The Biological Flora of Canada

1. *Vaccinium angustifolium* Ait., Sweet Lowbush Blueberry*

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This contribution on *Vaccinium angustifolium* Ait., Sweet Lowbush Blueberry (Ericaceae), is the first of a series presenting biological information on plants that are components of the flora of Canada. *Vaccinium angustifolium* is a deciduous low shrub endemic to North America, whose range in Canada extends from the east coast of Newfoundland to Lake Winnipeg in Manitoba. It occurs from Quebec 57°N to Virginia 38°N. To produce fruit the flowers usually require cross-pollination by wild bees or related insects. The fruit of *V. angustifolium* is edible and matures during late summer. During the past 30 yr in the Atlantic Provinces of Canada many fields abandoned from other forms of agriculture have been brought into stands of this species by burn-pruning and selective weed control.

Key Words: *Vaccinium angustifolium*, Sweet Lowbush Blueberry, biology, ecology, physiology, distribution, economic importance.

1. *Name*

Vaccinium angustifolium Ait.; section *Cyanococcus;* Ericaceae;
V. lamarckii Camp (Camp 1943, 1945);
V. pennsylvanicum Lam. (Robinson and Fernald 1908);
V. pensilvanicum Lam. (Fernald 1950); Sweet Lowbush Blueberry;
airelle à feuilles étroites (Marie-Victorin 1964).

2. *Description of the Mature Plant*

(*a*) *Raunkiaer life-form.* Chamaephyte. Winter-deciduous, broad-leaved low shrub with ascending branches, edible blue fruits, deep tap root; reproduces by seeds and rhizomes.

(*b*) *Shoot morphology.* Stems woody, average height 20 cm with maximum of 50 cm, generally glabrous, with raised lenticels, the bark variously pigmented from yellow to deep red in autumn; buds of two types, the larger flower buds borne terminally, the more lanceolate vegetative buds born proximally; leaves alternate in a spiral, simple, pinnately netted, serrate glandular, elliptic or ovate-oblong, apex acute, base obtuse, the ventral surface waxy green, the dorsal surface pale green and sometimes with light bloom; rhizomes woody bearing numerous shoots, new growth white or pinkish (Figure 1a, b).

(*c*) *Root morphology.* The radicle of the seedling develops into an extensive tap root system (Hall 1957); the root system is finely divided at the extremities and several authors state that there are no root hairs (e.g., Addoms and Mounce 1931).

(*d*) *Inflorescence.* The members of *Vaccinium* section *Cyanococcus* are characterized by flowers borne in racemes; members of section *Vaccinium* by contrast have flowers borne singly in the leaf axils. Flowers of *V. angustifolium* are typically pentacyclic with five sepals, five petals fused into a bell-shaped corolla, 10 stamens in two whorls of five and fused to the corolla, and a single pistil with inferior ovary. Fruit is a true berry bearing 10 pseudolocules each with a few to many small seeds. Bell (1957) found that the average number of perfect seeds was 13 and of imperfect seeds was 50 per berry. Some mutants were reported by Hall, Aalders, and Lockhart (1964). Both *Vaccinium* and *Gaylussacia* have inferior ovaries but the seeds of the former are much smaller.

(*e*) *Subspecies.* None.

*See La Roi (1977) for notice, guidelines and schedule for contributors.

FIGURE 1. Sweet Lowbush Blueberry Plant. A: Above, close-up of flowers; below, flowering plant. B: Above, close-up of fruit; below, fruiting plant.

(*f*) *Varieties and forms.* Fernald (1950) recognized a puberulent var. *hypolasium* and a smooth-leaved var. *laevifolium* House, but we do not, considering these to be part of the variation found in the species. We recognize the following forms: *V. angustifolium* Ait. forma *angustifolium* with green leaves, fruit with a heavy bloom, consequently a blue color, and straight stems, is the most frequent taxon (Vander Kloet 1978); *V. angustifolium* forma *nigrum* (Wood) Boivin is characterized by blue-green leaves, fruit with little or no bloom giving it a black color, and zigzag stems (Aalders and Hall 1963a); *V. angustifolium* forma *leucocarpum* (Deane) Rehder is a white-fruited form.

(*g*) *Ecotypes.* Forma *nigrum* tends to increase more rapidly than forma *angustifolium* in stands that are burned regularly (Hall et al. 1975).

(*h*) *Chromosome numbers.* Longley (1927) first reported 24 bivalent chromosomes for *V. angustifolium.* Newcomer (1941) *sub V. pennsylvanicum* also reported that five selections had $n = 24$ chromosomes. Darrow et al. (1942) are the only workers to report a diploid condition ($2n = 24$) but no voucher specimen for this count can be located (Vander Kloet 1978). Counts from clones of Canadian and Maine *V. angustifolium* all have $2n = 48$ (Hall and Aalders 1961; Bent and Vander Kloet 1976; Hersey and Vander Kloet 1976; Whitton 1964).

3. *Distribution and Abundance*

(*a*) *Geographic range. Vaccinium angustifolium* is a North American endemic, extending from Cape St. Francis on the eastern tip of Newfoundland to the Pine Falls area of Lake Winnipeg in south central Manitoba (Figure 2). It extends from 57°N in northern Quebec southward to isolated uplands in the Appalachian Mountains of Virginia, 38°N. A complete distribution map appears in Vander Kloet (1978).

