SOURCE-SINK INTERACTIONS IN FLOWERING AND FRUITING SOUTHERN HIGHBUSH BLUEBERRY

By

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Experiments were conducted to test the hypothesis that flower bud density (FBD) (flower bud·cm^{-1} cane length) affects vegetative budbreak and subsequent reproductive and vegetative development in two southern highbush blueberry (*Vaccinium corymbosum* L.) cultivars, 'Misty' and 'Sharpblue'. The effect of carbohydrate reserve concentrations on vegetative budbreak and subsequent reproductive and vegetative development was also examined.

The number of vegetative buds that broke dormancy and grew decreased as FBD increased on individual canes of field-grown plants or on entire plants of container-grown 'Misty' and 'Sharpblue' plants. Leaf area and leaf area:fruit ratios decreased as FBD increased. Although net CO_2 exchange rates (NCER) for individual leaves increased as FBD increased in 'Sharpblue' at the time of fruit

ripening, whole-canopy NCER at fruit ripening decreased as FBD increased in both 'Misty' and 'Sharpblue'. Fruit fresh weight increased and the fruit development period was shortened as the leaf area:fruit and whole-canopy NCER:fruit ratios increased.

Plants placed in a greenhouse with enriched (ENR) CO_2 concentrations (≈700 $\mu mol \cdot mol^{-1}$) for 38 days during December and Januuary had elevated root starch concentrations compared to plants placed in an ambient (AMB) CO_2 greenhouse (≈360 $\mu mol \cdot mol^{-1}$). ENR plants had increased vegetative budbreak compared to AMB plants in 'Sharpblue' but not in 'Misty'. However, leaf area and whole-canopy NCER were greater in ENR compared to AMB plants in both cultivars. Fruit FW was higher in ENR plants compared to AMB plants only in 'Sharpblue'.

Root and cane starch concentrations at bloom, 28 days after bloom (DAB), and at fruit harvest decreased as FBD increased in AMB plants, but in ENR plants, root and cane starch concentrations decreased as FBD increased only at bloom and only in 'Misty'. Root and cane starch concentrations decreased between dormancy and 28 DAB in AMB and ENR 'Misty' and 'Sharpblue' plants, but, except for root starch in 'Misty', root and cane starch increased at fruit harvest. Root and cane dry weights were similar as FBD increased in AMB and ENR 'Misty' and 'Sharpblue' plants.

Large, early ripening fruit commands the best prices for producers. These studies demonstrated that by reducing FBD or increasing carbohydrate reserve concentrations, producers could potentially increase fruit size and advance ripening.

CHAPTER 1
INTRODUCTION

Floral budbreak and fruit set in many southern highbush blueberry (SHB) (*Vaccinium corymbosum* L.) cultivars begin prior to vegetative budbreak. Field observations indicate that heavy flower and fruit loads may delay and reduce vegetative budbreak and shoot growth in some SHB cultivars. This is supported by the observation that partial removal of flower buds by shoot tip pruning will increase vegetative budbreak. This suggests that initial flower and fruit load can influence the timing and extent of vegetative budbreak and shoot growth in SHB.

Flower and fruit load affect the extent of vegetative growth in other fruit crops. Reduced growth or death of roots occurs during periods of rapid fruit growth or high fruit load and leads to decline in some plants (Avery, 1969; Cannell, 1985; Chamont, 1993; Head, 1969; Maggs, 1963). In tomato (*Lycopersicon esculentum* L.) (Hurd et al., 1979; Murneek, 1926) and apple (*Malus domestica* Borkh.) (Schechter et al., 1992), new leaf production is lower and final leaf size smaller on fruiting plants compared to nonfruiting plants. Fruiting plants often have lower overall leaf area than nonfruiting plants (Avery et al., 1979; Head, 1969; Kappel, 1991; Maggs, 1963; Schaffer et al., 1986c; Schechter et al., 1994). Although high flower

and fruit loads have been observed to decrease vegetative growth in SHB, the extent of this reduction and the subsequent effect on reproductive growth are unknown.

The reduction in shoot growth associated with high flower and fruit loads may have a significant effect on leaf area:fruit ratios and reproductive growth. The effect of leaf area:fruit ratios on fruit size, quality, and rate of development has been studied in numerous fruit crops, and thinning is practiced for some tree fruits to increase leaf area:fruit ratios and fruit size. In rabbiteye blueberry (*Vaccinium ashei* Reade), a leaf:fruit ratio of one large leaf (≈20 cm^2) per fruit was needed for optimum fruit production (Patten and Neuendorff, 1989). However, there is no information on the effects of leaf area:fruit ratios on fruit development in SHB.

Flower and fruit load may also affect the net CO_2 exchange rates (NCER) of the leaves. High fruit loads can lead to increases in NCER on an individual leaf basis. However, NCER of fruiting plants compared to nonfruiting plants may not be greater on a whole-canopy basis due to differences in overall leaf area. Whole-canopy NCER and carbohydrate production may be more important than individual leaf NCER and carbohydrate production in determining final fruit size and maturity in SHB, but that has not yet been researched.

The reduction in vegetative growth associated with high flower and fruit loads may be related to insufficient carbohydrate availability. The level

of carbohydrate reserves and the ability to mobilize reserves may be critical in determining the timing and extent of vegetative budbreak, which in turn would influence subsequent reproductive and vegetative development. Differences in flower bud number may lead to significant differences in reserve carbohydrate levels. Additionally, some carbohydrate reserves may not be easily mobilized depending upon location of the reserves. The use of carbohydrate reserves and the subsequent need for their replenishment are apparent, but the levels of carbohydrate reserves, their accessibility, and their role in vegetative budbreak have not been studied in SHB.

The hypothesis to be tested in this research is that flower and fruit load affect the time and extent of vegetative budbreak and canopy development. This in turn was expected to affect reproductive development in southern highbush blueberry cultivars. The specific objectives are to determine 1) the effects of flower bud and fruit density on vegetative budbreak and development, leaf and whole-canopy net CO_2 exchange rates, carbohydrate reserve levels, fruit size, and fruit ripening period and 2) the effects of different carbohydrate reserve levels on vegetative budbreak and development, whole-canopy net CO_2 exchange rates, fruit size, and fruit ripening period.

CHAPTER 2
REVIEW OF THE LITERATURE

The cultivated blueberry is a member of the family *Eriacaceae*, the subfamily *Vaccinioideae*, the genus *Vaccinium*, and the subgenus *Cyanococcus* (Camp, 1945). Section *Cyanococcus* is indigenous to North America and several species are native to Florida. Although blueberries are currently cultivated worldwide, North America still produces the majority of the blueberries consumed. Florida, with its early growing season and early ripening cultivars, has been able to capitalize on the high prices available in April and May, but many production problems exist.

Growing conditions for blueberry production in Florida and the southeastern U.S. differ from those in the traditional northern blueberry growing areas. Florida has milder winters, a longer growing season, and higher average temperatures. This has led to the development of different cultivars of blueberries for production under Florida conditions. The southern highbush blueberry (SHB) cultivars, tetraploid interspecific hybrids of *Vaccinium corymbosum* and *V. darrowi*, are a promising class that includes 'Sharpblue', 'Misty, 'Flordablue', 'Avonblue', 'Gulfcoast', 'Reveille', 'Bladen', 'Cooper', 'O'Neal', 'Marimba', 'Blue Ridge', and 'Cape Fear'. In

1995, cultivated blueberry acreage in Florida was approximately 2300 acres of which 1100 acres were SHB cultivars (Andersen et al., 1995).

The SHB cultivars differ in many traits from their northern highbush blueberry parents. A major difference is that many SHB cultivars have a delay in vegetative budbreak relative to floral budbreak compared to the northern highbush blueberry. A delay in vegetative development may affect both reproductive development and further vegetative development.

Blueberry Growth and Development

In northern highbush blueberry, the axillary bud primordia that develop into vegetative buds for next year's growth are initiated along the stem axis as the stem grows during the spring (Gough et al., 1978a). Flower buds in blueberry are initiated during the summer and continue to differentiate through the fall and winter (Bell, 1950; Gough et al., 1978b). In Rhode Island, floral bud differentiation in 'Bluecrop' highbush blueberry plants began in August, and cell division continued until December, before going dormant (Gough et al., 1978b).

Vegetative budbreak in *V. angustifolium* plants growing in Halifax, N.S., Canada began in early May and floral budbreak occurred 3-4 weeks later, when the vegetative branches were almost fully expanded (Bell, 1950). Northern highbush blueberry plants followed a similar pattern (Gough et al., 1978a; Shutak and Marucci, 1966). However, in many SHB cultivars growing in Florida, floral budbreak can begin 3-4 weeks before

vegetative budbreak. Thus vegetative budbreak and new shoot growth occur concomitantly with reproductive growth. Field observations indicate that heavy flower and fruit loads may delay and reduce vegetative budbreak and shoot growth in some SHB cultivars. The reduction in vegetative budbreak and shoot growth associated with high flower and fruit loads may be related to insufficient carbohydrate availability.

Carbohydrate Availability

Plants contain many vegetative and reproductive meristems. These meristems and organs need similar resources for growth, in particular, carbohydrates, nutrients, and water. Some organs remain carbohydrate users (sinks) most of their lives, while other organs such as leaves become producers (sources). The timing and amount of both carbohydrate use and carbohydrate production can be critical within a plant.

Carbohydrates for growth must come from storage or from current production. Carbohydrates are produced by photosynthesis, but photosynthates may be stored in various plant parts for future use. Carbohydrate storage is especially important for perennial plants that must have a source of carbohydrates for growth when carbohydrate production is limited, such as in early spring when the plant is leafless.

Carbohydrate Reserves

Carbohydrate and nutrient reserves can play a key role in reproductive and vegetative growth, with roots and stems composing major storage

sites. The importance of carbohydrate reserves in spring growth of deciduous trees is evidenced by the fact that growth and dry weight accumulation in fruit and developing stems and leaves occur before any plant parts are present for substantial photosynthesis (Quinlan, 1969; Tromp, 1983). Generally, the fruit trees studied have shown a reserve carbohydrate maximum in late autumn around leaf fall and a minimum in early spring at around budbreak (Brown et al., 1985; Hansen, 1967; Oliveira and Priestley, 1988). The loss of dry weight in the root system over winter indicates its significance as a storage organ in apple (*Malus domestica* Borkh.) (Quinlan, 1969). Annual fluctuations of carbohydrate in apple are not as dramatic as in some fruit trees, as new leaves develop rapidly and start exporting when only one third to one half expanded (Pate, 1989; Wardlaw, 1968). However, Hansen (1971a) found that more than half of the metabolites for initial growth of apple shoots and flowers were not from current photosynthesis. This was true only during the development of the first 5-6 leaves, after which current photosynthesis supplied the majority of assimilates for further vegetative growth and flowering. Reserve carbohydrate depletion was also greater than accounted for by dry mass accumulation in new growth, indicating that a large portion of the carbohydrates were used in respiration (Hansen, 1967).

