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Understanding Yield-Contributing Factors of Cranberry *(Vaccinium macrocarpon Ait.)*

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Abstract

Cranberry (*Vaccinium macrocarpon* Ait.) is an economically important fruit crop native to northeastern continental America. Despite its importance, the cranberry market can be volatile. While the dynamics governing the cranberry market are complex, growers and handlers would benefit from improved methods of yield prediction. Improving methods of prediction necessitates an enhanced understanding of the biology influencing bud initiation and development, fruiting, and other yield-contributing factors. The objective of this report is to provide a review of the literature addressing yield and its relevant biology as it pertains to cranberry. Consideration is given to the physiological, genetic, and environmental factors that affect yield. Understanding these factors will enable investigators to appreciate and account for them during the development of improved prediction and management practices for this unique and important crop. Furthermore, a review of the literature will provide guidance as to what are important areas of future research for cranberry and similar fruit species.

The American cranberry (*Vaccinium macrocarpon* Ait.) is a perennial, low-growing, evergreen vine native to northeastern continental America (Eck, 1990). The genus *Vaccinium* is a member of the Ericaceae family and includes other horticulturally important crops, including blueberry (*V. corymbosum* L., *V. angustifolium* Ait., and others) and ligonberry (*V. vitis-idaea* L.). Native Americans were among the first humans to use cranberries in their diets (Klingbeil and Rawson, 1975). Since then, the cranberry plant has been domesticated and cultivation has expanded. Some of the contributors to global cranberry production include the United States (US), Canada, Chile, and Europe (FAO, 2012; Stang, 1997). The US dominates global production and major cranberry-producing states are Wisconsin, Massachusetts, New Jersey, Oregon, and Washington (Cranberry Marketing Committee, 2008). Approximately 15,580 hectares (38,500 acres) of cranberry were harvested in the US during 2011 (NASS, 2012). Production of this high-value crop can make significant contributions to a local and/or regional economy. In Wisconsin, a leader in cranberry production, the annual total economic impact to the state averages $300 million and underscores the economic importance of this crop in producing regions (Keene and Mitchell, 2010).

The cranberry industry conducts an annual crop estimate for the following year in order to assist with setting crop prices and monitoring production levels. One commonly used method of prediction is based on visual assessment of buds during the year prior to harvest. According to this method, relatively large and round buds are considered to be mixed, while small and narrow buds are considered vegetative. During the harvest year, fruit set is tabulated and used to verify predictions made the previous year. Despite widespread use of this method, inaccuracy has been reported to exceed 15% and this margin of error may increase with the introduction of new cultivars (“hybrids”) that exhibit differ-

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ent production characteristics (Dittl, personal communication). A more accurate approach to yield prediction and an improved understanding of the biology governing fruiting of cranberry may allow for improved estimates of crop productivity. Multiple studies on individual factors related to yield of cranberry have been conducted, but a complete synthesis of these factors is lacking. The purpose of this paper is to review the current body of literature as it relates to cranberry yield. By understanding these factors, we can better account for them during the research and development of improved prediction and management practices.

Growth, Development, and the Importance of Buds

The growth habit of cranberry consists of runners bearing vertical shoots known as uprights. Terminal buds develop on uprights and are either vegetative or mixed (reproductive). Vegetative buds eventually produce leaf-bearing uprights, otherwise known as vegetative uprights. In contrast, mixed buds produce reproductive uprights that have leaves, flowers, and fruit. Both types of uprights eventually develop a vegetative or mixed bud that overwinter and it is the latter type that contains flower initials that produce fruit the following year. Previous studies have shown that individual uprights often exhibit biennial bearing, with reproductive uprights developing vegetative buds and vegetative uprights developing mixed buds (Eaton, 1978; Elle, 1996; Roper et al., 1993). Although this alternating pattern of mixed bud formation on these two types of growth leads to biennial bearing among individual uprights, overall yield tends to be relatively stable because a single bed contains a mixture of uprights. Interestingly, new cultivars have been reported to exhibit extensive return bloom (Roper, 2006; Zeldin, personal communication). Return bloom is the formation of mixed buds on reproductive uprights, which circumvents biennial bearing tendencies. This characteristic has become a primary selection criterion in cranberry breeding programs due to its potential to enhance yield (Zeldin, personal communication).

Bud break occurs by early June and is visible as new stem and leaf tissue elongates from over-wintering buds. After stems elongate, bloom occurs acropetally and each flowering upright produces a range of two to seven flowers (Brown and McNeil, 2006; Eaton, 1978). Fruit set occurs following pollination, which is facilitated by honeybees and native pollinators (Brown and McNeil, 2006; Cane and Schiffhauer, 2003; Evans and Spivak, 2006). Fruit development and maturation occurs in 60 to 120 days and generally one to three fruit per upright develops to maturity (Dana, 1990). Concurrent with fruit set and maturation, bud initiation and development for the following season occurs in the apical region of the upright, thus continuing the cycle of cranberry growth.