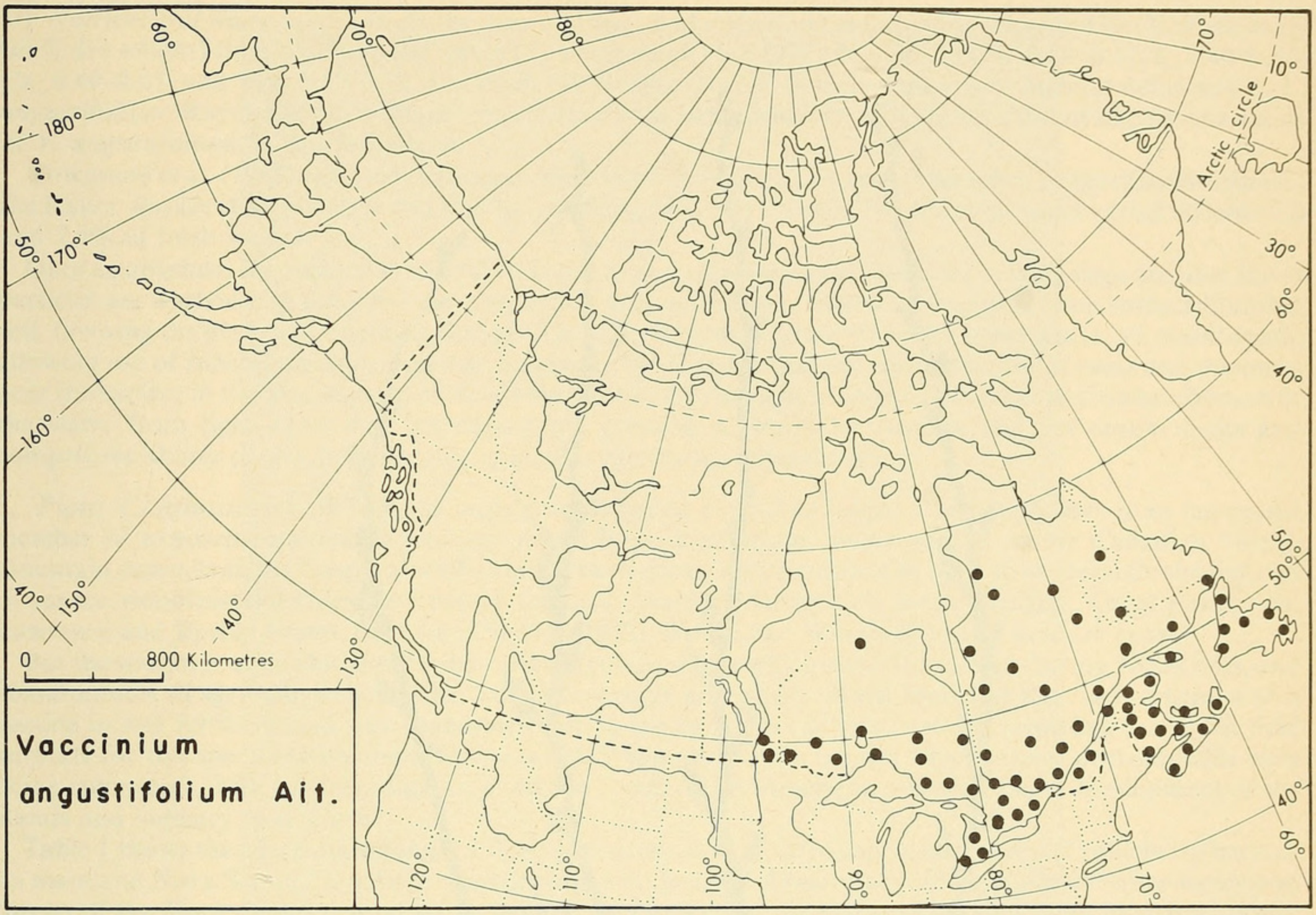

FIGURE 2. Canadian distribution of *Vaccinium angustifolium* from specimens in the Department of Agriculture Herbarium, Ottawa, Ontario (DAO); National Herbarium, National Museums of Canada, Ottawa, Ontario (CAN); and Acadia University Herbarium, Wolfville, Nova Scotia (ACAD).

(*b*) *Altitudinal range. Vaccinium angustifolium* extends from ca. sea level to 1300 m asl in Eastern Canada to 1300–1500 m asl in Virginia. On the higher points of the Adirondack Mountains *V. angustifolium* is replaced by *V. boreale* (Sweet Hurts) (Vander Kloet 1977).

4. *Physical Habitat*

(*a*) *Climatic relations. Vaccinium angustifolium* occurs in a large area of eastern North America and tolerates a wide range of climatic conditions. The variability of this species with regard to productivity is well established (Aalders and Hall 1963b; Hall, Aalders, and Wood 1966) but the adaptiveness of the species to different climatic conditions requires further study. A comparison of growth under different climatic conditions was conducted on uniform plant and soil media in 1965 and 1966 at Kentville, Nova Scotia; Normandin, Quebec; and St. John's West, Newfoundland. Linear shoot growth of 20 plants from seven clones at the three respective stations averaged 183, 141, and 111 cm per plant in 1965; and 195, 153, and 70 cm in 1966. The number of flower buds produced per plant averaged 126, 94, and 66 in 1965; and 88, 54, and 23 in 1966. Thus climatic conditions for growth varied widely among the three stations. Vegetative growth was not notably different between 1965 and 1966 at Kentville and Normandin, but much poorer in 1966 at St. John's West; reproductive growth was much better in 1965 than 1966 at all three stations.

In Eastern Canada, winter temperatures for *V. angustifolium* and other chamaephytes are generally ameliorated by a snow cover. Inadequate snow cover may be followed by shoot dieback to ground level in the Lac de St. Jean area (Poirier and Dubé 1969). Unusually warm weather and salt spray from a February hurricane, followed by cold temperatures, were probably responsible for extensive mortality of *V. angustifolium* flower buds (Figure 3) in the Fox River area of Nova Scotia in 1976. Cold winds off the Northumberland Strait are a factor in delaying the beginning of plant growth in Inverness County, Nova Scotia (Hall et al. 1963).

