 | 1.55 | 1.46 |
| Three Seasons | | | |
| Sand | 1.76 N.S. | 1.73 N.S. | 1.62 N.S. |
| Soil | 1.72 | 1.83 | 1.42 |
| Soil-Peat | 1.75 | 1.62 | 1.38 |
| Peat | 1.69 | 1.77 | 1.57 |

[z]Means within each column for each year do not differ significantly at the 5% level.

[y]Data not available.

Table 4. Average dry weight of vertical stems, leaves, rhizomes, and roots of lingonberries grown on four Alaskan substrates.

| Substrate | Dry Weight (mg) | | | |
|---|---|---|---|---|
| | Vertical stems | Leaves | Rhizomes | Roots |
| One Season | | | | |
| Sand | 44.5a | 67.8a | 72.4a | 4.9a |
| Soil | 40.8a | 78.0a | 82.2a | 4.4a |
| Soil-peat | 42.0a | 82.7a | 86.2a | 4.0a |
| Peat | 49.7a | 81.3a | 86.1a | 6.2a |
| Two Seasons | | | | |
| Sand | 42.0a | 67.5a | 79.4a | 5.0a |
| Soil | 41.6a | 61.7a | 80.8a | 4.9a |
| Soil-peat | 40.7a | 77.9a | 82.2a | 6.2a |
| Peat | 54.9a | 80.8a | 99.4a | 7.5a |
| Three Seasons | | | | |
| Sand | 35.3b | 66.3b | 119.8b | 12.4a |
| Soil | 44.4b | 55.9b | 119.7b | 3.5b |
| Soil-peat | 38.7b | 68.7b | 121.5b | 7.0b |
| Peat | 70.8a | 176.1a | 161.9a | 17.5a |

[z]Mean separation within each column for each year by Duncan's New Multiple Range Test, 5% level.

Table 5. Element concentration in whole-plant tissue samples of lingonberries grown in peat, soil, soil-peat, and sand substrates.

| Substrate | Tissue Concentration N % | P ppm | K ppm | Ca ppm | Mg ppm | Al ppm |
|---|---|---|---|---|---|---|
| One Season | | | | | | |
| Sand | 0.64a[z] | 622.37a | 2887.70a | 5917.40a | 1388.35a | 378.88a |
| Soil | 0.58a | 568.96a | 2716.20a | 6171.35a | 1345.45a | 468.55a |
| Soil-Peat | 0.58a | 551.52a | 2840.15a | 6062.85a | 1099.05a | 223.65a |
| Peat | 0.61a | 586.95a | 2666.20a | 5849.65a | 1245.50a | 269.73a |
| Two Seasons | | | | | | |
| Sand | 0.53b | 495.59a | 2135.75a | 5253.20a | 1015.11a | 292.80b |
| Soil | 0.59b | 638.51a | 2132.70a | 6421.50a | 1239.65a | 650.44a |
| Soil-Peat | 0.62b | 652.70a | 1779.25a | 6251.80a | 1231.25a | 520.90ab |
| Peat | 0.87a | 885.10a | 2871.20a | 5911.45a | 1228.10a | 302.52b |
| Three Seasons | | | | | | |
| Sand | 0.72b | 521.89b | 1684.60b | 6330.70a | 1336.05a | 338.88b |
| Soil | 0.92a | 693.21b | 2111.10b | 5847.00a | 1567.80a | 1078.36a |
| Soil-Peat | 0.67b | 728.96b | 1979.90b | 6167.60a | 1624.35a | 867.67a |
| Peat | 0.96a | 1041.30a | 3534.45a | 4355.30a | 1506.55a | 307.58b |

[z]Mean separation within each column for each year by Duncan's New Multiple Range Test, 5% level.