The current understanding of cranberry bud initiation and development is based on research conducted on native selections and older cultivars during the early-to-mid 1900s. The results of these studies suggest that bud development is initiated in late June to early July and development continues until spring of the following year (Goff, 1901; Lacroix, 1926; Roberts and Struckmeyer, 1943). Despite the importance of these early studies, they were often limited by small sample sizes and utilized cultivars that may not reflect the properties of newer cultivars being put into production. Imaging technologies have also evolved since the publication of these studies. As a result, questions remain regarding the timing and mechanisms responsible for bud initiation and development. With recent cultivar releases and associated improvements in return bloom, additional questions have surfaced regarding how bud initiation and development among newer cultivars compares to native selections and older cultivars. Investigations of model plant systems, namely Arabidopsis (*Arabidopsis thaliana* L.), have made significant contributions towards understanding the biology of flower bud initiation and development in annual plants. Such investigations may also provide a foundation to better understand the flowering biology of perennial plants, such as cranberry.

As reviewed by Blázquez (2005) and Turnbull (2011), many investigators working with Arabidopsis have demonstrated that the product of *FLOWERING LOCUS T* (*FT*) mediates flowering. Analyses of FT show that it has many characteristics of florigen, the universal flowering hormone initially proposed by Chailakhyan in 1937. In long-day plants, *FT* is transcribed in the leaves upon accumulation of the photoperiod-sensitive CONSTANS (CO) protein. This, in turn, elicits a cascade of expression that leads to flowering and is referred to as the *photoperiodic pathway*. FT homologs with similar activity have been discovered in other plant species, including the woody perennial apple (*Malus* spp.), providing evidence that this conserved signal is a critical regulator of flowering in many plant species (Tränkner et al., 2010).

Other pathways to floral evocation in Arabidopsis and related species have been proposed. In the *carbohydrate pathway*, accumulation of sucrose in the apex is associated with expression of regulators that specify floral organ identity (Blázquez et al., 1998; Lejeune et al., 1993). This finding may provide a partial explanation for biennial bearing tendencies in cranberry, whereby accumulation of carbohydrates in the buds of reproductive uprights may be limited during fruit set and simultaneous bud induction. Studies on the effects of shading and leaf removal on cranberry uprights support this explanation (Roper et al., 1992; Roper et al., 1995; Roper and Klueh, 1994). Apical accumulation of gibberellins also occurs and precedes floral initiation, which provides evidence that gibberellins are involved in flowering (Blázquez et al., 1998; Eriksson et al., 2006). Gibberellins have also been shown to influence flowering by leading to the expression of key genes involved in flowering (Mutasa-Göttgens and Hedden, 2009). Yet, gibberellins have an antagonistic effect on flowering in many woody perennial species (Jonkers, 1979; Wilkie et al., 2008). Vernalization is also known to be important for flower development among many woody perennial species, including Ericaceous plants (Stuart, 1961).

The discovery of multiple pathways that influence the expression of floral meristem identity genes demonstrates that the transition to mixed bud development and flowering is complex. Furthermore, the presence of multiple pathways enables plants to respond to a host of factors that signal conditions favorable to flower formation. While the information pertaining to the flowering biology of Arabidopsis is valuable, it is important to be mindful that the mechanisms responsible in perennial plants, like cranberry, may differ. Nevertheless, this work may provide a foundation for investigators as they work to better understand the flowering biology of cranberry.

Factors Influencing Yield of Cranberry

Recognized factors effecting yield of cranberry can be categorized as being physiological, genetic, or environmental. These factors are not mutually exclusive and their interactions can affect yield within a given growing cycle.

Physiological factors

Studies on yield components of cranberry have determined that the proportion of reproductive to vegetative uprights within a defined area of a bed is an important determinant of yield (Eaton and Kyte, 1978; Eaton and MacPherson, 1978). Eaton et al. (1983) also found fruit set was an important determinant, while seed number per berry and upright length were of less importance. Later studies by Baumann and Eaton (1986) confirmed the importance of fruit set over other components, such as berry size and flower number per unit length of upright.

Considerable focus has been placed on understanding factors that influence fruit set given its important role in determining current-season yields. Recall that a single upright produces five to seven flowers (Brown and McNeil, 2006). Yet, only one to three fruit per upright usually develops (Dana, 1990). Intraplant competition for resources was initially postulated as being responsible for the disparity between flower number and fruit set (Baumann and Eaton, 1986). Carbohydrate relationships, such as photosynthate partitioning and resource allocation, have been recognized to have an influence on fruit set and yield (Gifford et al., 1984). Baumann and Eaton (1986) suggested that first-developing fruits basipetal on an upright may have a greater priority for carbohydrates and other metabolites relative to later-developing acropetal fruits. Competition within an upright could promote fruit abortion and reduction of fruit set above basal fruits. Resource competition could also lead to the depletion of carbohydrates needed for the formation and development of competent mixed buds for the following season, which has been proposed as an explanation for biennial bearing (Baumann and Eaton, 1986; Strik et al., 1991).

