

NOMENCLATURE, TAXONOMY,
AND BIOSYSTEMATICS OF
VACCINIUM SECTION CYANOCOCCUS
(THE BLUEBERRIES) IN NORTH AMERICA.
I. NATURAL BARRIERS TO GENE EXCHANGE
BETWEEN VACCINIUM ANGUSTIFOLIUM AIT.
AND VACCINIUM CORYMBOSUM L.

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A number of clustering strategies such as flexible sorting (Lance and Williams, 1967), average link (Upgma), and Burr's (1970) incremental sum of squares (McNeill in preparation) and other techniques such as Rubin's (1967) clustering strategy (see Vander Kloet, 1972) were used on various subsets of 670 blueberry colonies collected along the Frontenac axis in Ontario and adjacent New York in 1970. Two morphologically distinct groups (*inter alia*) are consistently formed. One of these groups may be referred to the taxon *Vaccinium angustifolium* Aiton (sensu Hall and Aalders, 1961, and D. W. Smith, 1969, non Camp, 1945) and the other to *Vaccinium corymbosum sensu lato*.

Both of these taxa are tetraploid (Longley, 1927, Newcomer, 1941, Hall and Aalders, 1961, Löve and Löve, 1966). Darrow *et al.* (1944) reported that *Vaccinium angustifolium* was diploid; however, the supporting specimen they cite cannot be located. Since no cytological barriers to interbreeding exist between tetraploids, these taxa are considered compatible (Camp, 1942, 1945). They are sympatric in the sense that all the northern populations of *V. corymbosum* fall completely within the range of *V. angustifolium*. Furthermore, both species are acidophilic, although habitat preferences do exist. *Vaccinium corymbosum* occurs in a variety of wet habitats such as bogs, swamps, wet depressions, seepage slopes and ditch, river, and lake margins, while *V. angustifolium* occurs not only on a variety of dry sites such as granite outcrops, sand hills, headlands,

Table 1: Differences between *V. angustifolium* and *V. corymbosum* which may result in ethological isolation.

Taxon	habitat	plant height in cm	corolla length in mm	1971 mean blooming date
<i>V. angustifolium</i>	granite outcrops quartzite outcrops sandstone pavements oak parklands	10-60	4-6	May 18 $\pm$ 3 days
<i>V. corymbosum</i>	bogs swamps wet depressions	100-300	6-11	May 30 $\pm$ 4 days

poverty grass meadows and oak parklands, but also in raised bogs, along lake margins and along ditch banks where it occurs with *V. corymbosum*.

Along the Frontenac axis *Vaccinium corymbosum* occurs in bogs, swamps, occasionally in wet depressions on granite and quartzite outcrops while *V. angustifolium* occurs on sandstone pavements, oak parklands and on granite and quartzite outcrops where it comes into contact with *V. corymbosum*. Even here the taxa maintain their morphological distinctness although two, or at most three, hybrids were found in all localities where both species occur together.

It is against this background that the present investigation of the pollination syndrome (*sensu* Levin, 1971) of these two species was undertaken; Table 1 contrasts the characteristics which may lead to discrimination by the pollinator fauna and thus result in ethological isolation. Accordingly, in 1971, following a procedure described by Judd (1966), I collected pollinators on plants of these species. Pollinators were identified by M. Ivanochko (Vespidae), B. V. Peterson and G. E. Shewell (Diptera) and H. E. Milliron (other Hymenoptera) of the Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario. Table 2 lists the common bee species collected and their frequency of occurrence. It suggests that, in fact, the two species utilize different segments of the pollinator fauna. No honey bees and very few andrenids were caught on *V. corymbosum*; however, both taxa shared several of the *Bombus* spp. especially *Bombus bimaculatus*.

This overlap in pollinator taxa might not involve opportunities for pollen transfer if there were high pollinator specificity. Pollinator specificity was first reported by Aristotle, corroborated by Darwin (see Grant, 1950) and is still believed to be important (Heinrich, 1973). This concept is based on strict observation of preference for a single floral signal, i.e., the *Bombus ternarius* which I followed for 83 consecutive visits chose only *Vaccinium angustifolium* corollas.