Table 5. continued

| Substrate | Tissue Concentration Fe ppm | Mn ppm | Zn ppm | Cu ppm | B ppm |
|---|---|---|---|---|---|
| One Season | | | | | |
| Sand | 449.54a | 462.85a | 150.08a | 10.72a | 18.70a |
| Soil | 507.55a | 453.30a | 110.08a | 14.48a | 19.10a |
| Soil-Peat | 395.81a | 441.49a | 86.51a | 11.75a | 19.91a |
| Peat | 307.15a | 553.84a | 83.41a | 11.06a | 17.16a |
| Two Seasons | | | | | |
| Sand | 273.79c | 401.61a | 23.53a | 16.30a | 15.15a |
| Soil | 1928.35a | 476.42a | 25.51a | 10.34a | 21.78a |
| Soil-Peat | 694.93b | 437.50a | 22.81a | 16.62a | 20.86a |
| Peat | 353.13c | 624.03a | 35.45a | 16.92a | 20.25a |
| Three Seasons | | | | | |
| Sand | 686.65c | 495.02b | 34.07ab | 24.48a | 66.33a |
| Soil | 3039.25a | 333.69b | 27.22b | 30.45a | 66.47a |
| Soil-Peat | 1446.95b | 485.61b | 31.12ab | 19.62a | 86.21a |
| Peat | 311.47c | 939.81a | 41.70a | 11.09a | 76.76a |

[z]Mean separation within each column for each year by Duncan's New Multiple Range Test, 5% level.

Table 6. Characteristics of four Alaskan substrates.

| | Sand | Soil | Soil-peat | Peat |
|---|---|---|---|---|
| Organic Matter (%) | 0.3 | 1.4 | 5.3 | - |
| pH | 6.4 | 6.5 | 5.4 | 4.8 |
| Average Temperature[z] ($^{o}C$) | | | | |
| June | 13.4 | 13.2 | 13.2 | 13.1 |
| July | 16.0 | 15.8 | 15.9 | 15.8 |
| August | 15.8 | 15.0 | 15.2 | 15.0 |
| $(NO_3 + NO_2)$-N (ppm) | 4.2 | 101.0 | 3.4 | 3.9 |
| Bray-1 phosphate (ppm) | 24.1 | 26.2 | 21.7 | 5.9 |
| K (ppm) | 96.0 | 136.4 | 103.6 | 32.8 |
| Ca (ppm) | 1947.3 | 4251.5 | 1421.9 | 191.5 |
| Mg (ppm) | 370.5 | 808.1 | 282.5 | 34.1 |
| Mn (ppm) | 16.1 | 38.1 | 11.9 | 3.4 |
| Fe (ppm) | 148.1 | 992.7 | 315.6 | 36.3 |
| Al (ppm) | 1.4 | 7.9 | 1.0 | < 0.5 |
| Zn (ppm) | 2.1 | 27.7 | 0.9 | 0.5 |
| Cu (ppm) | 4.9 | 6.3 | 5.4 | 0.8 |

[z]Temperature data are for the 1980 growing season. Average temperatures for 1978 and 1979 differed by less than $1^{o}C$ from the 1980 data.

# EFFECT OF CHILLING ON BUD BREAK IN LINGONBERRIES

## Abstract

Three seedling populations of lingonberries from Fairbanks, Alaska, Oulu, Finland, and the Pasvik River Valley, Norway were exposed to 0, 170, 344, 513, 681, 843, 1013, and 1185 hours of continuous chilling (4 $\pm$ 1$^{o}$C) temperatures to determine chilling requirements necessary to satisfy rest. Both the Finnish and Alaskan populations required at least 681 hours of chilling to obtain maximum terminal vegetative bud break. Continuous chilling for 1185 hours was not sufficient to obtain maximum bud break in the Norwegian population. In the Finnish and Alaskan populations neither the percentage of stems exhibiting lateral bud break nor the number of lateral branches per stem differed among chilling treatments. Plants from Norway showed significantly greater lateral bud break in the 513- and 681-hour treatments than in all other treatments. At least 681 hours of chilling were necessary to achieve normal flowering in the Finnish population.

## Introduction

Dormancy is a period where active growth in terminal and lateral meristems temporarily is suspended (Wilkins 1969, Perry 1971). The cessation of active growth may be due to unfavorable environmental conditions or to an internally controlled rest period where growth does not occur even though external growing conditions appear favorable. Rest often is satisfied by exposing plants to a period of chilling temperatures (1 - 10$^{o}$C) varying in duration from 250 to over 1000 hours (Samish 1954, Vegis 1964). Investigations into rest and chilling re-

quirements have not been previously reported in the lingonberry, Vaccinium vitis-idaea L. The purpose of this study was to determine the chilling requirements of three populations of lingonberries by continuous chilling in a controlled environment. By imposing artificial chilling regimes, we hope to develop a research tool by which more than one growth cycle in lingonberries can be obtained annually.