Subsequent studies have provided support for the resource allocation hypothesis. Birrenkott and Stang (1990) found an approximate doubling of fruit set at upper positions after the selective removal of the lowest two flowers at pre-bloom and late-bloom, supporting the explanation that developing fruits represent a significant carbohydrate sink. Investigations on seasonal and developmental changes in nonstructural carbohydrate levels have confirmed that carbohydrates are at their lowest concentrations when basal flowers on an upright are setting fruit and upper flowers are slightly past anthesis, while carbohydrate concentrations are at their greatest prior to bloom (Birrenkott et al., 1991; Hagidimitriou and Roper, 1994). Such temporal and spatial variation confirms that, during the brief interval between flowering and fruit set, carbohydrate concentrations undergo dramatic fluctuations in uprights and fruit set represents a significant carbohydrate sink.

Investigations on the sources and translocation patterns of photosynthates have complemented the current understanding of carbohydrate relationships in cranberry. Roper and Klueh (1994) demonstrated that the removal of new leaves at fruit set results in reduced fruit set, count, size, and yield, whereas removal of one-year-old leaves or leaves post fruit set has significantly less effect. Similar defoliation studies have corroborated these findings (Roper et al., 1992; Vanden Heuvel and Davenport, 2005). With the photosynthetic rate of new leaves being about double that of one-year-old leaves, photosynthetic activity of these tissues are important sources of carbohydrates for fruit development (Hagidimitriou, 1993). Movement and partitioning studies show most of the carbohydrates produced from new leaves are allocated to fruit, further underscoring the importance of new leaves for fruit development (Birrenkott and Stang, 1990; Roper and Klueh, 1996). Patten and Wang (1994) found removal of old, new, or a combination of old and new leaves also reduced important yield components, such as the percentage of reproductive uprights and fruit set. Moreover, they found defoliation reduced development of large buds they assumed to be mixed. Based on these studies, it can be inferred that conditions reducing or interfering with photosynthesis, carbohydrate production, and translocation can exacerbate resource competition. This could consequently lead to reductions in fruit set, impede mixed bud development, and contribute to yield losses.

Plant signaling compounds, such as hormones and other growth-regulating metabolites are essential signaling agents that help regulate plant growth and development. Yet, they have not been extensively studied in cranberry. Studies on biennial bearing of apple and pear (*Malus* spp. and *Pyrus* spp., respectively) have shown that seed-produced gibberellins inhibit the initiation of mixed buds that would otherwise contribute to next year's crop (Jonkers, 1979). Gibberellins may act similarly in cranberry. Synthetic gibberellins (e.g. Gibrel and gibberellic acid (GA)) applied to cranberry has resulted in increased fruit set, with GA applied at bloom approximately tripling fruit set (Devlin and DeMoranville, 1967). However, formation of mixed buds was reduced. Reduction in mixed bud development is likely due to the increased concentration of gibberellins from the application of the synthetics and any additional seed-produced gibberellins. Fruit size was also reduced by the application of gibberellins, resulting in an abundance of unmarketable berries. Application of paclobutrazol, an inhibitor of gibberellin biosynthesis, increases mixed bud formation, further supporting the role of gibberellins in cranberry (McArthur and Eaton, 1989). Other growth promoting and inhibiting hormones, including their interactions, likely affect bud initiation and development, as well as other aspects of growth and development crucial for yield. Yet, information on how hormones and other growth-regulating metabolites influence bud initiation and development in perennial plants, like cranberry, is lacking.

While growers desire to maximize fruit set and overall yield, overproduction of flowers may be an innate adaptive strategy to enhance the reproductive success of a given plant (Burd, 1998). Brown and McNeil (2006) noted the natural tendency of terminal flowers on an upright to abort and speculated that terminal flowers may provide a reserve in the event that basal flowers are destroyed. Additionally, they speculated terminal flowers may function as pollen sources for later-blooming flowers. Other explanations for excess flower production in angiosperms have been put forth. Burd (1998) summarizes four explanations for excess flower production in plants with hermaphroditic flowers. The "reproductive assurance" explanation predicts that overproduction of flowers may be an insurance strategy against losses of ovaries due to herbivory, parasitism, unfavorable weather, or mechanical damage. Under the "bet hedging" explanation, excess flowers may enable plants to adjust the number of fruits they mature during years of abundant or lacking resources, including pollen. The "wider choice" explanation maintains that extra flowers enable plants to select only the most superior ovaries to invest in for eventual fruit and seed production. Lastly, the "attraction mechanism" predicts that the production of excess flowers may serve to attract pollinators needed for fertilization, thus enhancing reproductive success. Bees have already been documented as being important pollinators in cranberry production, making the "attraction explanation" one of several applicable explanations (Brown and McNeil, 2006; Cane and Schiffhauer, 2003; Evans and Spivak, 2006). With this evolutionary perspective, overproduction of flowers and low fruit set may be a natural mechanism to enhance the overall reproductive fitness of the cranberry plant.