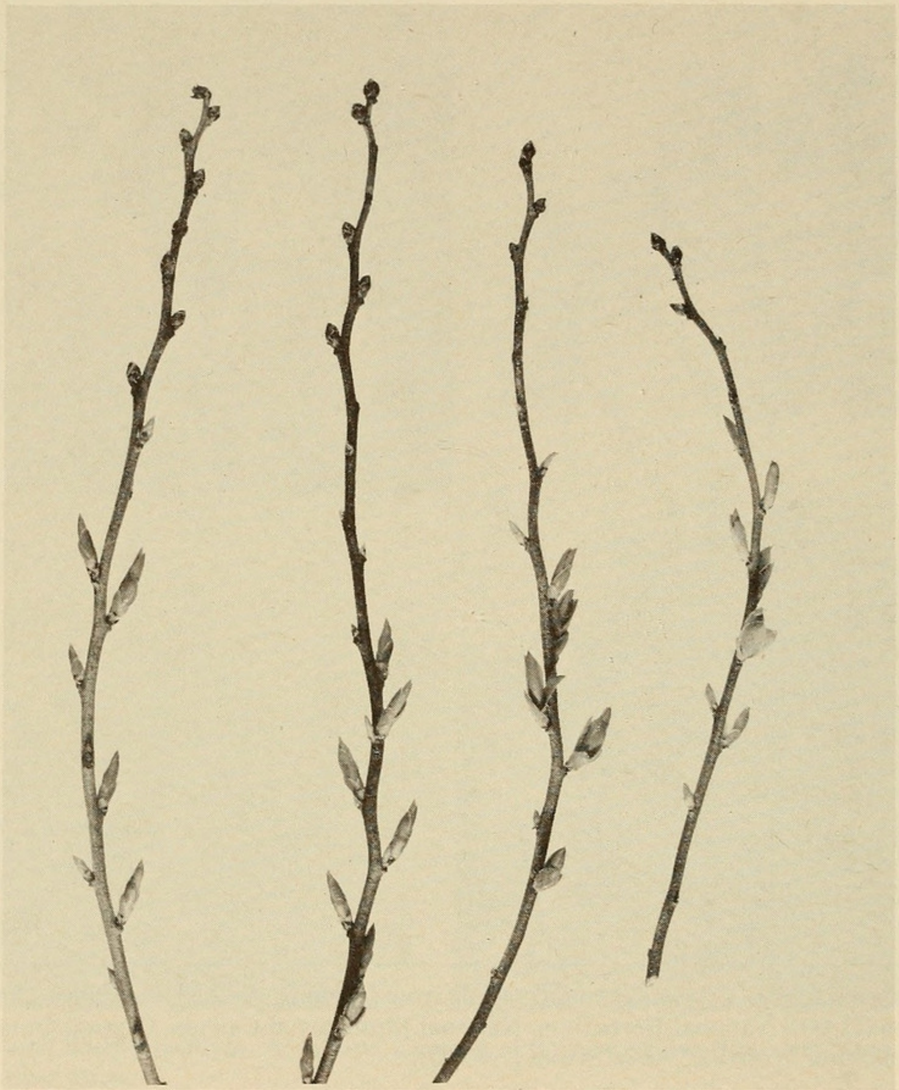

FIGURE 3. Winter injury on shoots of *Vaccinium angustifolium*.

In New Brunswick, Hall (1955) found that 0.5% of full sunlight under a *Picea rubens – Abies balsamea* canopy (Red Spruce – Balsam Fir) gave a minimum growth or just survival, 10% sunlight under a *Betula populifolia* canopy (Oldfield Birch) gave moderate vegetative growth but no flowering, and 50% sunlight (openings in canopy) gave flowering and fruiting.

Seed germination occurs only after periods of prolonged rainfall in late summer or early fall. Vander Kloet (1976a) found that seedling density was higher in a field sampled in Pictou County, Nova Scotia than in an old field at Leeds County, Ontario and he correlated this with higher precipitation and soil moisture.

Relative humidity may play an important role in fruit production. In dry years areas along the Atlantic coast have produced exceptional crops. Plants in the coastal fog belt are frequently covered with water droplets while plants farther inland experience stress from lack of moisture (e.g., withered berries, browned leaf margins).

(*b*) *Physiographic relations*. One of the most important factors limiting flowering and fruit development is the occurrence of late spring frosts on low-lying areas (Jackson et al. 1972b). Laboratory tests have shown that 6 h of −2.2°C were detrimental and a further reduction to −3.3°C for 6 h markedly reduced fruit set (Hall, Aalders, and Newbery 1971). *Vaccinium angustifolium* grows, yields, and reproduces well by rhizomes on both mineral and organic soils provided adequate moisture and aeration are available. It tolerates a wide range of soil conditions with best growth at low pH levels (Hall, Aalders, and Townsend 1964). In soils with much humus, most rhizomes grow in the top 5 cm. Jackson et al. (1972a) reported that soils such as Westbrook loam and Southampton sandy loam with a high percentage of stone or gravel provide the conditions most favorable to the emergence, growth, and development of seedlings.

(*c*) *Nutrient and water relations*. At the time of flower bud initiation the following suggested levels of nutrients (as % dry weight) should exist in the leaves (Townsend and Hall 1970): N, 1.50–2.00; P, 0.08–0.12; K, 0.40–0.55; Ca, 0.40–0.65; and Mg, 0.15–0.20. Lockhart (1959) first described the symptoms of mineral deficiency in *V. angustifolium*. Rayment (1965) clearly demonstrated the beneficial effects of applications of nitrogen to stands of *V. angustifolium* in Newfoundland.

Townsend et al. (1968) reported that sugars were lower, and starch was notably higher, in the rhizomes than in the leaves. Barker et al. (1963) found that the reducing sugars in fruits of five different clones varied between 7.4 and 7.9% of fresh weight.

Once established, the rhizone system of this species plays an important role in preventing slope erosion. If soil particles are washed into the network of rhizomes and shoots, new roots and shoots develop in the additional soil, favoring the plant and retaining the soil. The taproot system (Hall 1957) may penetrate to >1 m soil depth, allowing use of subsoil moisture reserves. Laycock (1967) states that the concentration of roots and rhizomes near the surface in the pine barrens of New Jersey allowed *V. angustifolium* and other species to absorb much of the water from light rains that fell during the growing season. The nutrient and pH requirements and competitive ability of this polymorphic species invite further investigation.

5. *Plant Communities*. Within the largely undisturbed part of its range, *V. angustifolium* is an important member of exposed headland vegetation, raised bogs, high moors, outcroppings on the Canadian Shield, mountain summits in the Gaspé, as well as in the herb–dwarf shrub stratum of open to moderately shaded pine to spruce woodlots and forests on coarse textured, mainly infertile soils in the Acadian, Great Lakes – St. Lawrence and Boreal Forest Regions of Rowe (1972), from Lake Winnipeg to the Atlantic coast.

But the species is most abundant in disturbance communities which result from clear-cutting, forest fires, and abandonment of agricultural land. The latter is especially noteworthy in the Maritime Provinces where, with a decline in soil fertility, land was abandoned during the early part of this century, providing many old field habitats for this species to colonize. Conners (1972) reports that by the late 1940s several of these fields were being cultivated. With the introduction of frozen foods on the American market a rapid development of the stands and industry took place.

Table 1 shows the contrasts among the floristic composition of three community types: (1) blueberry barrens on mainland Nova Scotia, (2) granite outcroppings near Kaladar, Ontario and, (3) the boreal conifer-hardwood forests of the Great Lakes region. Aside from *V. angustifolium*, the three community types have floristically little in common. Out of 71 species, excluding lichens and those with less than five occurrences, only *V. myrtilloides* (Sour-top Blueberry), *Gaultheria procumbens* (Teaberry), *Fragaria virginiana* (Wild Strawberry), *Rumex acetosella* (Sheep Sorel), and *Maianthemum canadense* (Wild Lily-of-the-Valley) are shared.

Maycock and Curtis (1960) have shown that *V. angustifolium* is an important component in both dry and wet sites of the boreal coniferous forest, but is unimportant on mesic sites. In Wisconsin, Curtis (1959) showed that it is the most prevalent groundlayer species in the northern dry forest and also an important constituent of northern dry-mesic forest, northern wet forest, bracken-grassland, and open bog. Lamoureux and Grandtner (1977) showed that this species was important in dune formation on Iles-de-la-Madeleine. Lavoie (1968) has described the Jack Pine (*Pinus banksiana*) forests with a *Kalmia angustifolia-Vaccinium* understory for the Lac de St. Jean area of Quebec. Community descriptions and tabulations of *V. angustifolium* in the Maritime Provinces are given by Hall (1955, 1959, 1975), Hall and Aalders (1968), and Hall et al. (1973, 1974, 1976).