Table 2: Numerical estimate of pollinators collected on *Vaccinium angustifolium* from four localities and on *Vaccinium corymbosum* from one locality.

Pollinators	Number caught on <i>V. angustifolium</i>	Number caught on <i>V. corymbosum</i>
<i>Bombus bimaculatus</i> *	49 (12)	20
<i>B. terricola</i>	30 (8)	3
<i>B. ternarius</i>	17 (4)	3
<i>B. impatiens</i>	12 (3)	2
<i>B. perplexus</i>	9 (2)	20
<i>B. affinis</i>	13 (3)	—
<i>B. griseocollis</i>	2 (+)	6
<i>B. pennsylvanicum</i>	2 (+)	2
<i>B. fervidus</i>	1 (+)	—
<i>B. vagans</i>	1 (+)	10
<i>B. sandersoni</i>	1 (+)	2
<i>Psithyrus ashtoni</i>	1 (+)	4
<i>Apis mellifera</i>	41 (10)	—
<i>Andrena carlini</i>	130 (38)	1
<i>A. vicina</i>	78 (19)	2
<i>A. crataegi</i>	6 (2)	1
<i>A. mandibulus</i>	—	1
<i>Nomada</i> spp.	14 (3)	—
<i>Osmia atriventris</i>	—	3
<i>Evylacus truncatus</i>	—	3
<i>Augochlora pura</i>	—	6

* () brackets indicate the average number of pollinators per locality.

The extent of flower constancy of bees can be verified by examination of the corbicular pollen loads. This is a time consuming procedure whose results are sometimes difficult to interpret. Grant (1950) has reviewed several pollen pellet analyses: those of Betts (1920), Brittain & Newton (1933), and Clements and Long (1923). Each of these workers reported that bees carried mixed pollen loads. However, Grant (1950, p. 384) reexamined some of Clements and Long's data and concluded that a 95% pure load in *Apis mellifera* is tantamount to a pure load. In effect Grant has belittled these reports.

In spite of these findings, the concept of ethological isolation remains entrenched in the literature and is frequently cited as part of the argument in favour of biological separation of taxa through floral signal isolation as in Levin (1971).

Since observation partially demonstrated ethological isolation between *Vaccinium angustifolium* and *V. corymbosum* colonies along the Frontenac axis, an examination was made of pollen pellets from a random sample of pollinators.

MATERIALS AND METHODS

From May 15, 1972, to June 10, 1972, five sampling areas were visited weekly, viz., (1) Rock Dunder, a 2 hm² granite outcrop near Morton, Ont. (031/309, 31 °/9 E). *Vaccinium angustifolium* colonies are abundant on this outcrop. (2) Burnt Hill, a 1.2 hm² granite outcrop near Morton, Ont. (035/297, 31 °/9 E). *Vaccinium angustifolium* colonies are abundant on this outcrop; moreover, in a small permanently wet depression a small population of *V. corymbosum* occurs. (3) Mt. Fitzsimmons, a steep granite outcrop near Lansdowne, Ont. (172/134, 31 °/8 E), supports a large population of *V. angustifolium* and along the margin of a *Nemopanthus mucronata* shrub carr (which occupies the centre of a small, permanently wet depression on top of the mountain) are several large colonies of *V. corymbosum*. (4) The Kaladar Jack Pine Ridge, a massive granite-gneiss ridge 0.5 km north of Kaladar, Ont. (312/475, 31

°/11 E) on which *V. angustifolium* occurs in abundance. (5) The Hebert Bog, near Upper Rock Lake, Frontenac County, Ont. (875/280, 31 °/8 W), a 2 hm² spruce bog which contains several large colonies of *V. corymbosum*, but no *V. angustifolium*. However, the surrounding granite-gneiss outcrops have several colonies of *V. angustifolium*.

At each of these sites, six colonies were chosen at random and every pollinator, which visited the colony in a ten minute period and hit at least three consecutive corollas, was trapped in a cyanide bottle, transferred to a vial of 70% alcohol, labelled, and stored in the refrigerator. In addition, flowers from all taxa in bloom at each sampling time were collected and, using the Wodehouse (1935) technique, reference pollen slides were prepared.