Fruit trees, such as apple, provide an example of how excess flower and fruit production can be managed in order to stabilize yield from year to year. Chemical thinning of tree fruits utilizes knowledge of carbohydrate and hormone relationships in the circumvention of biennial bearing and acquisition of fruits with adequate size. The appropriately timed application of synthetic auxins and cytokinins, such as naphthalene acetic acid (NAA) and 6-benzyladenine, respectively, removes excess flowers and fruits. Initiation of mixed buds and return bloom is subsequently promoted. Foliar application of nutrients, namely foliar-applied boron, has also been shown to increase fruit set and yield in several plants including sour cherry (*Prunus cerasus* L.) and avocado (*Persea americana* Mill. (Hanson, 1991; Lovatt, 1999). Yield has also been increased in *Vaccinium* crops, specifically cranberry and blueberry, through the foliar application of boron (DeMoranville and Deubert, 1987; Blevins et al., 1996). The mechanisms of increased fruit set due to boron are unclear. Plants may be deficient of boron early in the growing season, when soil temperatures are too low for adequate uptake (Swietlik and Faust, 1984). However, plants responding to boron often display no evidence of deficiency. Upon examination of reproductive tissues, plants given foliar treatments of boron generally display a greater number of pollen tubes reaching ovules and improved ovule viability (Blevins and Lukaszewski, 1998; Lovatt, 1999; Thompson and Batjer, 1950). Such findings suggest that the role of boron in improving yield may not be due to correcting nutrient deficiencies within vegetative tissues and has led to the speculation that there may be different nutritional requirements among vegetative and reproductive tissues of a plant.

Improving stress tolerance to abiotic and biotic factors has also contributed to increasing yields for many horticultural and agronomic crops. Maize (*Zea mays* L.) provides a classic example where increases in yield are often attributed to improved stress tolerance, particularly under conditions of high plant density and competition for resources (Tollenaar and Lee, 2002). Selection for improved stress tolerance, as well as subsequent energy and resource capture, has been the focus of many selective breeding programs seeking to enhance yield. The success of these breeding programs alludes to the importance of genetics in improving commercially important traits, such as yield. Increased yield of cranberry has already been noted among recent cultivar releases (Novy and Vorsa, 1993). Such promising results suggests that selective breeding will be essential in helping cranberry surpass current yield averages and come closer to meeting full yield potential. Furthermore, genetic and molecular tools provide a promising avenue towards gaining further insight on the mechanisms responsible for mixed bud development and fruit formation.

Genetic factors

Differences in cultivar performance have long been recognized in cranberry. For example, Elle (1996) determined differences exist in resource allocation strategies and genetic effects among the cultivars Ben Lear, Stevens, Early Black, Franklin, Howes, and Wilcox. Some cultivars currently in production are derived from native selections and/or crosses including native selections within the pedigree. Intracultivar heterogeneity has been increasingly noted among traditional cultivars of cranberry and may be responsible for yield variations within a perceived cultivar, despite similar environments and management practices (Fajardo et al., 2013; Novy and Vorsa, 1995). Such heterogeneity may be due to accidental hybridizations within commercial beds and the creation of rogue genotypes (Elle, 1996). Other potential sources of intracultivar heterogeneity include sharing of misidentified propagules among growers, seed germination from natives in the seed bank, and stolon encroachment from adjacent areas (Fajardo et al., 2013; Novy and Vorsa, 1995). Establishing new beds from plant material that has been verified as true-to-type can avoid the potential risks of intracultivar heterogeneity.

Several new cultivars have been released from selective breeding programs. These new cultivars are reputed to have greater yields relative to traditional cultivars (Novy and Vorsa, 1993). Enhanced fruit set, fruit size, color/total anthocyanin, and return bloom are a few of the promising characteristics of recently released cultivars (McCown and Zeldin, 2003). The characteristic of return bloom is of particular interest because it offers the potential to circumvent biennial bearing tendencies, which could increase yields. Furthermore, the issue of intracultivar heterogeneity has been found to be minimal among cultivars recently introduced to the cranberry industry (Fajardo et al., 2013). This may change over time due to some of the aforementioned factors, which is why many breeding programs have started to patent and protect plant material. New tools that enable cultivar verification are also becoming increasingly widespread and encouraged because yield limitations may be related to the genetic capacity of a given cultivar.