## Materials and Methods

Forty plants of uniform size were selected from each of three seedling populations of Vaccinium vitis-idaea. The seeds were collected from Fairbanks, Alaska (64.51N), the Pasvik River Valley, Norway (69.41N), and Oulu, Finland (65.00N). Plants from Alaska and Finland were identified as the arctic-montane subspecies minus, while plants from Norway were of the lowland subspecies vitis-idaea (Hulten 1949). At the beginning of this experiment plants from the Alaskan and Norwegian populations were two years old, and no flower buds were evident. Finnish plants were seven years old and contained numerous flower buds.

The plants were grown outdoors in 4-liter containers at the Horticultural Research Center, Excelsior, Minnesota. The substrate consisted of milled Sphagnum sp. peat. On August 15, 1980, all plants were transferred to a greenhouse with natural daylength conditions and with a minimum air temperature of 16°C. On October 1, five plants, selected at random from each population, were transferred to another greenhouse with 18°C minimum air temperatures. Daylength was extended to 20 hours with Sylvania Directlite incandescent bulbs. The remaining plants were placed in a refrigerated storage room in continuous darkness at 4 ± 1°C. Five plants, selected at random from each population,

were removed from the cold room at approximate weekly intervals and placed under the lights in the greenhouse. Plants from each population were removed from the cold room after 0, 170, 344, 513, 681, 843, 1013, or 1185 hours of continuous chilling.

The experiment was a randomized complete block design with subsampling. All experimental units contained five vegetative stems per plant selected at random with one plant per replicate. Observations on terminal vegetative bud break were made at three-day intervals for 60 days following the chilling treatment. After 60 days, the number of lateral buds to break and the percentage of stems exhibiting lateral and terminal bud break were recorded.

In the Finnish population, five reproductive stems per plant were selected at random. The number of florets per raceme, the percentage of stems with normal flowers, and the number of days to full bloom were recorded for each treatment. Full bloom was identified as the date at which 75 percent of the corollas were open.

All data were analyzed by the analysis of variance and Duncan's New Multiple Range Test at the 5 percent level.

## Results and Discussion

In the Alaskan population of lingonberries, 25 percent terminal vegetative bud break was achieved after 170 hours of chilling (Table 1). The number of days to 25 percent bud break was reduced significantly by treatments of 513 or more hours. Although 75 percent bud break was recorded in plants treated with 513 hours, the number of days to 75 percent bud break was reduced by more than half with an additional week, or 681 hours, of chilling temperatures. More than 10 days elapsed

between 25 and 75 percent bud break in plants treated with 513 hours. Plants in the 681-hour treatment achieved both 25 and 75 percent bud break after 15 days in the greenhouse. These results indicate a more rapid rate of bud break in the 681-hour treatment. The maximum percentage of terminal bud break was significantly greater in plants treated with 513 or more hours than in the 0-, 170-, or 344-hour treatments. Neither the percentage of stems exhibiting lateral bud break (Table 1) nor the number of lateral branches per stem (Fig. 1) differed significantly among chilling treatments.

The Norwegian population of lingonberries required at least 681 hours of chilling temperatures to achieve 25 percent terminal vegetative bud break (Table 2). Seventy-five percent bud break was observed only on plants treated with 1185 hours after 49 days in the greenhouse. A treatment of 681 or more hours was necessary to achieve the highest level of bud break amounting to 60-80 percent of the vegetative stems. Based upon observations of growth under field conditions where nearly 100 percent terminal vegetative bud break has been recorded, the maximum level of vegetative growth probably was not observed in this experiment for the Norwegian population. Of the 40 total plants in this experiment, only 4 reached 100 percent bud break after 60 days of observation. More than 1185 hours of chilling probably will be necessary to satisfy rest in this population.

Norwegian plants treated with 513 and 681 hours of chilling temperatures had significantly greater percentages of lateral bud break than plants treated with fewer or greater numbers of chilling hours (Table 2). In addition, more lateral branches per stem were produced

on plants treated with 513 and 681 hours of chilling than plants in the other treatments (Fig. 1).