Sweet cherry (*Prunus avium* L.) flower and vegetative buds open simultaneously and so, having very little leaf area at flowering, must draw

heavily on carbohydrate reserves in the spring (Keller and Loescher, 1989). In sweet cherry, carbohydrate reserves were higher in the roots than in other tissues but they did not substantially decrease until budbreak. Total nonstructural carbohydrates (TNC) in the roots declined drastically following full bloom in sweet cherry, indicating their importance for growth in the spring (Roper et al., 1988).

The contribution of carbohydrate reserves to reproductive growth may depend upon the timing of vegetative budbreak. Floral and vegetative budbreak occur simultaneously in 'Bonita' rabbiteye (*Vaccinium ashei* Reade) blueberry, but in the rabbiteye blueberry, 'Climax', floral development may occur 28 days before vegetative budbreak (Birkhold, 1991; Birkhold et al., 1992). Root dry weight and root and shoot soluble sugars and starch concentrations declined in 'Bonita' between dormancy (31 days before anthesis) and anthesis (0 DAA) (Darnell and Birkhold, 1996). 'Climax' root dry weight declined from dormancy until fruit harvest, while root carbohydrate concentrations declined from dormancy until 28 DAA. Carbohydrate reserves were estimated to contribute ≈5% of the C needed for fruit development in 'Bonita', while reserves account for ≈17% of the C required for 'Climax' fruit (Birkhold, 1991).

Carbohydrate reserve levels may affect fruiting and vice versa. Large differences in carbohydrate levels are seen between 'on' and 'off' seasons in alternate bearing trees. A positive relationship was found between starch

concentrations in pecan (*Carya illinoensis* (Wang) K. Koch) roots and in-shell nut production (Wood, 1989), suggesting that low levels of carbohydrate reserves were involved in causing an 'off' or nonbearing year. Nonfruiting, 'off' year, pistachio (*Pistacia vera* L.) trees had 144% more starch reserves than fruiting trees (Weinbaum et al., 1994). Starch levels were also drastically reduced during an 'on' year in 'Kinnow' mandarin (*Citrus reticulata* Blanco) (Jones et al., 1975) and 'Wilking' mandarin trees, while starch levels were highest in the 'off' years (Goldschmidt and Golomb, 1982). The 'off'/'on' starch content (mg·g DW^{-1}) ratio was 17.4 in the roots but only 2.0 in the trunk, suggesting that starch in the mandarin tree trunk is not easily mobilized or recycled.

In some trees, reproductive growth is almost totally dependent upon carbohydrate reserves. California buckeye (*Aesculus california*) trees store carbohydrates in the spring and early summer and then fruit in the autumn when the tree is leafless. Carbohydrates in the branches dropped from ≈17% to ≈10% (g·g DW^{-1}) during fruit production, while root bark and wood TNC dropped from 21% to 17% and 6% to 3%, respectively, during fruiting (Mooney and Hays, 1973). Girdling the branches and trunk led to greatly reduced fruit production in California buckeye, suggesting that root reserves were an important source of carbohydrates (Newell, 1991).

In most fruit trees, starch acts as the major carbohydrate storage form, and starch levels fluctuate during the year depending upon the growth

activity of the tree. The main depletion in carbohydrate reserves occurs during budbreak in the spring for most deciduous species, as carbohydrates are used for vegetative and reproductive budbreak. Carbohydrate reserves provide both the C skeletons for initial spring growth and much of the energy for the growth processes. As seen in alternate bearing trees, carbohydrate reserve levels affect reproductive growth, and reproductive growth affects carbohydrate levels. Carbohydrate reserve levels may also affect vegetative development, as found in several forage crops (Chatterton et al., 1974; Rice et al., 1996), but data are scarce in fruit crops.

Carbohydrate Production

All carbohydrates are ultimately produced by photosynthesis. The major organs responsible for photosynthesis are the leaves, although photosynthesis in other plant parts may be important at times.

Fruit photosynthesis

Fruit photosynthesis may be significant in fruit growth especially early in fruit development, and in plants where flowers develop prior to or concomitant with leaves and shoots (Kappes and Flore, 1985; 1986). Fruit photosynthesis contributed 14-15% of the carbon (C) needed for fruit growth and development in 'Climax' and 'Bonita' rabbiteye blueberry (Birkhold et al., 1992). Fruit photosynthesis contributed ≈85% of the C needed from 5 to 10 days after anthesis (DAA). Although fruit

photosynthesis can play a major role in early fruit development, it supplies only a small portion of the total carbohydrates needed.

Leaf photosynthesis and carbohydrate export

Current photoassimilates from the leaves are the major source of carbohydrates needed for growth. The total amount of photoassimilates available from the leaves will depend upon the rate of leaf photosynthesis, carbohydrate export from the leaf, and total leaf area.

Photosynthetic rates. Photosynthetic rates vary greatly between species and cultivars. Mean maximum photosynthetic rates of 13.3-13.7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ for 'Calred' peach, 'Marianna' plum (*P. cerasifera* Ehrh), and 'Mazzard' sweet cherry were higher than for 'Royal' apricot (*P. armeniaca* L.) (6.7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) but lower than for 'Nonpareil' almond (*P. dulci* (Mill) D. A. Webb) (18 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) (DeJong, 1983). Maximum photosynthetic rates for different varieties of apple were approximately 22 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Avery, 1977), although rates of 27.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ have been reported for spur leaves on flowering shoots of 'Starkrimson' apple (Fujii and Kennedy, 1985).

Photosynthetic rates reported for 'Woodard' rabbiteye blueberry were from 5.6 to 11 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Davies and Flore, 1986a; 1986b). Photosynthetic rates of 12.6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ were recorded for 'Climax' rabbiteye blueberry (Merhaut, 1993). Maximum photosynthetic rates for 'Bluecrop' highbush blueberry ranged from 6.6 to 14.3 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$

(Cameron et al., 1989; Davies and Flore, 1986a; 1986c; Moon et al., 1987a; 1987b). Photosynthetic rates for 'Jersey' and several other highbush blueberry cultivars were similar to 'Bluecrop' but maximum rates for *Vaccinium darrowi* were only 8.6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Moon et al., 1987a; 1987b). *V. darrowi* also had lower dark respiration rates than 'Bluecrop' or 'Jersey' (1.06 vs. 1.57-1.61 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and lower mesophyll conductances (53.3 vs 96.8-77.5 mmol $CO_2 \cdot m^{-2} \cdot s^{-1}$). The photosynthetic temperature optima were 14-22C for 'Bluecrop', 18-26C for 'Jersey', and 25-30C for *V. darrowi* (Moon et al., 1987b). Photosynthetic rates taken at temperatures ranging from 29-36C were 11.1-14.2 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ for 'Sharpblue' SHB (Merhaut, 1993). No information on photosynthetic rates is available for other SHB cultivars. Photosynthetic rates are an important aspect of carbohydrate production, and differences between SHB cultivars may be important in their overall carbohydrate economy.

Photosynthesis, carbohydrate export, and leaf ontogeny. Leaf characteristics change during their development. Net photosynthesis generally increases to a maximum before gradually declining. In tobacco (*Nicotiana tabacum* L.), maximum photosynthetic rates of 11.4-15.8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ were achieved from 35-45% full leaf expansion (≈14 days) (Rawson and Hackett, 1974). Net photosynthesis declined to one-third of the maximum values by full leaf expansion (≈40 days) and approached zero at ≈55 days. Respiration remained at 6-7% of net photosynthesis. In

'Deltapine 16' cotton (*Gossypium hirsutum* L.) plants, peak photosynthetic rates of 25 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ were attained at 75-90% of full leaf expansion (Constable and Rawson, 1980). The photosynthetic rate remained steady for 12 days and then declined to 20% of the maximum value during the next 40 days. Dark respiration reached a maximum of 0.34 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ within five days of leaf unfolding when leaves were undergoing maximum growth. In 'Jastor' bean (*Phaseolus vulgaris* L.) plants, maximum leaf photosynthesis was reached at 68% of full leaf expansion (Catsky and Solarova, 1976). Dark respiration was greatest in the leaf as it unfolded and declined rapidly to a minimum just prior to full leaf expansion. 'Montmorency' sour cherry and 'Bing' sweet cherry leaves reached maximum photosynthetic rates when greater than 80% expanded (Roper and Kennedy, 1986; Sams and Flore, 1982). Photosynthetic rates remained high for 2-4 weeks before gradually declining. Maximum photosynthetic rates of $\approx$6.9 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ occurred in strawberry (*Fragaria virginia* Duchesne) leaves 0-3 days after full leaf expansion. Coffee (*Coffea arabica* L.) leaves reached full expansion in about 30 days, but photosynthetic rates continued to increase to a maximum of 3.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ when the leaves were 60-90 days old (Yamaguchi and Friend, 1979). The increase and decrease in leaf photosynthetic rates with age in most plant species follow the same general pattern although both the rate and the timing of peak respiration and photosynthesis vary.

Initial development of leaves requires import of carbohydrates from other plant parts until leaves develop sufficiently to supply their own requirements for carbohydrates. Leaves then become net exporters of carbohydrates and a carbohydrate source for other plant parts. The transition of leaves from sink to source can be very important, especially at times when sink demands are high in other parts of the branch or plant.

Plant species and varieties vary as to when their leaves attain the ability to become net exporters of carbohydrates. Tomato (*Lycopersicon esculentum* L.) leaves began exporting when the whole leaf was only 10% expanded (≈10 days), although import continued and peaked at 15% expansion (13 days) (Ho and Shaw, 1977). Import remained at 2-3% until full leaf expansion (45 days). Grape (*Vitis vinifera* L.) leaves started exporting when 50-60% expanded (Hale and Weaver, 1962), while citrus leaves did not begin exporting until fully expanded (Kriedemann, 1969a; 1969b). Gross export in sour cherry was dependent upon time of leaf development as the 10th leaf did not begin exporting until 48-78% expanded, compared to the 7th leaf, which began exporting at 27% expansion (Kappes and Flore, 1989). When sink demand was increased by removing other source leaves, the 10th leaf began exporting when only 44-52% expanded (Kappes and Flore, 1989). Thus, the initiation of carbohydrate export from the leaves varies with species and may be affected by sink demand.

Effect of sink demand on photosynthetic rates. Sink demand affects leaf photosynthetic rates by influencing the leaf's carbohydrate export rates. Sink demand may affect carbohydrate export and net photosynthetic rates in mature leaves. Increasing sink demand has been reported to increase carbohydrate export and net photosynthetic rates in some crops. However, in other crops, changing the source-sink ratio did not always lead to changes in carbohydrate export or photosynthetic rates.