Environmental factors

The environment imparts a large influence on the yield potential of plants, including cranberry. Environmental factors affecting plant growth and development within a field setting include uncontrollable and controllable factors. Uncontrollable factors mainly relate to the climate of a location and include temperature, solar radiation, length of growing season, and other atmospheric conditions that affect plant growth and development. Controllable factors are those that can be managed through cultural practices and include fertility and pest control. Provision of irrigation is just one of several examples of how the effects of weather variables can be optimized by growers. Despite these approaches to optimize plant growth in a field setting, the environment still has a substantial effect on yield.

While multiple facets of the environment can influence plant productivity and ultimate yields, light and temperature are known to have the greatest effect on cranberries (Degaetano and Shulman, 1987; Franklin and Cross, 1948). Franklin and Cross (1948) evaluated the relationship between weather and cranberry yield in Massachusetts. Sunlight received from May through November (specifically May, August, September, and November) prior to the crop year and in February of the crop year were found to have the greatest effect on yield. Franklin and Cross speculated that sufficient sunlight during these periods of the growing cycle (August, September, and November) enabled plants to generate enough carbohydrates through photosynthesis to develop a mixed bud, withstand winter, and have enough reserves to grow the following season. The role of sunlight during the cooler months of February and May is speculated to be important in the prevention of developing oxygen-deficient conditions among flooded cranberry plants (Franklin and Cross, 1948). According to this assumption, sunlight promotes the release of oxygen, a product of photosynthesis. Furthermore, sufficient sunlight prevents respiration from exceeding photosynthesis and the subsequent depletion of carbohydrates. More recent studies, however, have demonstrated that oxygenation of spring floodwaters can actually lead to greater decreases in carbohydrates relative to floodwaters that remain unoxygenated (Botelho and Vanden Heuvel, 2005). Sunlight and associated radiant heat during flowering also favors pollinator activity, which is necessary for optimal pollination, fertilization, and fruit set (Cane and Schiffhauer, 2003).

Degaetano and Shulman (1987) measured the relationship of meteorological factors and yield in New Jersey from 1906 to 1984. Like Franklin and Cross (1948), light and temperature were found to be highly correlated with yield. Specifically, high temperatures during flowering and fruiting corresponded to low yields. Yield reductions during periods of high temperature were likely due to reduced pollen viability, dehiscence, dehydration, stigma viability, and subsequent fruit set (Sato et al., 2006). Vegetative upright production and development of mixed buds was promoted during warm temperatures experienced in the months of May, June, October, and November prior to harvest year (Degaetano and Shulman, 1987). Cold temperatures in late winter and early spring can also be beneficial in maintaining bud dormancy, which reduces the likelihood of premature growth and consequent frost damage to sensitive tissues. Temperature also affects nutrient uptake with a range of 18 to 24°C being optimal for the uptake of ammonium-based fertilizers (Roper et al., 2004).

Clearly, light and temperature affect plant productivity and resultant yields. Conditions interfering with optimal light and temperature conditions would consequently reduce yield. Light exclusion studies show carbohydrate concentrations are reduced by shading, but the effects on fruit set and yield were inconsistent (Roper et al., 1995). In a comparison among five cranberry production regions, DeMoranville et al. (1996) found moderate temperatures ranging between 16 to 30°C accounted for 80% of the variability associated with fruit biomass accumulation, whereas light had a less pronounced effect. Kumudini (2004) further explored the relationship between light and temperature. At temperatures between 15 to 35°C, saturating radiation levels were obtained at 600 to 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Such low saturating light levels can be achieved under partially cloudy conditions, which suggest that light should rarely be limiting within a field setting, provided shading within the canopy is minimal and floodwaters/ice are relatively clear. To date, however, no studies on light extinction within a cranberry canopy have been published.

Precipitation and soil-water relations are also critically important for shallow-rooted plants like cranberry. Cranberry roots are concentrated within the first 2.5 to 7.5 cm of the soil and lack root hairs (Dana, 1990; Eck, 1990). Soils of cranberry are predominately sand-based and drain rapidly. Moreover, cranberry stomata exhibit limited responsiveness to environmental conditions, which can lead to excessive evapotranspiration during unfavorably warm temperatures (Croft et al., 1993; Faraq and Palta, 1989; Hattendorf and Davenport, 1996). Observed midday depressions in leaf photosynthetic rates are likely to be related to heat and/or water stress and natural stomatal limitations, which can reduce photosynthetic efficiency (Kumudini, 2004). These combined features emphasize the importance of providing sufficient water for cranberry growth and development. In the study by Franklin and Cross (1948), precipitation was found to affect yield significantly. However, the importance of precipitation was not confirmed in the later study by Degaetano and Shulman (1987). This discrepancy is likely to be due to technological advances and changing production practices, such as the provision of irrigation and frost protection through sprinkler systems (Morzuch et al., 1983).