Plants from Finland exhibited 25 percent terminal vegetative bud break after 170 hours of chilling temperatures (Table 3). The number of days to 25 percent bud break was reduced significantly by 681 or more hours of chilling temperatures. Plants treated with 0, 170, 344, or 513 hours did not reach 75 percent bud break after 60 days of observation. The number of days to 75 percent bud break did not differ among treatments of 681 or more hours. Terminal bud break of greater than 90 percent was observed for chilling treatments of 681 or more hours. Neither the percentage of stems exhibiting lateral bud break (Table 3) nor the number of lateral branches per stem (Fig, 1) differed significantly among chilling treatments.

Normal flowers were produced on at least 80 percent of the reproductive stems receiving 513 or more hours of chilling temperatures (Table 3). Plants treated with 0, 170, or 344 hours had a greater incidence of abnormal racemes which included flower buds which expanded but failed to elongate, complete flower abortion, and normal development of one or more proximal florets with abortion of the more immature distal florets. Racemes on plants treated with 170 and 344 hours of chilling temperatures commonly included one to three florets which developed normally. Plants treated with 513 or more hours averaged between 8.2 and 12.3 normal florets per raceme. Flower buds on control plants did not develop. The number of days to full bloom was reduced significantly by chilling treatments of 681 or more hours.

The response of lingonberries to chilling treatments was similar for the Alaskan and Finnish populations. Both populations required at least 681 hours of chilling temperatures to achieve maximum terminal vegetative bud break in the shortest period of time. The response of these populations differed from the Norwegian population which probably will require more than 1185 hours of chilling to complete rest. The Norwegian population also differed from the others in the response of lateral buds to chilling temperatures. These results may be further evidence of differences between the subspecies vitis-idaea and minus. Previously, only morphologic characteristics distinguished the two subspecies (Hulten 1949). Further comparative studies using more populations from both subspecies will be necessary to verify this viewpoint.

This study has shown that at least 681 hours of continuous chilling temperatures will be necessary to satisfy rest and evoke a normal vegetative growth response in lingonberries. However, considerable variation among populations can be expected. Vegetative and reproductive growth appear to require similar chilling regimes to complete rest.

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Table 1. Response of vegetative buds of an Alaskan population of lingonberries to chilling regimes.

| Hours of chilling | Days to terminal vegetative bud break | | Percent bud break after 60 days | |
|---|---|---|---|---|
| | 25% | 75% | Terminal | Lateral |
| 0 | -[z] | - | 16.0b | 16.0a |
| 170 | 36.5a[y] | - | 36.0b | 20.0a |
| 344 | 27.3ab | - | 52.0b | 24.0a |
| 513 | 21.6bc | 32.8a | 84.0a | 16.0a |
| 681 | 15.0bc | 15.0b | 80.0a | 12.0a |
| 843 | 11.0c | 11.0b | 100.0a | 20.0a |
| 1013 | 11.0c | 11.0b | 96.0a | 8.0a |
| 1185 | 10.6c | 11.0b | 100.0a | 8.0a |

[z]The designated percentage bud break was not achieved after 60 days in the greenhouse.

[y]Mean separation within columns by Duncan's New Multiple Range Test. 5% level.

Table 2. Response of vegetative buds of a Norwegian population of lingonberries to chilling regimes.

| Hours of chilling | Days to terminal vegetative bud break | | Percent bud break after 60 days | |
|---|---|---|---|---|
| | 25% | 75% | Terminal | Lateral |
| 0 | -[z] | - | 4.0b | 4.0b |
| 170 | - | - | 0.0b | 8.0b |
| 344 | - | - | 0.0b | 20.0b |
| 513 | - | - | 8.0b | 52.0a |
| 681 | 60.0a[y] | - | 60.0a | 44.0a |
| 843 | 55.0ab | - | 60.0a | 16.0b |
| 1013 | 47.5b | - | 63.0a | 4.0b |
| 1185 | 45.6b | 49.0 | 80.0a | 4.0b |

[z]The designated percent bud break was not achieved after 60 days in the greenhouse.

[y]Mean separation within columns by Duncan's New Multiple Range Test, 5% level.