6. *Growth and Development*

(a) Morphology. In the lowbush blueberry seedling (Figure 4) the oblong-elliptical cotyledons are about 2 mm long. The first seedling leaves are much smaller and usually more elliptical than mature leaves, making identification of young seedlings difficult. Stages in seedling development are given by Eaton and Hall (1961). Plants rarely flower or produce rhizomes until 4 yr after germination (Hall 1953). After plants reach a total width of 30 cm and rhizome growth occurs in several directions, expansion of the clone is more rapid. Rhizomes may grow up to 10 cm/yr on mineral soils and up to 50 cm on organic soils. Clones with intact rhizomes 10 m long have been excavated in Kings County, Nova Scotia. The minimum age of a parent clone may be estimated by counting growth rings from rhizome cross-sections (Figure 5). The importance of rhizome growth in the expansion of the clone has been outlined by Barker and Collins (1963b).

(b) Physiology. Forsyth and Hall (1965) have shown that photosynthesis is more rapid in the early morning and that temperature, CO_2 and leaf age affect photosynthetic rates. Rates of apparent photosynthesis in shoots at different light intensities have been reported by Bonn et al. (1969). Red leaf infected leaves (see 9(*c*)) and genetic mutant leaves had abnormally lower photosynthetic rates (Hall, Forsyth, Lockhart, and Aalders 1966). Strong

TABLE 1 — *Vaccinium angustifolium* Aiton, associated species on six granitic outcroppings from Kaladar, Lennox-Addington County to Mount Fitzsimmons, Leeds County, eastern Ontario; two barrens* on mainland Nova Scotia; and 11 dry Boreal Conifer – Hardwood Forests of the Great Lakes Region**

	Frequency of occurrence (%)		
Species	Eastern Ontario	Mainland Nova Scotia	Great Lakes region
Bare ground, rock, or litter	789 (21.6)	1716 (17.2)	NA
Epipetric lichens	522 (14.3)	—	NA
Fruticose lichens	210 (5.8)	—	NA
Polytrichum commune	28 (0.8)	199 (2.0)	NA
Polytrichum juniperinum	151 (4.1)	—	NA
Polytrichum piliferum	33 (0.9)	—	NA
*Lycopodium annotinum****	—	—	(12)
Lycopodium clavatum	—	6	(21)
Lycopodium obscurum	—	44 (0.4)	(22)
Lycopodium complanatum	—	6 (0.06)	(1)
Pteridium aquilinum	—	59 (0.6)	(78)
Juniperus communis	91 (2.5)	—	—
Danthonia spicata	159 (4.4)	536 (5.4)	—
Deschampsia flexuosa	144 (3.9)	—	—
Poa compressa	30 (0.8)	—	—
Agrostis scabra	6 (0.2)	—	—
Panicum subvillosum	—	14 (0.1)	—
Oryzopsis asperifolia	—	—	(8)
Carex pensylvanica	228 (6.2)	—	(3)
Carex nigromarginata	23 (0.6)	—	—
Carex umbellata	8 (0.2)	—	—
Luzula multiflora	—	6 (0.06)	—
Clintonia borealis	—	—	(17)
Maianthemum canadense	15 (0.4)	8 (0.08)	(66)
Salix bebbiana	—	35 (0.35)	—
Betula populifolia	—	30 (0.3)	—
Corylus cornuta	—	—	(23)
Rumex acetosella	47 (1.3)	4 (0.04)	(1)
Comandra umbellata	66 (1.8)	—	—
Anemone quinquefolia	—	—	(8)
Dalibarda repens	—	—	(8)
Spiraea alba	18 (0.5)	—	(1)
Spiraea latifolia	—	60 (0.6)	—
Spiraea tomentosa	—	29 (0.3)	—
Amelanchier sanguinea	11 (0.3)	—	—
Amelanchier spicata	19 (0.5)	—	—
Prunus virginiana	9 (0.3)	—	—
Prunus serotina	7 (0.2)	—	—
Pyrus melanocarpa	163 (4.5)	—	—
Rubus arundelanus	12 (0.3)	—	—
Rubus hispidus	—	41 (0.4)	—
Rubus idaeus	—	—	(6)
Waldsteinia fragarioides	—	—	(18)
Fragaria virginiana	5 (0.1)	39 (0.4)	(3)
Potentilla tridentata	—	46 (0.5)	—
Potentilla simplex	—	84 (0.8)	—
Polygala paucifolia	—	—	(22)
Rhus copallina	9 (0.2)	—	—
Rhus typhina	11 (0.3)	—	—
Aralia nudicaulis	—	—	(33)
Cornus canadensis	—	389 (3.9)	(61)
Ledum groenlandicum	—	14 (0.1)	—
Rhododendron canadense	—	106 (1.1)	—

TABLE 1—*(Concluded)*

Species	Frequency of occurrence (%) Eastern Ontario	Mainland Nova Scotia	Great Lakes region
Kalmia angustifolia	—	3271 (32.7)	—
Arctostaphylos uva-ursi	61 (1.7)	—	—
Gaultheria procumbens	23 (0.6)	348 (3.5)	(21)
Vaccinium myrtilloides	32 (0.9)	1 (0.01)	(20)
Vaccinium angustifolium	528 (14.5)	2139 (21.4)	(51)
Vaccinium vitis-idaea	—	27 (0.27)	—
Gaylussacia baccata	54 (1.5)	—	—
Trientalis borealis	—	—	(39)
Melampyrum lineare	—	—	(19)
Linnaea borealis	—	—	(12)
Viburnum rafinesquianum	21 (0.6)	—	—
Lonicera canadensis	—	6 (0.06)	—
Diervilla lonicera	8 (0.2)	—	—
Helianthus divaricatus	26 (0.7)	—	—
Aster cordifolius	8 (0.2)	—	—
Aster macrophyllus	—	—	(33)
Solidago puberula	—	648 (6.5)	—
Solidago rugosa	—	6 (0.06)	—
Solidago graminifolia	—	15 (0.15)	(3)
Antennaria neglecta	—	12 (0.12)	(1)
Prenanthes trifoliolata	—	5 (0.05)	—
Hieracium aurantiacum	—	8 (0.08)	(12)
Hieracium pratense	—	5 (0.05)	—
34 spp. with fewer than 5 occurrences	46 (1.3)	10 (0.1)	NA
Totals	3650 (100)	10,000 (100)	11 Stands

*Data from Hall and Aalders (1968) slightly modified and reduced.
**Data from Maycock and Curtis (1960) slightly modified and reduced.
***Scientific nomenclature of vascular plants follows *Gray's Manual of Botany* (Fernald 1950).

vegetative growth results when plants of different provenances are given 16 h light and 8 h dark periods per 24 h at 18°C. Flower buds are formed when plants are given 12 h light and 12 h dark per 24 h at 18°C. Hall et al. (1970) have shown that leaf anthocyanin concentration increases as the temperature decreases. *Vaccinium angustifolium* leaves develop brilliant red or yellow coloration in autumn.

