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Challenges Facing Pollination and Fruit Set in Indigenous Blueberries (*Vaccinium angustifolium* Ait.)

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Introduction

As the turn of the century approaches, the lowbush blueberry (*Vaccinium angustifolium* Ait.) is becoming highly valued for its health benefits especially its antioxidant properties. Research performed by the USDA Human Nutrition Research Center on Aging at Tufts University has concluded that the blueberry is a leading source of antioxidant phytonutrients (Prior, 1998). Greater consumer usage will demand an increase in production efficiency. Consequently, research interests are focusing upon increased potential and actual yield through a better understanding of the growth, development, and optimal management practices for the crop.

Background of the Lowbush Blueberry

Lowbush blueberries are produced on over 42,000 ha of native stands in Maine, the Maritime provinces and Quebec (Heppler and Yarborough, 1991). *Vaccinium* species are long-lived, predominantly out-crossing, woody perennials native to North America (Bruederle et al., 1991). The plant flourishes in acidic, well-aerated, sandy soils high in organic matter (Korcak, 1986). Plants spread by rhizomes and fields originate when competing vegetation is removed. Most commercial fields are managed in a two-year cycle. Primarily vegetative growth occurs during the first year, while the second year consists of flowering and fruiting.

The lowbush blueberry is typically shallow-rooted plant with as much as 85% of the stem existing as a shallow underground

rhizome. The roots extend 6-25 cm below the soil surface and are often invaded by mycorrhizal organisms (Hancock, 1995). Although this plant is shallow rooted, it possesses a unique physiological trait of feeder roots that can be found as deep as 90 cm (Davies and Albrigo, 1983). These roots are important during periods of drought by providing water and mineral nutrients not available to the rhizomes (Hall, 1957).

Desirable lowbush traits include low stature, early fruit maturation, uniform ripening, drought resistance, precocity, fine picking scar, high productivity and sweetness (Galletta and Ballington, 1996). Undesirable traits include self-infertility, small fruit size, small stature, spreading habit, softness of fruit and low fruit acidity (Galletta and Ballington, 1996). Three traits of interest to blueberry breeders include fruit size, delayed bloom to avoid late spring frosts, and early ripening to take advantage of high market value (Finn and Luby, 1986).

The Lowbush Blueberry Flower and its Development

As with many woody species, flowers are initiated under field conditions the year preceding flowering and fruiting (Aalders and Hall, 1964). Bud formation is stimulated during short days and long nights with a photoperiod of less than 12 hours (Hancock, 1995). The ideal flower for maximum fruit production should possess a short corolla that widens at the middle to

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greater than 8mm and then narrows at the base (Lyrene, 1994b).

Buds remain dormant throughout the winter months (Hancock, 1995). Before the start of the growing season, the distal portion of a branch is characterized by a large, somewhat spherical terminal flower bud (Eck, 1966). Floral development begins in late June or early July; floral primordia appear late July and reproductive tissues are differentiated in August (Aalders and Hall, 1964). The flowers which open first are located closer to the base of the stem; then an upward succession is followed (Chiasson and Argall, 1996). The blueberry inflorescence is a raceme with the terminal bud opening last (Young, 1952). Flowering is a brief process, the blossom remains intact for only 7-10 days (Wood, 1962). By the seventh day pistil receptivity declines and between 15 and 60% of the blossoms set fruit (Wood, 1962).

The flower is urceolate (Lyrene, 1994a) and typically white in color (Eck, 1966). The corolla is bell-shaped and essentially closed with the petals united containing four or five lobes. There are eight to 10 stamens inserted at the base of the corolla which hang in a close circle about the style. The upper half of the anther is composed of two awns which allow for pollen dehiscence. *Vaccinium* ovaries have four or five cells, sometimes eight or 10 if there are false partitions and are considered "inferior" because they are attached to the calyx.

Self Incompatibility

Lowbush blueberries are capable of self-fertilization at low to moderate levels (Krebs and Hancock, 1988). It is not preferred as it results in little or no seed production and the seeds obtained are often sterile at maturity (VanderKloet, 1991). Cross pollination results in berries that are larger, ripen quicker, and have a higher seed count (Marucci, 1966). Due to large, sticky pollen tetrads that are not easily transferred by wind, wild clones are dependent upon insects for pollination (Marucci, 1966).

In 1993, Harrison et al. proposed that a post-zygotic mechanism, not self-incompatibility, caused the differences in reproductive fertility between self and cross-pollination. This is further supported by cytological evidence indicating self-pollen enters the embryo sac normally (Krebs and Hancock, 1988). Research has shown that 5% of all lowbush blueberry plants are male-sterile (Chiasson and Argall, 1996). Male-sterile plants possess shorter stamens, the pollen sacs are slightly shrunken and no pollen is produced (Hall and Aalders, 1961). In both selfing and out-crossing, fertility levels are under similar genetic constraints such as levels of inbreeding and the genetic constitution of the resulting zygote (Krebs and Hancock, 1988).