Conclusion

Several factors influencing yield of cranberry have been investigated and have contributed greatly to the current understanding of yield. Nevertheless, a cohesive study of yield has yet to be performed and applied within a field setting. The need to further understand yield-contributing factors has been recently emphasized with the introduction of several new cultivars that possess unique characteristics that differentiate themselves from traditional cultivars. Understanding the biological differences between traditional and new cultivars, as well as their implications on yield, will be crucial in the advancement of our understanding and management of this plant.

Literature Cited

Baumann, T.E. and G.W. Eaton. 1986. Competition among berries on the cranberry upright. J. Amer. Soc. Hort. Sci. 111(6):869-872.

Birrenkott, B.A. and E.J. Stang. 1990. Selective flower removal increases cranberry fruit set. HortScience 25(10):1226-1228.

Birrenkott, B.A., C.A. Henson, and E.J. Stang. 1991. Carbohydrate levels and the development of fruit in cranberry. J. Amer. Soc. Hort. Sci. 116(2):174-178.

Blázquez, M.A. 2005. The right time and place for making flowers. Science 309:1024-1025.

Blázquez, M.A, R. Green, O. Nilsson, M.R. Sussman, and D. Weigel. 1998. Gibberellins promote flowering of Arabidopsis by activating the LEAFY promoter. Plant Cell 10:791-800.

Blevins, D.G. and K.M. Lukaszewski. 1998. Boron in plant structure and function. Annu. Rev. Plant Physiol. Plant Mol. Biol. 49:481-500.

Blevins, D.G., C.L. Scrivner, T.M. Reinbott, and M.K. Schon. 1996. Foliar boron increases blueberry number and yield of two highbush blueberry cultivars in Missouri. J. Plant Nutr. 19(1):99-113.

Botelho, M.R. and J.E. Vanden Heuvel. 2005. High dissolved oxygen concentration of floodwater reduces carbohydrate concentration of cranberry uprights during flooding. HortScience 40(3):569-573.

Brown, A.O. and J.N. McNeil. 2006. Fruit production in cranberry (Ericaceae: *Vaccinium macrocarpon*): a bet-hedging strategy to optimize reproductive effort. Am. J. Bot. 93(6):910-916.

Burd, M. 1998. "Excess" flower production and selective fruit abortion: a model of potential benefits. Ecology 79(6):2123-2132.

Cane, J.H. and D. Schiffhauer. 2003. Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* (Ericaceae)). Am. J. Bot. 90(10):1425-1432.

Chailakhyan, M.K. 1937. Concerning the hormonal nature of plant development processes. Doklady Akad Nauk SSSR 16:227-230.

Cranberry Marketing Committee. 2008. 2008 Crop Year Retrospective. Accessed 8 Mar. 2013. <http://www.uscranberries.com>.

Croft, P.J., M.D. Shulman, and R. Avissar. 1993. Cranberry stomatal conductivity. HortScience 28:114-116.

Dana, M.N. 1990. Cranberry management, p. 334-362. In: G.J. Galletta and D.G. Himelrick (eds.). Small Fruit Crop Management. Prentice Hall. Englewood Cliffs, NJ.

Degaetano, A.T. and M.D. Shulman. 1987. A statistical evaluation of the relationship between cranberry yield in New Jersey and meteorological factors. Agr. Forest Meteorol. 40:323-342.

Devlin, R.M and I.E. DeMoranville. 1967. Influence of gibberellic acid and gibrel on fruit set and yield in *Vaccinium macrocarpon* cv. Early Black. Physiol. Plant. 29:587-592.

DeMoranville, C.J., J.R. Davenport, K. Patten, T.R. Roper, B.C. Strik, N. Vorsa, and A.P. Poole. 1996. Fruit mass development in three cranberry cultivars and five production regions. J. Amer. Soc. Hort. Sci. 121(4):680-685.

DeMoranville, C.J. and K.H. Deubert. 1987. Effect of commercial calcium-boron and manganese-zinc formulations on fruit set of cranberry. J. Hortic. Sci. 62(2):163-169.

Dittl, T. Research committee member. Wisconsin Cranberry Growers Association (WSCGA).

Eaton, G.W. 1978. Floral induction and biennial bearing in the cranberry. Fruit Var. J. 32:58-60.

Eaton, G.W. and T.R. Kyte. 1978. Yield component analysis in the cranberry. J. Amer. Soc. Hort. Sci. 103(5):578-583.