(c) Phenology. Vaccinium angustifolium overwinters in a leafless state, with twigs yellow to reddish brown. At Kentville, vegetative and flower buds swell in early May if air temperatures have exceeded 10°C for 3–4 d. Flowering occurs from late May to mid-June. In cooler coastal areas, flowering may be delayed 2–3 wk (Bell 1953). Leaf development precedes, is concomitant with, or follows flowering depending on the particular clone. Leaves harden by mid-July, turn red in late August, and absciss by late October. In seasons following a burn-prune, vegetative growth commences a week after flower bud expansion and terminates in early July. Termination of shoot growth as evidenced by a black tip in the apical meristem (Bell 1950) occurs earlier on older unpruned bushes (Barker and Collins 1963a). Berries ripen in early August at Kentville, 2–3 wk earlier than in Cumberland County, Nova Scotia (Aalders et al. 1972). Flower primordia begin to develop shortly after cessation of vegetative growth (Bell and Burchill 1955a), but continue until late October if air temperatures remain >0°C with extended periods greater than 10°C. Thus temperature is an important regulator of plant phenology. But other factors including day length are important (Hall et al. 1970). At Lac de St. Jean, Quebec, flower bud formation is poor in some years, probably owing to early frosts. Hall and Ludwig (1961) have shown that different clones react differently to day length and temperature. By winter, primordia of all the floral organs are microscopically recognizable (Bell and Burchill 1955b).

Kender (1968) found that growth potential of rhizome buds was greater in early spring and late summer than in July.

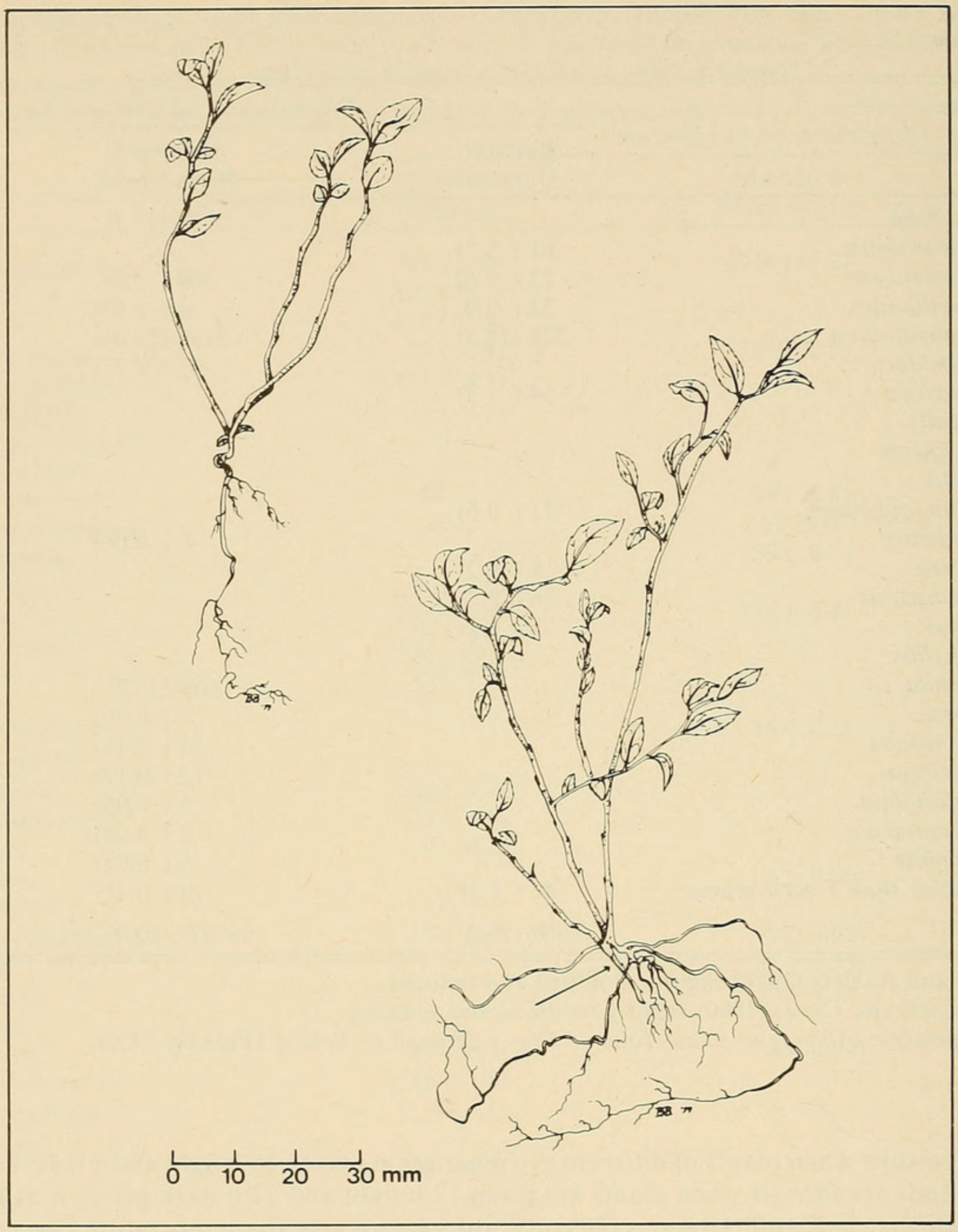

FIGURE 4. Sweet Lowbush Blueberry seedlings. Approximate age 3 yr upper left and 4 yr lower right. The latter has begun to form a rhizome (indicated by arrow).

7. *Reproduction*

(a) Floral biology. The flowers are insect pollinated, but not very attractive to bees, probably because the nectar volatiles are simple acetaldehyde and ethanol (Hall, Forsyth, Lightfoot, and Boch 1971). The stamens and pistil are functional as soon as the flower fully opens. The pistil remains highly receptive under field conditions for 4 d but fertility drops to about 20% by the 7th d (Wood 1962). Wood (1961a) also found that nectar volume and weight of nectar sugar increased with the flower age. After pollination the corolla turns pink and deteriorates very rapidly. This is associated with a marked increase in ethylene production (Hall and Forsyth 1967) and a high rate of respiration (Forsyth and Hall 1969) which persists through the small green fruit stage.