The effects of sink demand on photosynthetic rates may depend on location of the leaves in relation to the fruit. Leaves on fruiting spurs of 10-year-old 'Starkrimson' apple trees had 20-25% higher rates of photosynthesis per leaf area than leaves on vegetative spurs (Fujii and Kennedy, 1985). Leaves on nonfruiting branches or rosette leaves on fruit-bearing branches of 'Aporta' and 'Chelina' apple trees had photosynthetic rates ≈50% lower than leaves emerging from the fruit stalk (Kazaryan et al., 1965). Watson et al. (1978) found higher photosynthetic rates only in extension shoot leaves of fruiting 'Golden Delicious' trees compared to defruited trees, while there were no differences between spur leaves. Fruiting had no effect on the photosynthetic rate of mature 'Sturdeespur Delicious'/MM106 apple leaves, but girdling fruiting apple branches decreased shoot and spur leaf photosynthetic rates by ≈8-10%, while girdling nonfruiting branches decreased photosynthetic rates by ≈70% within 2 weeks (Schechter et al., 1994). Other researchers have found no

differences in the photosynthetic rates of spur and shoot leaves on bearing and nonbearing apple trees (Palmer et al., 1991; Rom and Ferree, 1986).

Leaves on girdled avocado (*Persea americana* Mill.) branches with one fruit had higher net photosynthetic rates and lower internal CO_2 concentrations than the leaves on branches with the fruit removed (Schaffer et al., 1987). Leaves on branches with no fruit had increased SLW, increased numbers of starch grains, and reduced leaf conductance and photosynthetic rates, suggesting to Schaffer et al. (1987) that starch accumulation may have inhibited photosynthesis. The rate of photosynthesis in mature wheat (*Triticum aestivum* L.) leaves declined rapidly when carbohydrate (glucose, fructose, sucrose, and starch) concentrations reached ≈100 mmol carbohydrate carbon·m^{-2} (Azcón-Bieto, 1983). This suggests end product inhibition of photosynthesis.

The effects of sink demand on photosynthetic rates may depend upon stage of development and crop load. There were no differences in leaf photosynthetic rates between fruiting and nonfruiting 'O'Henry'/Nemaguard peach trees during the early stages of fruit development, but photosynthetic rates were 11-15% higher in fruiting trees during the early part of stage III of fruit growth (DeJong, 1986). Rates of photosynthesis of 'Golden Queen' peach tree leaves increased during stage III of fruit development before decreasing after fruit harvest (Chalmers et al., 1975). The rate of export of ^{14}C labelled assimilates out of the leaves also decreased after harvest.

Although photosynthetic rates declined after harvest, rates remained relatively high, which Chalmers et al. (1975) suggested may be important for renewed root growth and reserve accumulation.

Photosynthetic rates in 'Bing' sweet cherry leaves increased during stage II of fruit development, but there were no differences between fruiting and nonfruiting trees as photosynthetic rates were affected more by leaf ontogeny and environment than by sink strength (Roper et al., 1988). In cherry, photosynthetic enhancement of leaves on fruiting compared to nonfruiting trees occurred when the leaf area:fruit ratio was 2 but not when the leaf area:fruit ratio was 4. Additionally, photosynthetic enhancement usually was observed only in the afternoon and not in the morning (Flore, 1985; 1986). Reducing crop load to zero by harvesting the fruit reduced photosynthetic rates to 65% of preharvest rates in sour cherry and peach; however, the rate of photosynthesis recovered somewhat after 4 weeks (Flore and Gucci, 1986). In sour cherry trees with different leaf:fruit ratios, the decline in photosynthesis after fruit harvest was inversely related to the leaf:fruit ratio (Flore, 1986). Flore (1986) suggested that photosynthetic response is dependent upon the carbohydrate translocation pool and that positive enhancement of photosynthesis will only occur when the concentration of carbohydrates in the translocation pool is low, such as occurs at low leaf:fruit ratios and in the afternoon. Also, depression of the photosynthetic rate after fruit removal will only occur when other sinks

cannot compensate for the increased amount of carbohydrate available and the carbohydrate pool builds up sufficiently to become inhibitory.

Carbohydrate use by other sinks and processes often increases when carbohydrates become more available, and so net photosynthesis is unaltered. Removal of the fruit from 'Bonita' eggplant (*Solanun melongena* L.) plants led to a temporary increase in leaf sugar content and a continual increase in starch content, while leaf nitrate (NO_3^-) content decreased, indicating that some of the carbohydrates previously allocated to fruit growth were possibly going to NO_3^- assimilation and storage (Claussen, 1986). Defruiting 'Frühstamm Hold' tomato plants initially decreased stomatal conductance and photosynthesis by 40%. However, recovery occurred by 24 hours, concomitant with increased nitrate reductase (NR) activity in the leaves (Hucklesby and Blanke, 1992). Therefore, N assimilation may be one of the other sinks in the plant that uses some of the excess carbohydrates available when one sink is removed.

The type of carbohydrate stored in the leaves may be important in determining photosynthetic responses to sink:source manipulations. Girdling leaves to prevent export of photosynthates for 7 days caused differing responses depending upon the type of carbohydrate stored in the leaves (Goldschmidt and Huber, 1992). Leaves of soybean (*Glycine max*, Merr.), cotton, and cucumber (starch storers), whose petioles had been heat girdled, had increased (190-589%) stomatal resistance and decreased

(51-59%) maximum photosynthetic rates (A_{max}-determined at 3% CO_2) compared to nongirdled leaves. Girdled spinach (*Spinaca oleracea* L.) leaves (sucrose storer) had only slightly reduced (16% inhibition) photosynthetic rates and almost no change in A_{max} compared to nongirdled leaves. Girdled tomato, sunflower (*Helianthus annuus* L.), broad bean (*Vicia faba* L.), bean, and pea leaves, which store both starch and sucrose, had reduced (62-84% inhibition) photosynthetic rates compared to nongirdled leaves but only slight reductions (13-35% inhibition) in A_{max}. Girdled leaves of a wild-type tobacco (*Nicotiana sylvestris*) (starch and hexose storer) and a starchless mutant (hexose storer) exhibited 93-100% inhibition in photosynthetic rates and 43-74% reductions in A_{max} compared to nongirdled leaves. Inhibition of A_{max} was negatively correlated to leaf starch content, but starch was not always directly responsible, as A_{max} in the starchless mutant tobacco was also inhibited.

When sucrose export from the leaf is reduced, photosynthates must be shunted elsewhere within the leaf or their production reduced. Plants with low acid invertase activity can store sucrose in their vacuoles and so remove excess sucrose and photosynthates. Plants with high acid invertase activity cannot store sucrose, as it is broken down into hexose sugars. Plants that do not store hexose sugars may store some of the excess carbohydrates as starch. Increased starch granules in some leaves such as *Citrus reticulata* Blanco resulted in deformation of their chloroplast structure

and inhibition of photosynthesis (Schaffer et al., 1986a). Starch may also inhibit photosynthesis by lengthening the CO_2 diffusion pathway due to increased leaf thickness (Mauney et al., 1979). Hexose sugars from sucrose hydrolysis can also be rephosphorylated and made into sucrose, thereby going through an "overflow" loop or "futile cycling" (Huber, 1989). Decreased availability of inorganic phosphate (P_i) as sugars are rephosphorylated can lead to decreased photosynthesis by decreasing triose-P/P_i exchange at the chloroplast membrane (Plaut et al., 1987). However, transgenic tobacco plants that expressed yeast-derived invertase in their apoplasts did not accumulate phosphoglyceraldehyde (PGA) in their chloroplasts, which would happen if P_i concentrations were low in the cytosol (Stitt et al., 1990). Instead, accumulation of carbohydrates and hexose sugars resulted in decreased levels of Calvin cycle enzymes and inhibition of photosynthesis, partly due to their effect on photosynthetic gene expression. Also, as sucrose hydrolysis exceeds the capacity of the hexose kinases to rephosphorylate the hexose sugars, hexose sugars may accumulate and affect the Calvin cycle by decreasing Rubisco and stromal Fru1,6Pase actvity (Goldschmidt and Huber, 1992). There are many different ways in which a plant can compensate for altered sink demand, but depending upon different factors within the plant at a given time, the response will vary.

The effects of sink demand on photosynthetic rates on an individual leaf basis may not hold true on a whole plant basis. The young, recently expanded leaves of fruiting 'Tribute' strawberry (*Frageria x ananassa* Duch.) plants had higher photosynthetic rates on a leaf area basis than similar leaves on deblossomed plants at various times during the first fruiting cycle (Schaffer et al., 1986b; 1986c). However, on a whole plant basis, deblossomed plants had greater overall leaf area and higher rates of net photosynthesis by weeks 4-6. Deblossomed plants also had increased leaf dry weight and total nonstructural carbohydrates in their leaves. Photosynthetic rates of older leaves on fruiting plants were similar to those on deblossomed plants (Schaffer et al., 1986b; 1986c). The amount of ^{14}C from labelled source leaves found in untreated leaves and fruit on fruiting plants was similar to that in untreated leaves in deblossomed plants (Schaffer et al., 1985). The majority of ^{14}C-photosynthates in the deblossomed plants were in the expanding leaves, indicating that assimilates that might have gone into fruit production were partitioned to new leaf production in deblossomed plants. Fruiting 'Hecker' strawberry plants (*Fragaria virginiana* Duchesne) also had increased rates of photosynthesis on a unit leaf area basis but not on a whole plant basis compared to deblossomed plants (Choma et al., 1982). There were no differences in dark respiration or stomatal conductance between fruiting and nonfruiting plants (Choma et al., 1982; Schaffer et al., 1986b). Thus net

photosynthesis on a whole plant basis may not change due to fruiting, but there is a lack of information about this in most fruit crops.

Carbohydrate Use and Sink Competition

Fruit growth is very dependent upon reserves and/or current photosynthates but photosynthates exported from the leaves or carbohydrates that the plant is able to acquire from reserves and translocate to areas of growth are insufficient to allow all meristems to grow simultaneously. Therefore, different organs within a plant must compete directly for available resources or develop strategies whereby sink number is adjusted or growth occurs at different times.

Flowering, fruit set, and early fruit development appear to be periods when reproductive strategies can adjust fruit load to carbohydrate and nutrient resource levels. In prickly pear cactus (*Opuntia ficus-indica* (L.) Miller), flowering and fruit production do not begin until a minimum dry weight:surface area ratio is exceeded in the individual cladodes (Garcia de Cortázar and Nobel, 1992). In cacao, flower production and then cherelle wilting and abortion allows cacao to adjust its crop load to carbohydrate supply (Valle et al., 1990). Mango can drop fruit anytime during fruit development, while fruit drop rarely occurs in coffee (Cannell, 1985). Citrus trees may have several periods of fruit drop during the season. Without a mechanism for shedding excess fruit when resources are limited, plants

grow very little and often undergo death of the shoot and root tips (Avery, 1970; Cannell, 1985; Smith, 1976).