Efficient Pollination

Pollination is the single most important factor determining wild blueberry production (Chiasson and Argall, 1996). The requirement for bees in blueberry pollination was discovered by Colville circa 1910; Phipps discovered this for the lowbush blueberry in 1928-1929 (cited in Marucci, 1966). North American bee species, such as *Bombus* spp., that sonicate the flowers are the most efficient pollinators (Lyrene, 1994a). The bee extracts pollen by positioning itself at the aperture of the pendent corolla tube and vibrating its flight muscles. This vibration causes the pollen to pour out of the anthers onto its face (Lyrene, 1994b). Anthesis lasts 7 to 10 days depending upon the cultivar and environmental conditions (Hancock, 1995). Blueberry pollen is normally shed in tetrads with the 4 products of a meiotic division remaining together (Lyrene and Ballington, 1986). The transfer of pollen must occur frequently since quality fruit requires the presence of fertilized ovules (Chiasson and Argall, 1996). Higher temperatures during flower development causes wider corolla apertures allowing better access to the anthers and stigma, increasing the effectiveness of bee pollination (Lyrene, 1994b).

Four major groups of pollinators may be present within commercial blueberry

fields; bumble bees, solitary bees, honeybees and most recently alfalfa leafcutter bees (Chiasson and Argall, 1996). The most frequent pollinators of the lowbush blueberry include *Andrena vicina*, *A. carlini*, *Bombus bimaculatus*, *B. terricola*, *B. ternarius* and *B. perplexus* (VanderKloet, 1978). However, blueberries have poricidally dehiscent anthers and do not freely shed pollen as a result of honeybee (*Apis* spp.) visits (Lyrene, 1994a).

Fruit Development

Fruit development is representative of a double sigmoidal growth curve (Edwards Jr. et al., 1970), similar to that of peach, cherry and fig (Young, 1952). Three stages of growth are observed in the blueberry fruit development. In Stage I, there is a rapid increase in the pericarp following fertilization (Young, 1952), lasting ~29 days (Finn and Luby, 1986). Stage II is characterized by retarded development of the pericarp, concurrent with rapid embryo development (Young, 1952), lasting 5 to 56 days, depending upon the species (Finn and Luby, 1986). A secondary period pericarpal development to fruit maturity occurs in Stage III (Young, 1952). The final stage lasts 16 to 26 days (Finn and Luby, 1986). Four days may be required for the fruit to completely change from green to blue (Young, 1952).

Extensive maturity and genotypic differences have been noted in the chemical composition of lowbush blueberry fruit (Kalt and Mc Donald, 1996). Levels as well as the ratio of sugar and acid fractions are related to keeping quality of blueberries (Ballinger and Kushman, 1970). Fruit are noted for high soluble solids, a small, shallow scar (Ballington et al., 1984) and containing equal amounts of glucose and fructose and little sucrose (Kalt and Mc Donald, 1996).

Blueberries contain many seeds (Hancock, 1995), are usually bright blue in color, about 5-7 mm in diameter and have an excellent flavor (Eck, 1966). On average ripe blueberries contain 85% water, 0.7% protein, 0.5% fat, 1.5% fiber and 15.3% carbohydrates (Hancock, 1995). Color is affected by the total anthocyanin

content, the quantity and structure of surface wax, the pH, distribution of individual anthocyanins and the formation of metal complexes of anthocyanins (Sapers et al., 1984). Total anthocyanins range from 85 to 270 μg per 100 mg and are generally located in the epidermis and the hypodermis (Hancock, 1995).

Environmental Limitations on Development

Bloom, fruit development and ripening are all affected by the environment. In some areas, irrigation has been important in increasing crop production (Andersen et al., 1979). Relative drought tolerance has been attributed to the waxy leaf cuticle which may partially occlude the stomatal antechamber and lower stomatal conductances and subsequently water losses during drought (Davies and Johnson, 1982). In the lowbush blueberries, berries were very small during years of extreme drought (Young, 1952). Although moisture has an effect on fruit size, no effect was observed on the duration of Stages II and III in fruit development (Young, 1952). Fruit quality characteristics related to soluble solids vary depending on fluctuations in environmental factors, such as temperature and moisture (Ballington et al., 1984).

The Future

The consumer demand for products will elevate as the healthful antioxidant properties of the lowbush blueberry are further explored. Breeding efforts are limited due to the fact that the fruit are marketed as an indigenous or 'wild' crop. Therefore, increased demand can be met by improving production efficiency through a greater understanding of the physiology of the crop. Enhancing the conditions conducive to maximum bloom, pollination and fruit set will allow growers to optimize yields. In addition to current work, future research is required on an improved understanding of the morphological, phytochemical, abiotic, and biotic mechanisms governing floral induction and initiation, pollination and fruit set will provide a greater understanding.

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