Glasshouse studies indicate that flowers selfed using pollen from the same flower or any flower of the same clone do not generally set fruit (Aalders and Hall 1961). The results of intercrossing and selfing six clones of *V. angustifolium* are given in Table 2. The vascular anatomy of the ovary has been described by Bell and Giffin (1957).

(b) Seed production and dispersal. It is rare to find a seedless fruit of *V. angustifolium* even in highly productive clones. Table 2 shows the number of seeds per berry in crosses completed in 1977 and 1978 among six clones.

Seeds are spread in the droppings of birds and mammals. The American Robin (*Turdus migratorius*) is a major seed disperser in southwestern New Brunswick as it often feeds and migrates just before fruit harvest by man (Eaton 1957). We have found seeds of *V. angustifolium* in the droppings of Black Bear (*Ursus americanus*), Red Fox (*Vulpes vulpes*), and Raccoon (*Procyon lotor*).

TABLE 2—Cross- and self-fertility of six selected clones of *Vaccinium angustifolium* in glasshouse trials, Kentville, Nova Scotia, 1977–1978

Female	Male	Percent of pollinated flowers forming fruits[1]	No. seeds per berry[2]	No. seeds per 100 pollinations	Percent seed germinations[3]
Augusta	× Brunswick	100	31	3100	88
	× Chignecto	70	24	1680	97
	× 510	65	25	1625	98
	× ME3	81	55	4485	93
	× ME4161	61	49	3026	88
	× Self	56	10	568	89
Brunswick	× Augusta	0	—	0	—
	× Chignecto	0	—	0	—
	× 510	2	16	39	94
	× ME3	2	20	49	90
	× ME4161	0	—	0	—
	× Self	0	—	0	—
Chignecto	× Augusta	74	30	2249	88
	× Brunswick	65	17	1131	91
	× 510	55	24	1298	90
	× ME3	56	28	1548	98
	× ME4161	45	25	1125	95
	× Self	0	—	0	—
510	× Augusta	12	46	580	84
	× Brunswick	95	34	3230	80
	× Chignecto	80	33	2632	86
	× ME3	11	41	461	82
	× ME4161	0	—	0	—
	× Self	0	—	0	—
ME3	× Augusta	18	37	644	89
	× Brunswick	65	39	2535	94
	× Chignecto	14	38	521	89
	× 510	6	22	140	95
	× ME4161	1	14	18	93
	× Self	0	—	0	—
ME4161	× Augusta	42	21	892	97
	× Brunswick	29	23	673	93
	× Chignecto	26	16	410	90
	× 510	39	23	907	91
	× ME3	75	30	2235	92
	× Self	14	6	77	74
Crosses		30.6%	29	1241	82
Selfs		11.7%	8	108	90

[1]Based on a sample of 20–80 hand-pollinated flowers.
[2]Seeds used here were the perfect ones, according to Bell (1957).
[3]Based on four lots of 50 seeds each, or on fewer if 200 not available.

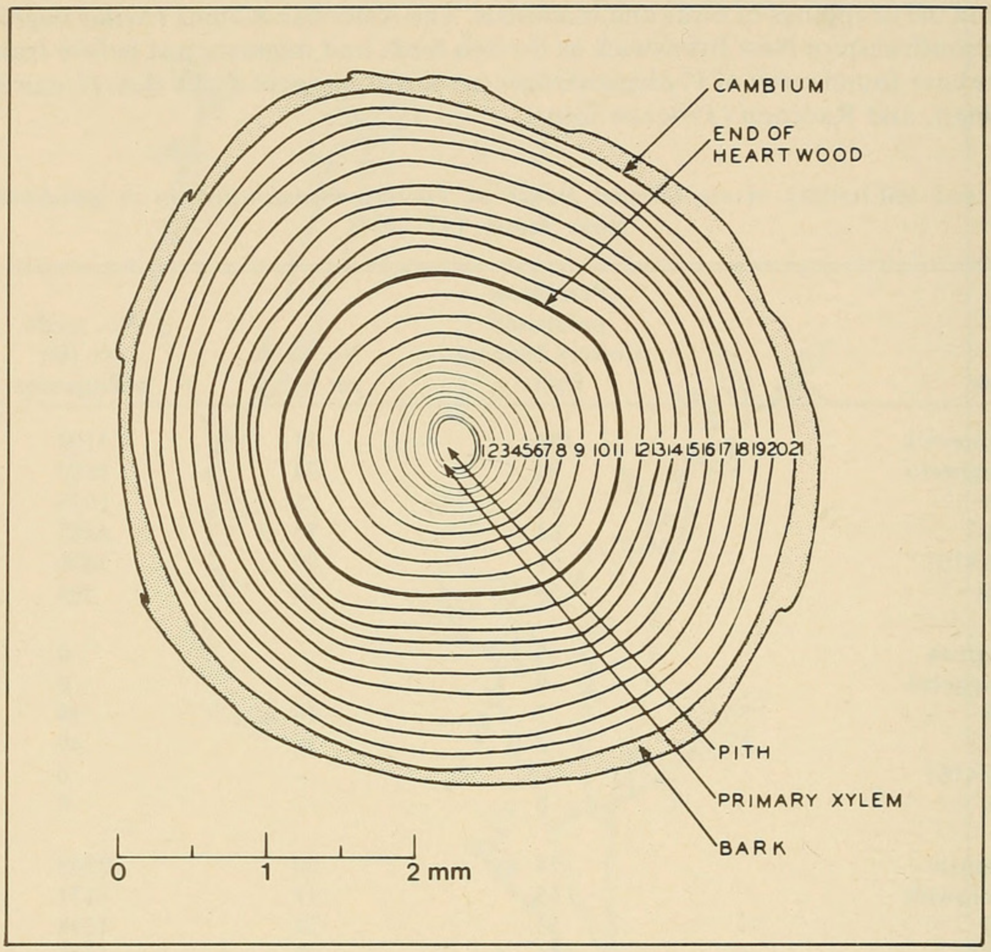

FIGURE 5. Cross-section of a *Vaccinium angustifolium* rhizome showing 21 growth rings. Counting these rings provides an estimate of the minimum age of the parent clone.

The number of seed (up to 64) found in a berry depends on genetic factors and environmental conditions. If weather is favorable (warm and dry) for insect pollination during the period of stigma receptivity, berries will have higher seed counts.