The movement of resources from a source to a sink is important within a plant as it allows organs to grow and develop by importing needed materials. The control over this movement is what determines when organs get different resources. Sink strength is the term for an organ's ability to compete for resources. Sink strength is composed of two main components, sink capacity and sink activity. Sink capacity is determined by a sink's size, while sink activity is a sink's potential carbohydrate uptake rate per unit time (Hansen, 1989). Sucrose is the main carbohydrate translocated in most plants, although other sugars may predominate depending upon the species. Sink activity is determined by a sink's capability to remove the translocated sugar from the unloading area so that a concentration gradient is maintained for continued translocation to the sink. When sink capacity and activity of different sinks are equal, then partitioning is inversely proportional to the distance from the source (Cook and Evans, 1983).

Sink strength and carbohydrate allocation will vary with plant organ and growth stage of the plant. On cucumber and tomato plants during flowering, the general order is roots > young leaves > inflorescences (Chamont, 1993; Ho et al., 1989). After fruit set, this order may change to

seeds > fleshy fruit parts = shoot apices and leaves > flowers > cambium > roots > storage (Cannell, 1985; Ho et al., 1989).

Carbohydrate Allocation to Fruit

Fruiting has been recognized as a competitive and possibly exhaustive process for decades (Murneek, 1924; 1925). Fruiting may account for a large proportion of the annual dry weight increment in different plant species and cultivars at different times. Apple fruit may account for 35-70% of the total annual dry weight increment (Forshey et al., 1983; Hansen, 1970; Heim et al., 1979; Heinicke, 1937; Maggs, 1963; Schechter et al., 1994). The proportion of the annual dry weight increment going into the fruit of 'Golden Queen' peach increased from ≈30% in young trees (4-6 years old) to ≈70% in mature trees (15 years old) (Chalmers and van den Ende, 1975). Fruit made up over 72% of the dry weight increment during a 3-month period in 4-year-old coffee plants and averaged ≈44% over the year (Cannell, 1971; 1985). Fruit accounted for 19-32% of the annual dry weight production in black currant plants (*Ribes nigrum* L.) (Hansen, 1986). In wild blueberry plants, annual biomass allocation to fruit ranged from 3.9 to 86.3% depending upon plant age, with 3- to 11-year-old plants allocating >50% to fruit biomass production (Pritts and Hancock, 1985). Twenty-year-old plants allocated approximately 25% of their total annual biomass increase to fruit, while 30-year-old plants allocated only about 5% to fruit.

Leaf Area:Fruit Ratio

Fruit compete with each other for carbohydrates. The cultural practice of removing or thinning the fruit from trees, which increases the leaf area:fruit ratio, has been practiced for decades to improve fruit size and quality. The leaf area per fruit needed for maximum fresh weight, dry weight, and sugars in apple was 526-1205 cm^2 (≈40-75 leaves) depending upon cultivar (Haller and Magness, 1925). As the number of leaves per fruit in 'Golden Delicious' apple trees increased from 20 to 80 leaves per fruit, the percentage of soluble solids and larger sized fruits increased, although total yield per tree was similar (Ferree and Cahoon, 1987). A minimum of 2-3 leaves (225-335 cm^2) per fruit was needed for optimum fruit growth (103-140 g) on girdled 'Hayward' kiwifruit (*Actinidia deliciosa*) laterals (Lai et al., 1989; Snelgar et al. 1986; Snelgar and Thorp, 1988). In sour cherry, 1.5-2.0 leaves:fruit were required for optimal fruit size (Flore, 1985). In 'Lambert' and 'Bing' sweet cherries, as the leaves per fruit increased from ½ to 9 leaves:fruit, the average fruit weight, soluble solids, and firmness increased (Facteau et al., 1983; Spayd et al., 1986). Although Hansen (1986) claimed that small fruits do not respond to thinning, lightly cropped 'Baldwin' black currants with 80-90% of their racemes removed had increased fruit size compared to fruit from control plants (Hansen and Ostermann, 1988). A decrease in crop load in 'Wolcott' blueberry was related to an increase in berry size, dry matter content, sugar content, and

soluble solids in expressed juice, but to a decrease in berry keeping quality, total yield, and fruit development period (Ballinger et al., 1963). Based on fruit maturity, a leaf:fruit ratio of 1 large leaf (≈20 cm^2) per fruit was estimated to be needed with 'Tifblue' rabbiteye blueberry (Patten and Neuendorff, 1989). The effect of crop load and leaf area needed for optimum fruit size and quality for SHB cultivars is not known.

The Effect of Fruiting on Vegetative Biomass Allocation

Fruit not only compete with other fruit but with vegetative meristems as well. Competition for resources between fruit and other plant parts will depend upon the allocation to reproductive growth, the total amount produced, and upon the plant species. Murneek (1926) observed that reproductive-vegetative competition in tomato began immediately after fruit set, with the plant weakened in its vegetative development from that point. Tomato plants without fruit had higher root dry weight than plants with fruit and the root fresh weight was approximately 3.7 times that of fruiting plants (Murneek, 1926). More recently, Hurd *et al.* (1979) found that during the period of 50-60 days after first anthesis, up to 90% of the fresh weight gain was partitioned to the tomato fruit before decreasing to around 80%. During this same time period, the rate of new leaf production was lower, the duration of leaf expansion was shorter (30 days vs. 40-50 days), and the final size of the individual leaves was smaller (one third to one half the area of the largest leaves) on fruiting plants compared to defruited

plants, but the fresh weight per unit area remained constant. Root growth stopped ≈4 weeks after first anthesis, although some roots had started to die within a week after first anthesis. Root growth rate in cucumber decreased from days 35 to 40 after planting and from 60 days to harvest, which corresponded to periods of high fruit load (Chamont, 1993). If root growth declined in inverse ratio to fruit load, then no roots died.

Fruiting affected vegetative growth in apple trees, with root growth reduced 25-48% in fruiting trees compared to deblossomed trees (Avery, 1969; Avery et al., 1979; Head, 1969; Maggs, 1963; Schechter et al., 1992; Schechter et al., 1994). The rate of leaf production was slower, leaf size was smaller, and overall leaf dry weight was reduced in fruiting trees compared to deblossomed trees. Fruit accounted for 37-66% of the total dry weight increment in fruiting trees while the roots and leaves accounted for 12-24% and 14-26% of the total dry weight increment, respectively. Apple trees with fruit had higher scion:rootstock ratios than deblossomed trees, indicating that root growth is reduced more than shoot growth in fruiting apple trees.

Cropping was an important factor affecting growth rate in peach (Chalmers and van den Ende, 1975; Dann et al., 1984; Miller and Walsh, 1988). Vegetative growth rate was inversely related to fruit growth rate, with vegetative growth, including root growth, most rapid during stage II of fruit growth and slowest during stage III. The appearance of new white

roots was inversely related to the presence of fruit. Young, nonbearing trees had new white roots throughout the growing season, but mature, bearing trees had a bimodal pattern of new white root production, namely, before budbreak and after fruit removal (Glenn and Welker, 1993). As the peach trees aged and grew, the shoot (excluding fruit and leaves):root dry weight ratio increased from near one in young peach trees to close to four in mature trees, but a constant allometric relationship between the logarithm of the shoot and root dry weights remained (Chalmers and van den Ende, 1975). This would indicate that the pattern of biomass allocation to the shoot and the root remained similar. Fruits are often dominant sinks and depending upon their stage of development may affect biomass allocation to vegetative organs. However, there is no information on changes in vegetative biomass allocation due to differences in crop load in SHB.

Reproductive structures are not always dominant sinks. Vegetative sinks can be very competitive. Partial defoliation and leaf shading of oil palm decreased fruit production but rarely reduced vegetative dry matter increase (Corley, 1973). Nine to 11 months after removing the top third of fruiting citrus trees, root growth and total leaf biomass in the pruned trees had recovered and were equal to unpruned trees, but fruit biomass was only 24% that of unpruned trees (Eissenstat and Duncan, 1992).

Vegetative parts of the kiwi vine can outcompete the fruit for assimilates. Only when girdled did kiwifruit respond to 5:1 leaf:fruit ratios,

producing larger fruit than at 1:1 ratios, indicating that a large portion of the carbohydrates produced in the lateral was going elsewhere in the vine (Woolley et al., 1991). Application of CPPU (N-(2-chloro-4-pyridyl)-N-phenylurea), a cytokinin-active compound, increased individual fruit fresh weight an average of 36 grams whether the vine was carrying a low crop load or a moderate crop load, suggesting that ample carbohydrates existed if the fruit could compete for it.

Fruit sink strength varies with stage of development. Once established, fruits are generally strong sinks and can account for a large portion of the annual biomass increment of a plant. However, even in established fruits, there are stages when sink strength or demand appears to be reduced and vegetative growth may be less restricted. This may be important in SHB as vegetative buds must compete with already developing fruit for carbohydrates.

Respiration

Carbohydrates are not only accumulated in biomass but must also be expended in respiration to provide energy for numerous plant processes involved in producing and maintaining that biomass. Respiration may account for 27-60% of the C fixed daily by photosynthesis (Gordon et al., 1977; Lambers, 1985; Lambers et al., 1981; Lambers et al., 1989; Poorter et al., 1990). Plant respiration was approximately 60% of gross photosynthesis in kiwifruit (Buwalda et al., 1992). In 24 nonwoody species,

27-50% of the daily fixed C (calculated from whole shoot net photosynthetic rates and shoot and root respiration rates) was respired the same day and was negatively correlated with whole plant relative growth rates (Poorter et al., 1990).

Respiration can be divided into three major components: growth respiration; maintenance respiration; and ion uptake respiration. Growth respiration is associated with the costs of plant growth and is related to the growth rate of the plant. It is also dependent upon the composition of the dry matter accumulated and the biosynthetic pathways involved in its production (Lambers, 1987; Penning de Vries et al., 1974). Maintenance respiration is involved in maintaining the cellular structures and processes within the dry matter already accumulated. Maintenance respiration is used primarily for protein turnover, maintaining ion gradients, and membrane (lipid) maintenance and is related to the amount of biomass present, tissue composition, and growth conditions, especially temperature (Lambers, 1987; McCree and Silsbury, 1978; Penning de Vries, 1975). Ion uptake respiration supplies the energy for nutrient ion uptake and transport and is related to the rate of ion uptake (Lambers, 1987; Van der Werf et al., 1988; Veen, 1980).

Respiration and temperature

Maintenance respiration is strongly temperature dependent, while growth respiration is generally temperature independent except as

temperature affects relative growth rates or metabolic pathways of biosynthesis (Amthor, 1989; Walker and Thornley, 1977). Respiration increases exponentially with temperature with a Q_{10} of ≈2 (DeJong et al., 1987; Grossman and DeJong, 1994; McCree and Silsbury, 1978; Szaniawski and Kielkiewicz, 1982).