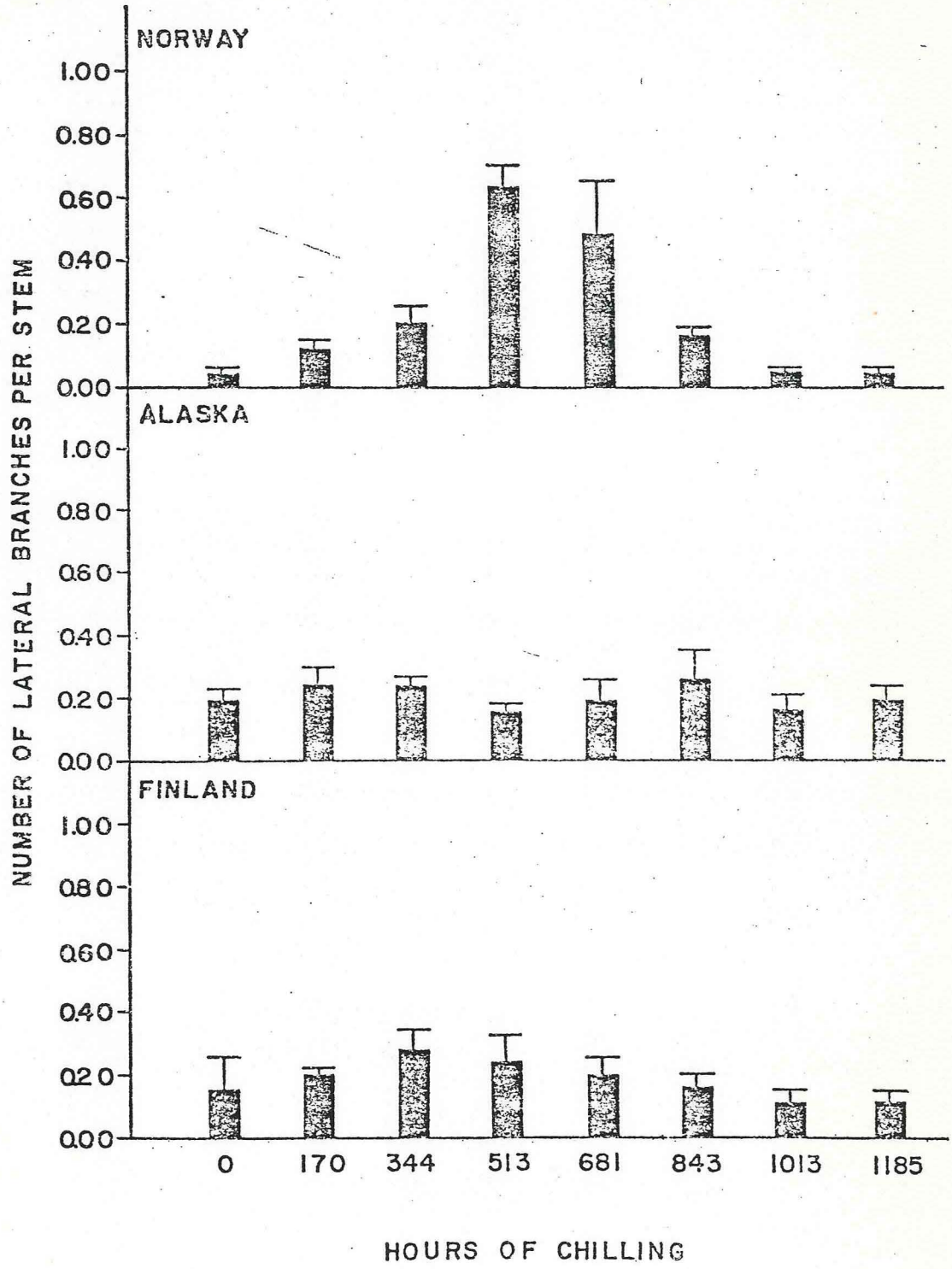
Table 3. Response of vegetative and reproductive buds of a Finnish population of lingonberries to chilling regimes.