(c) Seed viability and germination. Fresh seed of *V. angustifolium* extracted from well ripened berries germinates readily at 21°C under 16 h light per 24-h period (Table 2) and usually takes 21 d. Germination is greater in light than in dark (G. W. Wood, personal communication). Seeds can be stored dry or frozen in fruit for 6 mo with no major reduction of viability (Aalders and Hall 1975). Seeds of *V. angustifolium* germinate well when sown on a soil mix, pH 4.7 in the glasshouse.

(d) Vegetative reproduction. Asexual reproduction occurs when the rhizomes are cut or killed by fire, shading, burrowing and/or frost action whereas sexual reproduction predominates in areas where the soil has recently been denuded by cultivation, flooding, or blow down of forest trees.

Plants may be propagated from either rhizome or stem cuttings. At Kentville, stem cuttings are taken just after black tip formation (6(*c*)) in early July and rooted under intermittent mist for 6 wk, with about 80% success (Hall et al. 1977). Studies of *in vitro* culture techniques for propagation are in progress (Nickerson and Hall 1976; Nickerson 1978).

8. *Population Structure and Dynamics*

Since dispersal is through bird and mammal droppings, one would expect a clumped dispersion pattern, and random sampling of three abandoned meadows with 28 1-m^2 quadrats in Pictou County, Nova Scotia gave a mean $\pm$ SE of 1.1 $\pm$ 0.39 seedlings, variance of 4.54, and a variance mean ratio of 4.3:1, confirming that expectation. One quadrat had a clump of 17 seedlings, the remainder one or none, rarely two seedlings. Seedlings may initially be clumped but as Vander Kloet (1976a) has shown, both in Nova Scotia and Ontario, seedling mortality is very high, i.e., > 99% of germinating seeds died even under partially controlled conditions.

The shoot crown diameters of plants established by seed can be converted to age classes according to a formula devised by Eaton and Hall (1961). Using this size-age relationship, Vander Kloet (1976b) found a marked difference in the age structure of *V. angustifolium* in old fields in eastern Ontario and eastern Nova Scotia. In the former, all seed-established plants exceeded 40 yr of age; in the latter the 11–20 yr age class was the most frequent.

On stable habitats such as mountain summits, exposed headlands, or outcroppings in the Canadian Shield, colonies of *V. angustifolium* may attain considerable age. Clones attain large size (>10 m diameter) and age (>150 yr). Vander Kloet (unpublished data) studied the species composition and population patterns of granitic outcrop communities in the Thousand Island region of Ontario and New York over a 10-yr period. Little or no change in species composition or abundance was observed; however, the positions of colonies of *V. angustifolium, Juniperus communis* (Common Juniper), and *Pyrus melanocarpa* (Black Chokeberry) shifted laterally. Vigorous peripheral branches of *Juniperus* shaded out colonies of *Vaccinium* and *Pyrus*, while the latter two invaded the senescing centers of *Juniperus* colonies. Similarly *Pyrus* and *Vaccinium* invaded the senescent portions of each other's colonies.

Turnover rates in *V. angustifolium* populations may be more rapid in the maritime provinces where the species is often a common component of old field succession, reaching peak abundance 15–25 yr after abandonment. By the judicious use of fire, this seral stage can be maintained as blueberry barrens for many years. Ordinarily the low growing *V. angustifolium* is soon shaded out by a variety of hardwood or conifer tree species. Once the forest canopy fully develops, it becomes uncommon and/or sterile. *Vaccinium myrtilloides* has a much higher survival potential than *V. angustifolium* in the mature Acadian boreal forest (Hall 1959).

9. *Interaction with Other Species*

(a) Competition. Competing plant species may be treated in four ecological site groups: (1) undisturbed natural; (2) post-logging; (3) old field; (4) blueberry crop.

On undisturbed natural sites within its range of suitable habitats, *V. angustifolium* has many competitors, as may be seen in Table 1. In relatively stable and oligotrophic *Pinus banksiana* woodlands and *Picea mariana* (Black Spruce) forests of the Boreal Forest and Great Lakes – St. Lawrence Regions (Rowe 1972) east of Lake Winnipeg, its major competitors for nutrients, water, and light in the herb–dwarf shrub stratum include *V. myrtilloides, Cornus canadensis* (Bunch Berry), *Gaultheria hispidula* (Creeping Snowberry), *Coptis groenlandica* (Goldthread), *Pteridium aquilinum* (Bracken Fern), *Clintonia borealis* (Corn-lily), *Comptonia peregrina* (Sweet-fern), *Maianthemum canadense*, and *Lycopodium* spp. Major competitors in the low shrub stratum include *Kalmia angustifolia* (Lambkill), *Ledum groenlandicum* (Labrador-tea), and *Diervilla lonicera* (Bush Honeysuckle).

On post-logging sites in eastern Canada, surviving and/or invading *V. angustifolium* populations must compete with surviving species that respond favorably to clearing, e.g., *Pteridium aquilinum* (Cody and Crompton 1975), *Dennstaedtia punctilobula* (Hay-scented Fern) (Cody et al. 1977), and *Cornus canadensis* (Hall and Sibley 1976), as well as with aggressive invader species, e.g., *Epilobium angustifolium* (Fireweed).

On old field sites in the Acadian Forest Region (Rowe 1972) *V. angustifolium* is an important seral species in the transition stage between field and forest. On coarse-textured soils in old fields of Prince Edward Island, *Myrica pensylvanica* (Bayberry) succeeds *V. angustifolium* before the *Picea glauca* excludes both (Hall 1975). On light sandy soils of the Lac de St. Jean of Quebec, *Comptonia peregrina* is a major invader of blueberry stands (Lavoie 1968).

Members of the blueberry crop group offer competition because they thrive under the cultural practices pertaining to lowbush blueberry culture. Probably the strongest competitor for space is *Kalmia angustifolia* (Hall et al. 1973). Its stem growth following burn-pruning exceeds that of *V. angustifolium* (Hall and Aalders 1968). Fertilizing stands of lowbush blueberry increases the growth of *Pyrus melanocarpa* relative to that of *V. angustifolium* (Hall et al. 1978). On poorly drained areas *Rhododendron canadense* (Rhodora) and *Spiraea latifolia* (Meadow-Sweet) (Hall et al. 1974) replace *V. angustifolium*.

(b) Symbiosis. The principal native pollinators in Maine and eastern Canada are species of Halictidae and Andrenidae although a few species of Bombidae, Anthophoridae, Colletidae, and Xylocopidae are of some importance (Boulanger et al. 1967). In eastern Ontario Vander Kloet (1976c) found that the solitary bees *Andrena vicina* and *A. carlini*, and the bumblebees *Bombus bimaculatus, B. terricola*, and *B. ternarius* were the important pollinators. Wood (1961b) found honeybees effective during a short period of bloom in New Brunswick.