Temperature in one organ may affect respiration in other organs also. An increase in root temperature increased maintenance respiration not only of the root but also of the shoot in sunflower (Szaniawski and Kielkiewicz, 1982). An increase in shoot temperature in eastern hemlock [*Tsuga canadensis* L. (Carriere)] resulted in an increase in shoot respiration but a decrease in root respiration (Szaniawski and Adams, 1974).

Fruit respiration

In 'Golden Delicious'/M9 apple trees, fruit respiration increased from June to October (Blanke and Wibbe, 1991). At night, the tree respired approximately 22% of the C fixed during the day from June to October and fruit respiration accounted for 6.7% of the nighttime tree respiration. Fruit respiration in peach averaged slightly more than leaf respiration in July and approximately 16-20% of the total carbohydrate requirements of the peach fruit was used in respiration (DeJong and Walton, 1989; Grossman and DeJong, 1994). Respiration accounted for approximately 22.6% of the carbohydrate needed for 'Hayward' kiwifruit fruit growth (Walton and DeJong, 1990). 'Weymouth' and 'Jersey' highbush blueberry and

'Woodard' and 'Tifblue' rabbiteye blueberry fruit respiration per gram fresh weight increased at the end of stage II and during early stage III (Shimura et al., 1986). 'Climax' and 'Bonita' rabbiteye blueberry fruit respiration per gram fresh weight was high during early fruit growth and then declined before increasing again during ripening (Birkhold, 1991). Respiration accounted for ≈37% of the C needed for fruit development (Birkhold et al., 1992).

Summary

Quality fruit production depends upon an ample supply of carbohydrates. Carbohydrates may be supplied by current photosynthesis in the fruit and leaves and from carbohydrate reserves. Photosynthates from the leaves are the most important source of carbohydrates for fruit production. Therefore, the establishment of the vegetative canopy is critical for fruit production. However, in SHB, the establishment of the photosynthetic canopy may be very dependent upon carbohydrate reserve levels and flower and fruit load as floral budbreak and fruit set begins prior to vegetative budbreak. Fruits are very strong carbohydrate sinks and vegetative budbreak in SHB must compete with developing fruit. Thus, heavy flower and fruit loads may severely reduce carbohydrate allocation to vegetative buds and developing shoots. This would result in a decrease in vegetative budbreak and leaf area development, which in turn would decrease carbohydrate production and potentially decrease fruit yield.

However, information is lacking on the manner and extent of the competition between reproductive and vegetative sinks in SHB.

CHAPTER 3
FLOWER BUD DENSITY AFFECTS VEGETATIVE AND REPRODUCTIVE DEVELOPMENT IN FIELD-GROWN SOUTHERN HIGHBUSH BLUEBERRY PLANTS

Introduction

Reproductive development is often an exhaustive process that affects the whole plant, as the demand for carbohydrates by reproductive organs can be high (Murneek, 1924; 1925). Reproductive growth requires carbohydrates for C-skeletons for growth and for respiration to provide the energy for growth and maintenance.

Fruit photosynthesis may provide a portion of the carbohydrates needed for fruit growth (Birkhold et al., 1992; Kappes and Flore, 1985), but most of the carbohydrates typically must come from current photosynthesis in the leaves or carbohydrate reserves. If carbohydrate supplies are insufficient to meet the demands of the different reproductive and/or vegetative sinks, competition occurs and sink development is affected. For example, reduced vegetative development in fruiting plants compared to nonfruiting plants has been observed in tomato (*Lycopersicon esculentum* L.) (Hurd et al., 1979; Murneek, 1926), apple (*Malus domestica* Borkh.)

(Avery et al., 1979; Head, 1969; Maggs, 1963), and strawberry (*Fragaria virginiana* Duchesne) (Schaffer et al., 1986c).

In most cases where carbohydrate competition and allocation have been researched, vegetative development precedes floral budbreak and fruit set. For example, inflorescences in strawberry and tomato arise from the axils of leaves after the canopy has partially developed. In apple, 18-20% of the total canopy at harvest is present at full bloom (Ferree, 1980; Forshey et al., 1983), while in northern highbush blueberry (*Vaccinium corymbosum* L.), floral budbreak occurs when vegetative branches are almost fully expanded (Bell, 1950). However, in many southern highbush blueberry (SHB) cultivars, floral budbreak and fruit set begin prior to vegetative budbreak. Field observations indicate that heavy flower and fruit loads may delay and reduce vegetative budbreak and shoot development in some SHB cultivars, while partial removal of flower buds by shoot tip pruning increases vegetative budbreak and shoot development. Thus, flower and fruit load appear to have a significant effect on vegetative budbreak and subsequent shoot development in SHB, although data are lacking.

Reproductive development can be affected by carbohydrate production and availability mediated through leaf area:fruit ratios. Total leaf area will in part determine carbohydrate production and availability and the number of fruit will influence carbohydrate allocation. The effect of leaf area:fruit ratios on fruit size and quality and the fruit development period

(FDP) has been examined in several species of fruits including apple (Ferree and Cahoon, 1987; Haller and Magness, 1925), cherry (*P. avium* L.; *P. cerasus* L.) (Facteau et al., 1983; Flore, 1985; Roper and Loescher, 1987), and northern highbush blueberry (Ballinger et al., 1963). Generally, as the leaf area:fruit ratio increases, fruit size, quality, and rate of development increase asymptotically. The reduction in canopy development associated with high flower and fruit load may reduce reproductive development by reducing leaf area:fruit ratios. However, the effect of flower and fruit load on leaf area:fruit ratios and the effect of leaf area:fruit ratios on reproductive development have not been studied in SHB.

Based on the above discussion and field observations, the following research hypothesis was proposed. Initial flower bud and fruit density affect the timing and extent of vegetative budbreak and canopy development, which in turn affect reproductive development in certain SHB cultivars. The specific objectives were to determine 1) the effects of varying flower bud densities on vegetative budbreak and canopy development and 2) the effects of leaf area:fruit ratio on fruit size, quality, and development period.

Materials and Methods

The experiment was conducted at the Horticultural Research Unit near Gainesville, FL, in 1995 using ten 'Misty' and ten 'Sharpblue' SHB plants.

The plants were approximately 5-years-old and were planted 0.8 m apart in a single row oriented north-south. Soil type was a Kanapaha fine sand (loamy, siliceous, hyperthermic, Grossarenoc, Paleudults) amended with peat at the rate of 38 $m^3 \cdot ha^{-1}$. The strip of soil extending 0.8 m on each side of the row was covered with a 8-12 cm layer of pine bark mulch. Plants were fertilized with 9.2 $kg \cdot ha^{-1} \cdot month^{-1}$ of granular 16N-2P-7K fertilizer. Irrigation and weed control practices followed standard recommendations (Williamson and Lyrene, 1995). The total number of chill hours (≤7C) accumulated was 600-700 h (Ag Weather Information Services, Auburn, AL). The experiment was conducted within a randomized block design, considering the degree of flower bud thinning as the treatment and plants as blocks. The plants were nested within the two cultivars and all plants within a cultivar appeared within the same section of a row in the field. Repeated measures over time were observed on individual canes, which were nested within individual blueberry plants. On most plants, three canes were selected, although three plants had only two suitable canes so additional canes were selected on other plants. Canes were chosen that had a main stem with at least two lateral stems. Canes were 1-3 years old and were 112-642 cm long with an average length of 320 cm. The entire length of each cane with its lateral stems was measured from the point of attachment to the subtending cane, and the total number of flower buds per cane was counted. Initial flower bud density (FBD) (flower bud $number \cdot cm^{-1}$

cane length) was determined. To establish a range of flower bud density, flower buds were hand thinned at evenly spaced intervals along the canes during dormancy in February, 1995. The different treatments randomly assigned to different canes on each plant were as follows:

1. No flower buds removed
2. Every third flower bud removed
3. Every second and third flower bud removed

The canes not selected for the experiment were allowed to flower and fruit with no flower bud adjustment. Floral and vegetative budbreak were measured on a weekly basis and ripe fruits were harvested every 3-5 days until 80% of the fruit were ripe. Full bloom for a particular flower bud was when the majority of the florets had open corollas. Fifty and eighty percent full bloom were when 50% and 80% of the flower buds were at full bloom, respectively. Fruit development periods (FDP) were calculated as the number of days from 80% full bloom to 80% ripe fruit. Fruit soluble solids were determined on a subsample of 5 fruits from each cane at each harvest date with an Abbe refractometer Mod. 10460 (Cambridge Instrument, Inc., Buffalo, NY). Canes were harvested after 80% of the fruit was picked. Leaf area was measured using a LI-COR Model LI-3000 portable leaf area meter (LI-COR, Lincoln, NE) and the leaves and current year's stems were dried to a constant weight at 70C to determine their dry weights. The canes were frozen and held at -30C until lyophilized and dry weights

measured. Lyophilized canes were ground in a Wiley mill to pass a 20-mesh screen, and subsamples were analyzed for sugar and starch levels. Sugars were extracted from 50 mg of tissue by boiling in 80% ethanol (1:100 w/v) for 2 min. Extracts were shaken for 20 min and centrifuged, the supernatant decanted, and the pellet re-extracted twice. The supernatants were combined, and final volumes were measured. Sample pigment was removed by adding 35 mg activated charcoal, and soluble sugars were assayed using the phenol-sulfuric acid method (Buysse and Merckx, 1993; Dubois et al., 1956). Tissue starch content was determined by suspending the insoluble fraction from the 80% ethanol extraction in 2.0 ml 0.2 N KOH and boiling for 30 min. After cooling, pH was adjusted to 4.5 with 1.0 ml 1.0 M acetic acid, and 1.0 ml of *Rhizopus* amyloglucosidase (10 $mg \cdot ml^{-1}$) (Sigma Chemical Co., St. Louis, MO) in 0.2 M calcium acetate buffer (pH 4.5) was added. Samples were incubated in a shaking water bath for 24 h at 37C. After incubation, samples were centrifuged and the supernatant decanted. Sample pigment was removed by adding 35 mg activated charcoal, and glucose liberated from starch hydrolysis was quantified by the phenol-sulfuric acid method.

SAS (SAS Institute, Cary, NC) was used for statistical analyses. Since FBD varied over wide ranges for each of the three treatments, FBD was analyzed with regression as a continuous variable rather than a discrete variable. PROC GLM was used for analysis of variance and regression

analysis, PROC CORR was used to test correlations, and PROC MIXED was used to analyze for consistent patterns in vegetative budbreak regression slopes. Variability among plants was assessed but was found not to be statistically significant and so the plant effects were not used in the model. Total cane length was used as a covariate to account for differences in initial cane size.

Results and Discussion

Mean FBD before treatment application was greater for 'Misty' (0.28 flower buds·cm^{-1} cane length) than for 'Sharpblue' (0.22 flower buds·cm^{-1} cane length). This concurs with field observations that 'Misty' usually sets more flower buds than some of the other SHB cultivars. After flower buds were removed according to their assigned treatments, FBD ranged from .07 to .34 flower buds·cm^{-1} cane length in 'Misty' and from .05 to .27 flower buds·cm^{-1} cane length in 'Sharpblue'.