The vial containing the pollinator in 70% alcohol was shaken in order to transfer the pollen grains from the insect body into the alcohol, which was then decanted and centrifuged; after the supernatant was poured off, four drops of glycerol were added to the pollen pellet, mixed, and a single drop put on a slide, covered and sealed with a clear fingernail polish.

The slide was scanned under high power and the first 50 grains identified and recorded, using in the first instance the prepared reference slides and secondly the pollen atlases of Richard (1970) and of Kapp (1969).

RESULTS

Of the 50 pollen loads examined, only one was pure; i.e., the pollen load was composed entirely of pollen grains which could be assigned to *Vaccinium angustifolium*. The remaining 49 were mixed. However, if the investigator's error, the presence of wind borne pollen on the collecting sites, and accidental straying by the pollinator are taken into account, a cumulative background contamination of 10% or even 20% could occur. Even with such a liberal allowance for error, only 22% of the loads examined could be assigned to the "pure" class.

Table 3: Pollen load analysis of pollinators visiting *Vaccinium angustifolium* and *V. corymbosum* along the Frontenac axis.

pollen load	low <100 grains	moderate 100-10,000 grains	high >10,000 grains
pure loads			
>80%	1	2	8
mixed loads			
2 spp.	4	5	6
mixed loads			
3 spp.	7	3	—
mixed loads			
4 spp.	14	—	—

Table 3 gives these results in terms of “pure” and mixed classes only, since no difference in the ratio of pure to mixed could be detected in either loads examined from bees collected on corollas of *Vaccinium angustifolium* or *V. corymbosum* or in loads examined from different genera of bees. Out of the loads from four *Apis mellifera* examined one carried a pure load; out of the 19 loads from *Andrena* spp. six carried pure loads; out of the 16 loads from *Bombus* spp. four carried pure loads. No difference in constancy could be detected between sites.

CONCLUSION

This random collection of pollinators had few that were constant to a single floral signal. Linsley *et al.* (1963, 1964) have argued that pollinator specificity is a plastic response subject to modification by immediate circumstances. It is most pronounced in areas of high food-plant density. At low food-plant density, a pollinator is apt to feed on any suitable plant. This latter condition seems to fit the Frontenac axis condition quite well. Many of the plant species on these outcrops break dormancy during

the last week of April and begin to bloom in the mid-May period, for example, *Arctostaphylos uva-ursi* L., *Fragaria virginiana* Duchesne, *Amelanchier sanguinea* Pursh (DC.), *Amelanchier spicata* (Lam.) K. Koch., *Amelanchier arborea* (Michx. f.) Fern., *Prunus pensylvanica* L. f., *Prunus virginiana* L., *Aronia melanocarpa* (Michx.) Britton, and *Comandra umbellata* (L.) Nutt. Also, hibernating queen bees emerge at this time; these queens may try a number of different floral signals before they begin to specialize. Twenty-seven bees (or 58%) of the random sample had fewer than 100 pollen grains on their entire body.

The analysis of the loads suggests that ethological isolation between *Vaccinium angustifolium* and *V. corymbosum* does not exist along the Frontenac axis. Although this evidence is fairly conclusive for this area it would be unreasonable to generalize from such a local sampling regime. A valid generalization would have to be based on a wider sampling of the entire range of the species. Hence, using the same collecting technique as described above, pollinators were collected from several populations of *V. angustifolium* and *V. corymbosum* in Nova Scotia. Additional pollinators were also collected from several other *Vaccinium* section *Cyanococcus* species, when they occurred with either *V. angustifolium* or *V. corymbosum* in both Nova Scotia and Florida, in order to assess the level of constancy between *V. angustifolium* or *V. corymbosum* and their sister groups.