Mycorrhizal associations in *V. angustifolium* were described by M. MacArthur (1955. Mycorrhiza in the blueberry. *In* Horticulture Division, Central Experimental Farm, Ottawa, Progress Report 1949-53. pp. 71–72) but the fungi involved were not identified.

(c) Predation and parasitism. Foliage of *V. angustifolium* is eaten by Black Bear (*Ursus americanus*), Eastern Cottontail (*Sylvilagus floridanus*), and White-tailed Deer (*Odocoileus virginianus*). Fruits are eaten by a number of mammals and many birds (Martin et al. 1951).

The important insects are Blueberry Maggot, *Rhagoletis mandax* Cn.; Black Army Cutworm, *Actebia fennica* (Tausch.); Chainspotted Geometer, *Cingilia catenaria* (Drury); Blueberry Flea Beetle, *Altica sylvia* Mall.; Blueberry Casebeetle, *Chamisus cribripennis* (LeConte) (see Wood 1978); Blueberry thrips, *Frankliniella vaccinni* Morgan and *Catinathrips kainos* O'Neill; Blueberry Tipworm, *Contarinia vaccinii* Felt.; sawflies, *Neopareophora litura* Klug, *Pristiphora idiota* Nort., *Pristiophora* sp.; Red-striped Fireworm, *Aroga trialbamaculella* Chamb.; and Stem Galler, *Hemadas nubilipennis* Ashm.

The stage of the life cycle of these insects which affects *V. angustifolium*, the manner of infection, the symptoms for recognition, and other details are given in Hall et al. (1975).

The important fungal diseases (Conners 1967) are monilinia blight caused by *Monilinia vaccinii-corymbosi* (Reade) Honey; botrytis blight (*Botrytis cinerea* Pers.); red leaf (*Exobasidium vaccinii* Wor.); witches-broom (*Pucciniastrum goeppertianum* (Kühn) Kleb.); dieback (*Diaporthe vaccinii* Shear); powdery mildew (*Microsphaera penicillata* (Wallr. ex Fr.) Lev. var. *vaccinii* (Schw.) W. B. Cke.); leaf rust (*Pucciniastrum vaccinii* (Wint.) Jorstad); leaf spot (*Septoria* sp.); Gloeosporium leaf spot (*Gloeosporium minus* Shear); and canker (*Godronia cassandrae* Pk. f. *vaccinii* Groves). A *V. angustifolium* plant which showed symptoms of shoestring virus disease was reported by Lockhart and Hall (1962).

(d) Toxicity and allelopathy. None reported to date.

10. *Evolution and Migration.* Camp (1942), on the basis of meager and unsubstantiated evidence (Vander Kloet 1978), assumed that *V. angustifolium* was a diploid species (i.e., gametes had 12 chromosomes) but as was pointed out in section 1(*h*) this cannot be confirmed. Therefore his allopatric speciation model for the species is also doubtful since Camp (1942) argued, rightly, that processes leading up to speciation in diploid populations differ markedly from those which give rise to tetraploid species. Vander Kloet (1977) has postulated a recent hybrid origin for *V. angustifolium*. He proposes that *V. boreale* migrated south or moved down mountain slopes where it came into contact with *V. pallidum* Ait. (Upland Low Blueberry) of oak-pine woods. Both of these species are diploids and by spontaneous chromosome doubling in a hybrid, an allotetraploid species is plausible.

Probably *V. angustifolium* migrated into the northern part of its habitat from the southern United States following the retreat of the last glacial ice. Birds doubtless accelerated this migration by dispersing seeds across water bodies and other habitat barriers.

An initial attempt has been made to separate clones of *V. angustifolium* on the basis of chlorophyll and anthocyanin content of bark from shoots (Wood and Barker 1963).

11. *Response Behavior*

(a) Fire. In natural communities or managed forests *V. angustifolium* survives wild fire or controlled burning below ground. Recolonization occurs by rhizome sprouting. Commercial stands are burn-pruned every second year resulting generally in unbranched stems which have more flower buds per stem and more flowers per bud than on older wood. There were no significant differences between fall- and spring-burned plants with respect to amount of shoot growth and number of flower buds per shoot (Hall, unpublished). Burning after the plants were in full leaf was detrimental to new shoot growth and flower bud formation (Eaton and White 1960). Black (1963) found that total fruit production over a 9-yr period was greater from burning every second year than from burning every third year. Smith and Hilton (1971) found that improved lowbush blueberry performance in Ontario after burning resulted mainly from the stimulative effects of nutrients in ash deposited on the surface soil.

(b) Grazing and harvesting. In New Brunswick, sheep were observed to graze grasses and sedges selectively rather than feed on *V. angustifolium* and *V. myrtilloides* (Hall, I. V. 1954. Ecological studies. *In* Dominion blueberry substation, Tower Hill, New Brunswick progress report 1949–1953. Canada Department of Agriculture. pp. 18–23). Removal of shoot tips by browsing White-tailed Deer (*Odocoileus virginianus*) results in lateral branching.

(c) Flooding. During the dormant period *V. angustifolium* can withstand considerable flooding such as that which occurs in many bogs, but it is not characteristic of wet habitats such as marshes or lake margins.

(d) Drought. During prolonged drought in early summer shoot growth is reduced. Dry weather later in the season results in shriveling of fruit and reduced flower bud formation. Irrigation prior to harvest substantially increases fruit size.

(e) Herbicides. 2,4-D causes a twisting of the terminal growth followed by browning and leaf fall. No data are available on other herbicides.

12. *Relationship to Man*

The fresh fruits of *V. angustifolium* have been a part of man's diet in North America since prehistoric times. Indians dried and pulverized fruits for blending with meat (Hedrick 1919). European settlers collected and preserved the fruit for jam, jelly, and preserves as well as eating them raw. These are still the main uses, but new products such as muffin mixes, ice cream, yogurt, and wine (Hope 1965) are using considerable quantities of fruit. For commercial use the fruits are quick-frozen by passing them through a tunnel of air at −29° to −34°C. For many years the only fruit markets for the species were in Canada and the United States. Recently the fruit has found some acceptance in western Europe where it competes with the European *V. myrtillus* L.

The area of lowbush blueberries under management is expanding each year in the Atlantic Provinces, which have programs for assisting growers to develop existing stands of *V. angustifolium.* Agriculture Canada is also providing funds through the New Crop Development Fund to determine the cost and feasibility of establishing plantings of this species within its range.

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