Fifty percent bloom occurred on 9 March 1995 for both 'Misty' and 'Sharpblue'. Eighty percent bloom was on 19 March and 23 March for 'Misty' and 'Sharpblue', respectively. Since floral budbreak and fruit set overlapped with each other and fruit density (fruit·cm^{-1} cane length) was not adjusted in this study, it was not possible to separate the effects of FBD from the effects of fruit density. Fruit density increased with increased FBD in 'Misty' and 'Sharpblue' and was similar for the two cultivars (Fig. 3-1).

The number of vegetative buds that broke and grew per unit cane length decreased as FBD increased in both cultivars (Fig. 3-2). Vegetative budbreak was delayed as FBD increased in 'Misty' ($p = .0001$) and 'Sharpblue' ($p = .0019$). The delay in vegetative budbreak was 6-10 days between the highest and lowest FBDs. Vegetative budbreak was over 90% complete at all FBD by 28 March. The number of new vegetative shoots was greater for 'Sharpblue' than for 'Misty', indicating that cultivar also has a large effect on vegetative response to FBD (Fig. 3-2).

Total leaf area and leaf area:fruit ratio decreased with increased FBD in both cultivars (Fig. 3-3 and 3-4). New stem length and leaf and new stem dry weight also decreased with increased FBD, but since the correlations between leaf area, leaf dry weight, new stem length, and new stem dry weight were greater than $r = 0.93$ in both cultivars, only leaf area is presented. Total leaf area and leaf area:fruit ratio were greater in 'Sharpblue' than 'Misty' across all FBDs (Table 3-1).

The delay and reduction in vegetative budbreak as FBD increased indicates that the development of the photosynthetic canopy was delayed and reduced. In a similar manner, canopy development is delayed and reduced in response to fruiting in other crops. The rates of leaf production, final leaf size, and total leaf area were less on fruiting plants compared to nonfruiting plants in tomato (Hurd et al., 1979), apple (Maggs, 1963; Schechter et al., 1994), pistachio (Weinbaum *et al.*, 1994), strawberry

(Schaffer et al., 1986c), and sweet cherry (Kappel, 1991). Tomato, strawberry, apple, and pistachio have some leaf area when fruit set occurs, and further vegetative budbreak and leaf area development is reduced in fruiting plants compared to nonfruiting plants. In sweet cherry, floral and vegetative budbreak occur simultaneously and leaf area at fruit harvest was approximately 13% less on fruiting trees than on nonfruiting trees (Kappel, 1991). Vegetative budbreak and total leaf area in the present experiment were reduced 60-68% and 33-46% at high FBD compared to low FBD in 'Misty' and 'Sharpblue', respectively (Fig. 3-2 and 3-3). The larger reduction in leaf area of blueberry compared to sweet cherry may be caused by later vegetative budbreak relative to floral budbreak in SHB or by the fact that new vegetative growth competes better with fruit growth in sweet cherry than it does in SHB.

The reduction in total leaf area and leaf area:fruit ratios with increased FBD also affected fruit development. Fruit fresh weight decreased with decreased leaf area:fruit ratio (Fig. 3-5). The decrease in fruit size with a decrease in leaf area:fruit ratio is similar to that in many fruit crops, including apple (Ferree and Cahoun, 1987; Haller and Magness, 1925), peach (Overholser and Claypool, 1931; Weinberger, 1931), and cherry (Flore, 1985; Facteau et al., 1983; Roper and Loescher, 1987). In northern highbush blueberry, where leaf area development begins prior to floral budbreak and fruit development, berry size decreased with an increase in

crop load, although specific leaf area:fruit ratios were not given (Ballinger et al., 1963). Based on fruit maturity, a leaf area:fruit ratio of 20 cm^2 per fruit was needed for optimum fruit production in 'Tifblue' rabbiteye blueberry (Patten and Neuendorf, 1989). The results from the present study suggest 20-30 cm^2 (one large leaf) per fruit is needed for large, early ripening fruit.

'Misty' berries were larger than 'Sharpblue' berries (Table 3-1), and the increase in fruit fresh weight with increased leaf area:fruit ratio was greater in 'Misty' than in 'Sharpblue' (Fig. 3-5). The less dramatic response observed in 'Sharpblue' may be a result of 'Sharpblue' allocating a larger portion of its carbohydrates into components such as fruit soluble solids or carbohydrate reserves, both of which were significantly greater in 'Sharpblue' than in 'Misty' at fruit harvest (Table 3-1).

Total fruit soluble solids at fruit harvest increased as the leaf area:fruit ratio increased (Fig. 3-6). Similar increases in soluble solids as the leaf area:fruit ratio increased have been found in apple (Facteau et al., 1983; Ferree and Cahoon, 1987), sweet cherries (Roper and Loescher, 1987; Spayd et al., 1986), and blueberries (Ballinger et al., 1963). In 'Wolcott' blueberry, light crop load berries averaged 13.3°Brix while heavy crop load berries averaged 12.0°Brix (Ballinger et al., 1963).

The FDP decreased with increased leaf area:fruit ratio in 'Misty' but not in 'Sharpblue' (Fig. 3-6). Although no differences in FDP were found with 'Sharpblue' in this study, Patterson (1997) estimated that the last 25%

of the fruit on heavy cropped 'Sharpblue' would be too small and late maturing to be marketable. The FDP in 'Wolcott' blueberry decreased with a decrease in crop load, although actual FDP values were not given (Ballinger et al., 1963). The FDP was shorter for 'Sharpblue' than for 'Misty' across all treatments (Table 3-1). The FDP for both was shorter than the 85 day FDP seen in self-pollinated 'Sharpblue' or the 62-68 day FDP seen in cross-pollinated 'Sharpblue' (Lyrene, 1989). This could reflect differences in growing conditions and would also indicate that berry development was not limited by lack of cross-pollination.

Flower and fruit thinning often reduce total fruit yield (Ballinger et al., 1963; Snelgar et al., 1986; Weinberger, 1931). In 'Misty', cumulative fruit yield decreased with increased FBD for harvests through May 10. By May 16, cumulative berry yield was similar for all FBD and by May 30, cumulative yield was greater with increased FBD. In 'Sharpblue', cumulative berry yield was greater with increased FBD at all harvest dates. Blueberry prices are always highest during the early harvest period, and flower bud thinning did not reduce total fruit yield in 'Misty' until after May 30. Thus, flower bud thinning may be beneficial in some SHB cultivars.

Cane sugar concentrations at fruit harvest were similar regardless of leaf area:fruit ratio in both cultivars; however, cane starch concentrations increased from 26 to 40 $\mu g \cdot mg\ DW^{-1}$ as leaf area:fruit ratio increased from 2 to 40 $cm \cdot fruit^{-1}$. Cane sugar concentrations were higher in 'Misty' than in

'Sharpblue' across all treatments, but cane starch concentrations were higher in 'Sharpblue' than 'Misty' (Table 3-1). This probably reflects an increase in the capacity to replenish carbohydrate reserves prior to fruit ripening in 'Sharpblue'.

In conclusion, vegetative budbreak, shoot growth, and leaf area:fruit ratios were reduced as flower bud density increased in the SHB cultivars, 'Misty' and 'Sharpblue'. Additionally, as leaf area:fruit ratio decreased, fruit fresh weight and soluble solids were reduced in both cultivars, and harvest was delayed in 'Misty'. Large, early fruit will command a higher price for producers, and it may be advantageous to decrease flower bud number in some SHB to increase fruit size and quality and hasten ripening. For example, 'Misty' may require that up to one third of its flower buds be removed in order to stimulate vegetative budbreak and canopy and reproductive development. Although FBD and fruit density were not separated in this experiment, there appears to be an early effect of FBD, which may be critical for vegetative budbreak and development and warrants further investigation.

Table 3-1. The effect of cultivar on vegetative and reproductive development measured at fruit harvest in 'Misty' and 'Sharpblue' southern highbush blueberry.

	'Misty'	'Sharpblue'	Significance
Total leaf area (cm^2)	1812[z]	3464	***[y]
Leaf area:fruit ratio (cm^2:#)	14.9	37.0	***
FDP (days)	59.9	52.1	***
Berry FW (g)	1.62	1.48	**
Soluble solids (°Brix)	11.7	13.7	***
Cane sugar ($ug \cdot mg^{-1}$ DW)	40.9	35.5	***
Cane starch ($ug \cdot mg^{-1}$ DW)	31.5	42.2	***

[z]Values are means adjusted using flower bud density as a covariate.
[y]**, ***, indicate significant statistical differences within the row at the 0.01 and 0.001 levels, respectively.

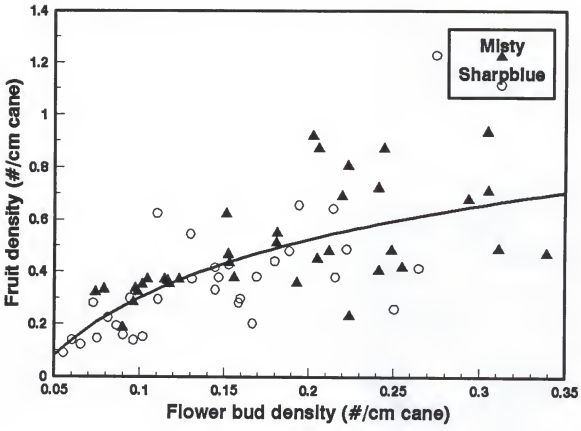

Figure 3-1. Fruit density versus flower bud density in 'Misty' and 'Sharpblue' SHB: $y = 1.04 + 0.32\ln x$, $r^2 = 0.45$, $P < 0.001$.

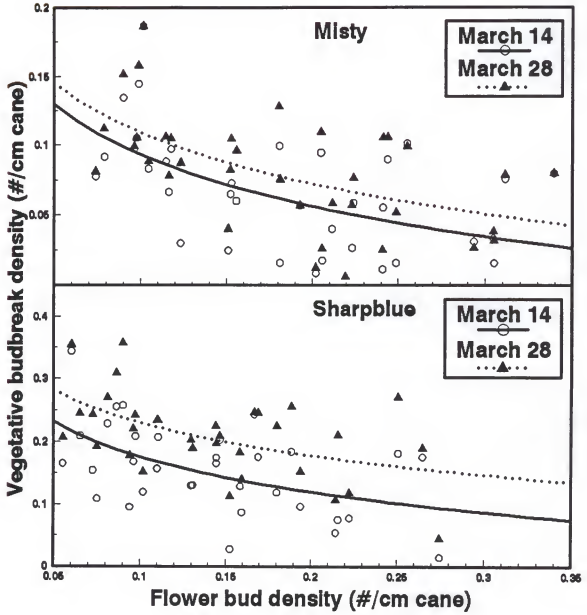

Figure 3-2. Vegetative budbreak of 'Misty' and 'Sharpblue SHB as affected by flower bud density: 'Misty': March 14 ($y=-0.030-0.053\ln x$, $r^2=0.29$, $P<0.001$); March 28 ($y=-0.013-0.053\ln x$, $r^2=0.31$, $P<0.001$); 'Sharpblue': March 14 ($y=-0.030-0.090\ln x$, $r^2=0.30$, $P<0.001$); March 28 ($y=-0.024-0.089\ln x$, $r^2=0.34$, $P<0.001$).