Eaton, G.W. and E.A. MacPherson. 1978. Morphological components of yield in cranberry. Hort. Res. 17:73-82.

Eaton, G.W., A.Y. Shawa, and P.A. Bowen. 1983. Productivity of individual cranberry uprights in Washington and British Columbia. Sci. Hortic.-Amsterdam 20:179-184.

Eck, P. 1990. The American Cranberry. Rutgers University Press. New Brunswick, NJ.

Elle, E. 1996. Reproductive trade-offs in genetically distinct clones of *Vaccinium macrocarpon*, the American cranberry. Oecologia 107:61-70.

Eriksson S., H. Bohlenius, T. Moritz, and O. Nilsson. 2006. GA_4 is the active gibberellin in the regulation of LEAFY transcription and Arabidopsis floral initiation. Plant Cell 18:2172-2181.

Evans, E.C. and M. Spivak. 2006. Effects of honey bee (Hymenoptera: Apidae) and bumble bee (Hypenoptera: Apidae) presence on cranberry (Ericales: Ericaceae) pollination. J. Econ. Entomol. 99(3):614-620.

Fajardo, D., J. Morales, H. Zhu, S. Steffan, R. Harbut, N. Bassil, K. Hummer, J. Polashock, N. Vorsa, and J. Zalapa. 2013. Discrimination of American cranberry cultivars and assessment of clonal heterogeneity using microsatellite markers. Plant Mol. Biol. Rep. 31(2):264-271.

Faraq, K.M. and J.P. Palta. 1989. Ultrastructure and surface morphology of cranberry plant (*Vaccinium macrocarpon* Ait.) with reference to Ethrel penetration. Acta Hort. 241:378-384.

Food and Agriculture Organization (FAO) of the United Nations. 2012. FAOSTAT: Cranberries. 15 Apr. 2013. <http://faostat3.fao.org/home/index.html>.

Franklin, H.J. and C.E. Cross. 1948. Weather in relation to cranberry production and condition. Mass. Agr. Expt. Stn. Bulletin 450.

Gifford, R.M., J.H. Thorne, W.D. Hitz, and R.T. Giaquinta. 1984. Crop productivity and photoassimilate partitioning. Science 225:801-808.

Goff, E.S. 1901. Investigation of flower-buds. Ann. Rept. Wisconsin Agr. Exp. Sta. 18:304-319.

Hagidimitriou, M. 1993. Carbohydrate partitioning and photosynthesis in cranberry. Univ. of Wisconsin-Madison, PhD Diss.

Hagidimitriou, M. and T.R. Roper. 1994. Seasonal changes in nonstructural carbohydrates in cranberry. J. Amer. Soc. Hort. Sci. 119(5):1029-1033.

Hanson, E.J. 1991. Sour cherry trees respond to foliar boron applications. HortScience 26(9):1142-1145.

Hattendorf, M.J. and J.R. Davenport. 1996. Cranberry evapotranspiration. HortScience 31(3):334-337.

Jonkers, H. 1979. Biennial bearing in apple and pear: a literature survey. Sci. Hortic.-Amsterdam 11:303-317.

Keene, A.A. and P.D. Mitchell. 2010. Economic impact of specialty crop production and processing in Wisconsin. Publication from Agriculture and Applied Economics at the University of Wisconsin-Madison. 19 Apr. 2013. <http://www.wiscran.org/special/libfile_files/media/317.pdf>.

Klingbeil, G.C. and J.M. Rawson. 1975. Wisconsin cranberry lore. University of Wisconsin-Extension. Madison, WI.

Kumudini, S. 2004. Effect of radiation and temperature on cranberry photosynthesis and characterization of diurnal change in photosynthesis. J. Amer. Soc. Hort. Sci. 129(1):106-111.

Lacroix, D.S. 1926. Cranberry flower-bud investigations. J. Agric. Res. 33(4):355-363.

Lejeune, P., G. Bernier, M.C. Requier, and J.M. Kinet. 1993. Sucrose increase during floral induction in the phloem sap collected at the apical part of the shoot of the long-day plant *Sinapsis alba* L. Planta 190(1):71-74.

Lovatt, C.J. 1999. Timing citrus and avocado foliar nutrient applications to increase yield and fruit set. HortTechnology 9(4):607-612.

McArthur, D.A.J. and G.W. Eaton. 1989. Cranberry growth and yield response to fertilizer and paclobutrazol. Sci. Hortic-Amsterdam 38:131-146.

McCown, B.H. and E.L. Zeldin. 2003. 'HyRed', an early, high fruit color cranberry hybrid. HortScience 38(2):304-305.

Morzuch, B.J., J. Kneip, and D.C. Smith. 1983. An econometric approach to modeling the effects of weather and technology on cranberry yields. Mass. Agr. Expt. Stn. Bulletin 683.