| Hours of chilling | Days to terminal vegetative bud break | | Percent bud break after 60 days | | Stems with normal flowers (%) | Number of florets per raceme | Number of days to full bloom |
|---|---|---|---|---|---|---|---|
| | 25% | 75% | Terminal | Lateral | | | |
| 0 | -[z] | - | 20.0b | 16.0a | 0.0a | 0.0b | - |
| 170 | 39.7a[y] | - | 28.0b | 20.0a | 4.0a | 1.0b | 49a |
| 344 | 32.7a | - | 44.0b | 32.0a | 28.0a | 2.3b | 42a |
| 513 | 28.3a | - | 64.0b | 16.0a | 80.0b | 11.0a | 40ab |
| 681 | 18.8b | 22.6a | 92.0a | 16.0a | 86.0b | 10.6a | 33b |
| 843 | 16.3b | 20.0a | 100.0a | 8.0a | 100.0b | 8.2a | 36b |
| 1013 | 17.0b | 18.0a | 96.0a | 12.0a | 100.0b | 10.0a | 33b |
| 1185 | 14.2b | 16.8a | 100.0a | 12.0a | 90.0b | 12.3a | 30b |

[z] The designated percent bud break was not achieved after 60 days in the greenhouse.

[y] Mean separation within columns by Duncan's New Multiple Range Test, 5% level.

Figure 1. Development of lateral branches of three lingonberry populations in response to different durations of chilling temperatures.


NORWAY
ALASKA
FINLAND
1.00
0.80
0.60
0.40
0.20
0.00
NUMBER OF LATERAL BRANCHES PER STEM
0
170
344
513
681
843
1013
1185
HOURS OF CHILLING

# SUMMARY

The purpose of this research was to study certain aspects of vegetative and reproductive growth of Vaccinium vitis-idaea in order to establish a foundation for future research into the domestication of this plant for improved berry production in Alaska. The five research projects in combination with the literature review fulfill this goal by providing a comprehensive assessment of vegetative and reproductive growth of the lingonberry as well as elucidating potential methods for increasing growth through cultivation practices.

The study of patterns of vegetative and reproductive growth provided general information not previously available on seasonal aspects of growth in wild populations of lingonberries. These data will also provide a basis for comparison in future projects dealing more specifically with lingonberries in cultivation. For instance, the effects of changes in environmental factors such as soil moisture, plant nutrient availability, etc., on growth can be analyzed more effectively by comparing the resulting growth patterns with information from wild populations.

This study also revealed the importance of entomogamy on both fruit quality and quantity. Future experiments must include identification of the natural insect pollinators of the lingonberry as well as the potential for the introduction of honeybees as pollinators both in natural and cultivated stands.

A major area of concern in future research projects will be to identify more specifically the reasons for the very low fruit yields encountered in the wild populations. Poor weather and lack of insect pollination have identified as sources of yield reductions, but other factors, such as freezing temperatures during anthesis, plant nutrition and soil moisture imbalances may contribute to the problem.

The gibberellic acid study showed that although GA does increase seedless fruit development, it is not effective under natural conditions in increasing fruit set. Based upon present experimental conditions, it does not appear feasible to use GA to increase yield in the absence of natural pollinators or during poor weather conditions. This experiment should be repeated using higher concentrations of GA. In addition, future experiments in cultivated fields should be considered since plants in cultivation may react differently to GA applications than those in the wild.

Because of the diversity of the natural habitat of lingonberries, it was necessary to determine those aspects of plant growth in the wild which must be emulated in cultivated field situations. The experiment with different shade regimes showed that it will not be necessary to select for lingonberries which will tolerate full sunlight. In addition, it will not be necessary to introduce shade cloth to cultivated fields to provide shade for maximum plant establishment.

The substrate experiment determined not only the optimum growing

medium for lingonberries, but also the location of future experiments. Boggy,acid soils may provide the best substrate for lingonberry growth, but additional factors such as bog drainage and permafrost must be considered. Future experiments should include experimentation with specific Alaskan sites in order to clarify these results. This experiment also established a base of all future field studies with lingonberries.

The final project on the determination of chilling requirements was the first study, other than general taxonomic investigations, to compare the two subspecies of lingonberry. This study showed that differences between the subspecies may be greater than previously anticipated. This study also provided basic information on the chilling requirements of lingonberries which can be used to facilitate controlled environment experimentation with lingonberries. Because the number of chilling hours was not sufficient to satisfy rest in the Norwegian population, this experiment should be repeated with additional hours of chilling temperatures. To determine if true differences exist between subspecies, more populations from both subspecies should be tested. The experiments also should be extended to include the satisfaction of chilling requirements under natural, outdoor conditions.