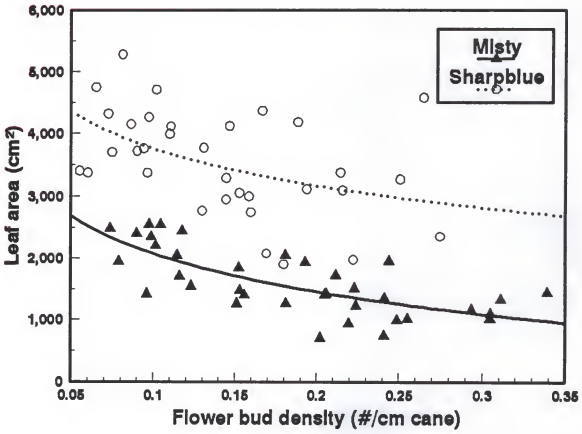

Figure 3-3. Total leaf area of 'Misty' and 'Sharpblue' SHB as affected by flower bud density: 'Misty' ($y = -1410 - 908 \ln x + 4.4$length, $r^2 = 0.77$, $P < 0.001$); 'Sharpblue' ($y = -969 - 858 \ln x + 8.6$length, $r^2 = 0.80$, $P < 0.01$). The regression lines and data points shown indicate adjustment at the average value of the cane length covariate.

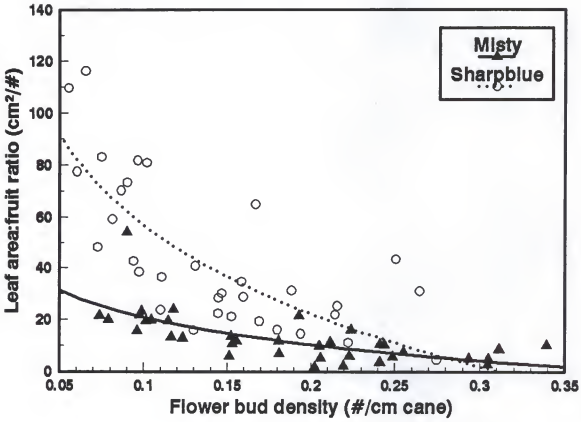

Figure 3-4. Leaf area:fruit ratio of 'Misty' and 'Sharpblue' SHB as affected by flower bud density: 'Misty' ($y=-14.6-15.5\ln x$, $r^2=0.47$, $P<0.001$); 'Sharpblue' ($y=-44.4-45.4\ln x$, $r^2=0.29$, $P<0.001$).

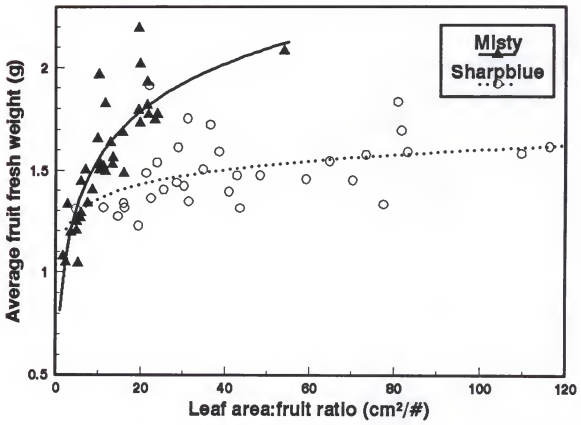

Figure 3-5. Fruit fresh weight of 'Misty' and 'Sharpblue' SHB as influenced by leaf area:fruit ratio: 'Misty' ($y = 0.78 + 0.34\ln x$, $r^2 = 0.74$, $P < 0.001$); 'Sharpblue' ($y = 1.11 + 0.11\ln x$, $r^2 = 0.21$, $P < 0.01$).

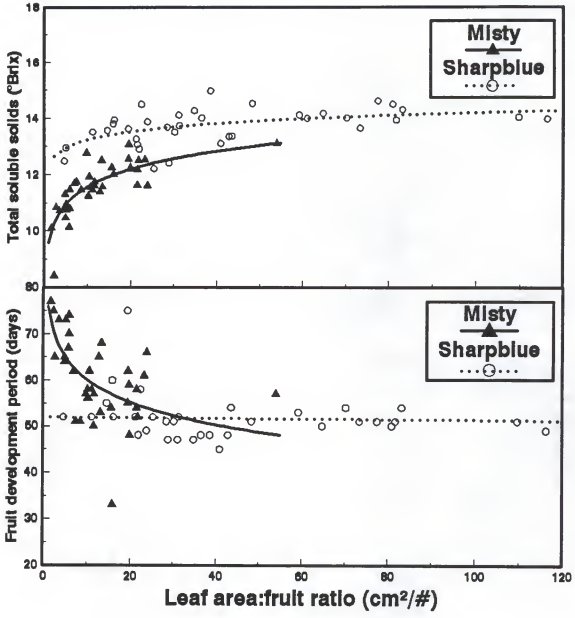

Figure 3-6. Total fruit soluble solids (TSS) and fruit development period (FDP) of 'Misty' and 'Sharpblue' SHB as affected by leaf area:fruit ratio: TSS: 'Misty' ($y = 9.4 + 0.9\ln x$, $r^2 = 0.39$, $P < 0.0001$); 'Sharpblue' ($y = 12.3 + 0.4\ln x$, $r^2 = 0.39$, $P < 0.0001$); FDP: 'Misty' ($y = 76.8 - 7.2\ln x$, $r^2 = 0.36$, $P < 0.001$); 'Sharpblue' (n.s.). Data points are the means of fruit sampled from each cane.

CHAPTER 4
FLOWER BUD DENSITY INFLUENCES VEGETATIVE AND REPRODUCTIVE DEVELOPMENT IN CONTAINER-GROWN SOUTHERN HIGHBUSH BLUEBERRY PLANTS

Introduction

Competition for carbohydrates occurs whenever sink demands are greater than source availability. Sink demands arise because carbohydrates are needed for C skeletons for growth and for respiration to provide energy for growth and maintenance of new and existing plant parts. Competition can be especially keen when sink demands are high and/or when source availability is reduced. Sink demand is high during flowering and fruiting and source availability is reduced in deciduous species in the spring before foliation occurs. In these cases, reserves provide an interim supply of carbohydrates critical for initial development of fruit and leaves, but are exhaustible.

Current leaf photosynthesis supplies most of the carbohydrates for new growth, therefore development of the canopy in the spring is critical for fruit growth and continued vegetative growth. In many deciduous fruit crops, vegetative budbreak and leaf development precede floral budbreak, thus, initial vegetative development does not compete with developing fruit.

For example, in apple (*Malus domestica* Borkh.), 18-20% of the total canopy at harvest is present at full bloom with the canopy completely developed by 3 weeks after bloom (Ferree, 1980; Forsey et al., 1983). In grape (*Vitis vinifera* L.), anthesis does not occur until approximately 8 weeks after vegetative budbreak (Williams et al., 1994). However, in many southern highbush blueberry (*Vaccinium corymbosum* L.) (SHB) cultivars, floral budbreak and fruit set begin prior to vegetative budbreak. Field observations indicate that heavy flower and fruit loads may delay and reduce vegetative budbreak in some SHB cultivars. This is supported by the observation that partial removal of flower buds by shoot tip pruning increases vegetative budbreak. However, there are no data on flower or fruit load effects on vegetative budbreak in SHB.

Flower and fruit development compete not only with vegetative budbreak but with subsequent canopy development as well. In tomato (*Lycopersicon esculentum* L.), competition begins immediately after fruit set with reduced vegetative development, including decreased rate of leaf production and smaller final leaf size, in fruiting plants compared to defruited plants (Hurd et al., 1979; Murneek, 1926). Reduced vegetative development in fruiting vs nonfruiting plants has been reported in apple (Avery et al., 1979; Head, 1969; Maggs, 1963), strawberry (*Fragaria virginiana* Duchesne) (Schaffer et al., 1986b; 1986c), pistachio (*Pistacia vera* L.) (Weinbaum *et al.*, 1994), and cherry (*P. avium* L.; *P. cerasus* L.)

(Kappel, 1991; Keller and Loescher, 1989). Reduced canopy development accompanied by heavy fruit loads has also been observed in commercial SHB plantings. Since reproductive development begins prior to vegetative budbreak and development in SHB, the reduction in vegetative development due to fruit growth may be quite severe. However, this effect has not been quantified.

The extent of vegetative development can affect leaf and/or whole plant canopy net CO_2 exchange rates (NCER) and carbohydrate production. Leaf NCER is often higher in fruiting plants compared to defruited or nonfruiting plants in apple (Gucci et al., 1995; Hansen, 1970), avocado (Schaffer et al., 1987), and strawberry (Schaffer et al., 1986b; 1986c). Although leaf NCER may be higher in fruiting compared to nonfruiting plants, whole-canopy NCER may not be higher in fruiting plants as total leaf area is often reduced (Choma et al., 1981; Schaffer et al., 1986b; Wibbe et al., 1993). However, most studies have only compared fruiting vs nonfruiting plants and there is little information available on the effects of varying crop load on whole-canopy NCER.

The extent of canopy development will in part determine the leaf area:fruit and whole-canopy NCER:fruit ratios and can influence final fruit size, quality, and rate of development. The leaf area:fruit ratio required to maximize fruit size and quality and/or reduce the fruit development period (FDP) varies with species and cultivar, but has been examined in several

species of fruits including apple (Ferree and Cahoon, 1987; Haller and Magness, 1925), peach (*Prunus persica* (L.) Batsch) (Overholser and Claypool, 1931; Weinberger, 1931), cherry (Facteau et al., 1983; Flore, 1985; Roper and Loescher, 1987), and blueberry (Ballinger et al., 1963). Generally, as the leaf area:fruit ratio increases, fruit size, quality, and rate of development increases asymptotically. However, the effect of leaf area:fruit or whole-canopy NCER:fruit ratios has not been studied in SHB.

In summary, field observations indicate that heavy flower bud and fruit loads may delay and reduce vegetative budbreak and canopy development in some SHB cultivars. This, in turn, could potentially decrease leaf area:fruit and whole-canopy NCER:fruit ratios, and lead to decreased fruit size and rate of development. The hypothesis tested in the present study is that increased flower bud and fruit density decreases vegetative budbreak, vegetative development, and whole-canopy NCER. This in turn decreases reproductive development in SHB. The specific objectives were to determine 1) the effects of varying flower bud densities on vegetative budbreak, plant development, leaf and whole-canopy NCER, and carbohydrate concentrations and 2) the effects of leaf area:fruit and whole-canopy NCER:fruit ratios on fruit size, quality, and development period.