Description of additional sampling sites (methodology is the same as above): (1) From February 28 to March 3, 1973, 13 pollinators were collected on corollas of *Vaccinium myrsinites* and *V. corymbosum* which occur along margins of and in fire trenches cut through pine flatwoods, and on the fringes of Lake Annie near Archbold Biological Field Station in Highlands County, Florida. (2) From May 27 to June 15, 1973, 87 pollinators were collected on five sites throughout Nova Scotia: a shrub zone, which contained both *V. corymbosum* and *V. angustifolium* colonies, surrounding Lake George, near Port Maitland, Yarmouth County; sand hills with *V. myrtilloides* and *V. angusti-*

folium on the northern edge of Wolfville, Kings County; a blueberry (*V. angustifolium*) headland near High Head, Yarmouth County; an abandoned pasture, which has been invaded by *V. angustifolium* and *V. myrtilloides*, 1.5 km N of West Branch, Pictou County; and finally an extensive blueberry barren (*V. angustifolium*) 2.6 km W of Merland, Antigonish County.

Results: The results, given in table 4, show the same pattern as those given in table 3. Again the incidence of low pollen loads is associated with mixed pollen loads, and vice versa, a high pollen load with a tendency towards specificity.

Table 4: Pollen load analysis of pollinators visiting *Vaccinium* § *Cyanococcus* in Florida and Nova Scotia heath communities.

pollen load	pollen load		
	low <100 grains	moderate 100–10,000 grains	high >10,000 grains
pure loads			
>80%	5	9	12
mixed loads			
2 spp	14	10	9
mixed loads			
3 spp	13	2	5
mixed loads			
4 spp	16	4	1

Moreover, these data do not support any more readily than the previous data the concept of ethological isolation in *Vaccinium* section *Cyanococcus*. Indeed the opposite seems to be more valid; pollinator activity increases the probability of gene exchange between taxa. The differences between taxa, such as those given in Table 1, are probably the result of selection pressures of the habitat.

In 1970, a series of warm nights, which began on April 22 and continued until May 5, resulted in rapid floral axis

expansion in *Vaccinium corymbosum* colonies in bogs and depressions (indeed several precocious colonies of *V. angustifolium* on the surrounding upland outcrops had already begun to bloom). However, on the nights of May 5 and 6, the temperature fell to -3°C and -2°C respectively in the hollows, while on the slopes and uplands the temperature remained at 0°C and 1°C respectively, causing severe frost damage to the expanded flower buds of *V. corymbosum* while the *V. angustifolium* flowers were not damaged at all.

On August 21, 1970, only the serotinous colonies of *Vaccinium corymbosum* bore fruit; the frost damaged shrubs had a few green berries which had been infected by *Molina* spp. and contained no ripe ovules.

Brown, McKay and Chapman (1968) give May 15 as the mean date for the last occurrence of 0°C for the sample area. But since the topography is heterogeneous, the probability of frost occurring at a later date in the hollows is very high (Geiger, 1966, p. 393).

Vaccinium growth and development is closely related to night-time temperatures (Geiger, 1966, p. 439). But if night-time temperatures fall below -2.2°C for more than two consecutive hours irreversible frost damage occurs (Hall, Aalders and Newbery, 1971). In short, along the Frontenac axis, selection is against precocious shrubs of *V. corymbosum*.

The reverse holds for *Vaccinium angustifolium*; here selection acts against serotinous colonies. The soil on the granite and quartzite ridges and outcrops is very shallow and discontinuous, which, in conjunction with $40\text{--}45^{\circ}\text{C}$ temperatures at ground level during June, July and August, and unpredictable precipitation, often result in severe summer droughts (Vander Kloet, 1973). Consequently, late flowering colonies of *V. angustifolium* produce few if any mature berries. I have observed racemes of wilted green berries and fully formed leaf abscission layers on July 1, 1970 and 1973. In those years only the colonies that flowered between May 5 and May 12 fruited abundantly.

It is these countervailing selective pressures which account for the phenological difference given in Table 1. Moreover, since the pollinator data suggest some constancy and some specialization in feeding behaviour, the different flower size and plant height may well restrict some cross-pollination between the species. It is not a single factor but rather a combination of all these factors — habitat, phenology, plant height, corolla length, and pollinator frequency and constancy — which is effective in the evolution and the retention of the species' distinctiveness.

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