Mutasa-Göttgens, E. and P. Hedden. 2009. Gibberellin as a factor in floral regulatory networks. J. Exp. Bot. 60(7):1979-1989.

National Agricultural Statistics Service (NASS). 2012. Noncitrus fruits and nuts 2011 summary. United States Department of Agriculture (USDA). Accessed on 25 Aug. 2012. <http://www.nass.usda.gov/>.

Novy, E.M. and N. Vorsa. 1993. Cranberry variety fruit yield and yield components. Abstract. HortScience 28(4):258.

Novy, R.G. and N. Vorsa. 1995. Identification of intracultivar genetic heterogeneity in cranberry using silver-stained RAPDs. HortScience 30(3):600-604.

Patten, K.D. and J. Wang. 1994. Leaf removal and terminal bud size affect the fruiting habits of cranberry. HortScience 29(9):997-998.

Roberts, R.H. and B.E. Struckmeyer. 1943. Blossom induction of the cranberry. Brief paper. Plant Physiol. 18(3):534-536.

Roper, T.R. 2006. The physiology of cranberry yield. Compilation of articles published in the Wisconsin Cranberry Crop Management Newsletter. Volume (XIX). 15 Apr. 2013. <http://scholarworks.umass.edu/cranberry_factsheets/16/>.

Roper, T.R. and J.S. Klueh. 1994. Removing new growth reduces fruiting in cranberry. HortScience 29(3):199-201.

Roper, T.R. and J.S. Klueh. 1996. Movement patterns of carbon from source to sink in cranberry. J. Amer. Soc. Hort. Sci. 121(5):846-847.

Roper, T.R., J. Klueh, and M. Hagidimitriou. 1995. Shading timing and intensity influences fruit set and yield in cranberry. HortScience 30(3):525-527.

Roper, T.R., A.R. Krueger, C.J. DeMoranville, N. Vorsa, J. Hart, and A.P. Poole. 2004. Rate of ammonium uptake by cranberry (*Vaccinium macrocarpon* Ait.) vines in the field is affected by temperature. HortScience 39(3):588-590.

Roper, T.R., K.D. Patten, C.J. DeMoranville, J.R. Davenport, B.C. Strik, and A.P. Poole. 1993. Fruiting of cranberry uprights reduced fruiting the following year. Note. HortScience 28(3):228.

Roper, T.R., E.J. Stang, and G.M. Hawker. 1992. Early season leaf removal reduces fruit set and size in cranberry (*Vaccinium macrocarpon* Ait.). Note. HortScience 27(1):75.

Sato, S., M. Kamiyama, T. Iwata, N. Makita, H. Furukawa, and H. Ikeda. 2006. Moderate increase of mean daily temperature adversely affects fruit set of *Lycopersicon esculentum* by disrupting specific physiological processes in male reproductive development. Ann. Bot. 97:731-738.

Stang, E.J. 1997. The emerging cranberry industry in Chile. Acta Hort. 446:159-163.

Strik, B.C., T.R. Roper, C.J. DeMoranville, J.R. Davenport, and A.P. Poole. 1991. Cultivar and growing region influence return bloom in cranberry uprights. HortScience 26(11):1366-1367.

Stuart, N.W. 1961. Initiation of flower buds in Rhododendron after application of growth retardants. Science 134(3471):50-52.

Swietlik, D. and M. Faust. 1984. Foliar nutrition of fruit crops. Horticulture Reviews 6:287-355.

Thompson, A.H. and L.P. Batjer. 1950. The effect of boron in the germinating medium on pollen germination and pollen tube growth for several deciduous tree fruits. Proc. Amer. Soc. Hort. Sci. 56:227-230.

Tollenaar, M. and E.A. Lee. 2002. Yield potential, yield stability, and stress tolerance in maize. Field Crop Res. 75:161-169.

Tränkner, C., S. Lehmann, H. Hoenicka, M. Hanke, M. Fladung, D. Lenhardt, F. Dunemann, A. Gau, K. Schlangen, M. Malnoy, and H. Flachowsky. 2010. Over-expression of an *FT*-homologous gene of apple induces early flowering in annual and perennial plants. Planta 232(6):1309-1324.

Turnbull, C. 2011. Long-distance regulation of flowering time. J. Exp.Bot. 62(13):4399-4413.

Vanden Heuvel, J.E. and J.R. Davenport. 2005. Effects of light, temperature, defoliation, and fruiting on carbon assimilation and partitioning in potted cranberry. HortScience 40(6):1699-1704.

Wilkie, J.D., M. Sedgley, and T. Olesen. 2008. Regulation of floral initiation in horticultural trees. J. Exp. Bot. 59(12): 3215-3228.

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