Materials and Methods

1995 Experiment

Two-year-old 'Misty' and 'Sharpblue' SHB plants were obtained from a commercial grower in August, 1994 and transplanted into 12L containers using a 1:1 (v/v) peat:perlite mix. Plants were maintained outside on a gravel bed in Gainesville, FL. Plants were fertigated with a 20N-8.8P-16K water-soluble fertilizer (Peters, Grace-Sierra Horticultural Products Co., Milpitas, CA) at 200 mg N·liter^{-1} twice a week until the beginning of October when the plants were allowed to slow growth and enter dormancy. On 24 January, 1995, the plants were defoliated by hand and placed in coolers at 6C for 31 days to ensure adequate chilling for breaking endodormancy. After the chilling period, the plants were moved outside to a gravel bed for the rest of the experiment. Plants were placed in alternating rows of 'Misty' and 'Sharpblue' oriented north-south. Total numbers of flower buds were counted, the total lengths of all canes and stems were measured for each plant, and flower bud densities (FBD) (flower bud number·cm^{-1} cane length) were calculated. Plants of each cultivar were grouped in three blocks according to cane length, with 24 plants per block. Three FBD treatment levels were randomly assigned within each cultivar and block. Flower bud density was adjusted to one of three levels:

1. FBD: 0.05 - 0.12

2. FBD: 0.13 - 0.18

3. FBD > 0.18

Flower buds were removed at evenly spaced intervals along the canes to decrease FBD or small stems with very low FBD were removed to increase overall plant FBD. Plants were sprayed every two to three weeks with captan or benomyl, and were fertigated weekly with 20N-8.8P-16K water-soluble fertilizer at 200 mg N·liter^{-1}.

Plant measurements

Floral and vegetative budbreak were measured on a weekly basis and ripe fruit were harvested every 3-5 days until 80% of the fruit were ripe. Bloom for a particular flower bud was when the majority of the florets had open corollas. Fifty and eighty percent bloom were when 50% and 80% of the flower buds were at bloom, respectively. The FDP was calculated as the number of days from 50% bloom to 50% ripe fruit. Vegetative buds were considered breaking when they were at least 0.5 cm extended. Whole plants were randomly harvested from within each treatment level and block at the following times: 1) immediately after the chilling period (dormancy), 2) 14 days after 50% bloom (14 DAB), 3) 42 days after 50% bloom (42 DAB), and 4) 80% ripe fruit (fruit harvest). The second harvest was done at 80% bloom but since harvests were done at 50% bloom in the 1996 experiment, results from this experiment are also put in terms of 50%

bloom. The third harvest time represented ≈one-half way through the FDP. At each harvest, plants were divided into roots, previous years' canes, new stems, leaves, and flowers or fruit. Leaf area was measured using a LI-COR Model LI-3000 portable leaf area meter (LI-COR, Lincoln, NE) and the leaves and current year's stems were dried to a constant weight at 70C to determine dry weights. The roots and canes were frozen and held at -30C until lyophilized and dry weights measured.

Net CO_2 exchange rate measurements

Net CO_2 exchange rates (NCER) of the whole blueberry plant canopies were determined immediately after completion of chilling, at 80% bloom, four weeks after 80% bloom, and at the beginning of fruit ripening. Whole-canopy NCER was measured using an open flow system with an Anarad AR600R infrared gas analyzer (IRGA) (Anarad Inc., Santa Barbara, CA). Whole plants were enclosed in a 1 m x 1 m x 1 m plexiglass chamber covered on the inside with Propafilm C (ICI Films, Wilmington, DE). Roots were enclosed in a Tedlar gas sampling bag (Fisher Scientific) sealed at the base of the canes. Photosynthetic photon flux (PPF), provided by a 400W metal halide lamp (Sylvania Lumalux Lu400), was 1750-2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of the canopy. CO_2 concentrations of incoming ambient air, pumped from outside the building to the chamber, were 373 ± 10 $\mu mol \cdot mol^{-1}$. Vapor pressure was measured with a General Eastern 1100DP dew point hygrometer (General Eastern Corp., Watertown, MA). Vapor pressure

deficit was maintained at <1 kPa (Moon et al., 1987a). Air flow into the chamber was regulated using Manostat 36-546-305 flow meters (Manostat, New York, NY). Fans built into the chamber circulated the air and the temperature was held at 25 ± 1C using a water-filled reservoir below the light source and a water-cooled heat sink inside the chamber. Leaf and chamber temperatures were monitored using copper-constantan thermocouples and a digital thermometer (Model AD2036, Analog Devices, Norwood, MA). Reference and sample gas subsamples were pulled from the gas entering and leaving the chamber, respectively, and dried by passing through magnesium perchlorate before entering the IRGA for analysis. Differential CO_2 concentration was recorded after it stabilized for at least 15 min.

1996 Experiment

Two-year-old 'Misty' and 'Sharpblue' SHB plants were obtained from a commercial grower in July, 1995 and transplanted into 12L containers using a 1:1 (v/v) peat:perlite mix. Plants were maintained outside on a gravel bed in Gainesville, FL. Plants were fertigated with a 20N-8.8P-16.6K water-soluble fertilizer at the rate of 200 mg N·liter^{-1} twice a week until the middle of September when the plants were allowed to slow growth and enter dormancy. Plants were sprayed with either propiconazole or a mixture of benomyl and captan every two to three weeks throughout the course of the experiment. Plants were placed in an open-ended tunnel greenhouse on

15 December, 1995. PPF was >1450 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on clear days. The plants were protected from freezes and the temperatures in the greenhouses averaged 1.5C warmer than the outside temperatures. The plants were transferred back outside to a gravel bed and placed in alternating rows of 'Misty' and 'Sharpblue' oriented north-south on 22 January, 1996. The total number of chill hours (≤7C) accumulated was >950 h (Ag Weather Information Services, Auburn, AL). Total numbers of flower buds were counted and the total lengths of all canes and stems were measured and FBD was calculated for each plant. Two FBD treatment levels were randomly assigned within each cultivar as follows:

1. FBD = 0.07 - 0.16
2. FBD > 0.17

FBD was adjusted by removing flower buds along the canes to decrease FBD or small stems with very low FBD were removed to increase overall plant FBD. Plants were fertigated weekly with 20N-8.8P-16.6K water-soluble fertilizer at the rate of 200 mg N·liter^{-1}. Plants were protected from freezing temperatures by moving them into a greenhouse when necessary.

Plant measurements

Measurement of floral and vegetative budbreak and calculation of FDP were done as previously described. Ripe fruits were harvested every 3-5 days until 50% of the fruit were ripe. Whole plants were randomly

harvested from within each treatment range at each of the following times: 1) immediately after removal from the greenhouse (dormancy), 2) at 50% bloom (0 DAB), 3) 28 days after 50% bloom (28 DAB), 4) and at 50% ripe fruit (fruit harvest). At each plant harvest, plants were divided into roots, previous years' canes, new stems, leaves, and flowers or fruit. Leaf area was measured using a LI-COR Model LI-3000 portable leaf area meter (LI-COR, Lincoln, NE) and the leaves and current year's stems were dried to a constant weight at 70C to determine dry weights. The roots and canes were frozen and held at -30C until lyophilized and dry weights measured. Lyophilized roots and canes were ground in a Wiley mill to pass a 20-mesh screen, and subsamples were analyzed for sugar and starch levels.

Carbohydrate analysis

Root and cane soluble sugars were extracted from 50 mg of tissue by boiling in 80% ethanol (1:100 w/v) for 2 min. Extracts were shaken for 20 min and centrifuged, the supernatant decanted, and the pellet re-extracted twice. The supernatants were combined, and final volumes were measured. Sample pigment was removed by adding 35 mg activated charcoal, and soluble sugars were assayed using the phenol-sulfuric acid method (Buysse and Merckx, 1993; Dubois et al., 1956). Tissue starch content was determined by suspending the insoluble fraction from the 80% ethanol extraction in 2.0 ml 0.2 N KOH and boiling for 30 min. After cooling, pH was adjusted to 4.5 with 1.0 ml 1.0 M acetic acid, and 1.0 ml of *Rhizopus*

amyloglucosidase (10 $mg \cdot ml^{-1}$) (Sigma Chemical Co., St. Louis, MO) in 0.2 M calcium acetate buffer (pH 4.5) was added. Samples were incubated in a shaking water bath for 24 h at 37C. After incubation, samples were centrifuged and the supernatant decanted. Sample pigment was removed by adding 35 mg activated charcoal, and glucose liberated from starch hydrolysis was quantified by the phenol-sulfuric acid method.

Net CO_2 exchange rate measurements

Whole-canopy NCER of 'Misty' plants was determined at 50% bloom, four weeks after 50% bloom, and at the beginning of fruit ripening. Whole-canopy NCER of 'Sharpblue' plants was measured at the beginning of fruit ripening. Whole-canopy NCER was determined as previously described.

Single leaf NCER measurements were taken on five recently matured leaves on randomly selected plants using a portable closed gas exchange system equipped with a one liter cuvette (LI-6200, LI-COR, Lincoln, NE). Measurements were taken on clear days between 11-17 April, 1996 when the fruit was beginning to ripen. Measurements were taken under ambient temperatures (28 ± 2C), relative humidity (20 ± 5%), CO_2 concentrations (371 ± 11 $\mu mol \cdot mol^{-1}$) and PPF (>1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Three measurements were taken per leaf and averaged.

Statistical Analysis

Although FBD was targeted into 2 or 3 different levels, a range of FBD resulted, therefore regression analysis was used to evaluate the data.

Total cane length was used as a covariate to adjust for differences in plant size. Cane lengths averaged over both cultivars were 178 cm in 1995 and 475 cm in 1996. When cane length was used as a covariate, blocks were never statistically significant and so were not used in fitting regression curves. SAS (SAS Institute, Cary, NC) was used for statistical analyses. PROC GLM was used for analysis of variance and regression analysis, PROC CORR was used to test correlations, and PROC MIXED was used to analyze for consistent patterns in vegetative budbreak regression slopes.

Results and Discussion

In 1995, FBD after treatment application ranged from 0.05 to 0.39 and 0.05 to 0.31 flower buds·cm^{-1} cane for 'Misty' and 'Sharpblue', respectively. In 1996, FBD ranged from 0.07 to 0.31 and 0.07 to 0.26 flower buds·cm^{-1} cane for 'Misty' and 'Sharpblue', respectively. In 1995, 50% bloom (0 DAB) occurred on 21 March or 24 days after removal from chilling for both 'Misty' and 'Sharpblue'. In 1996, 50% bloom (0 DAB) occurred approximately 18 days after removal from the greenhouses. The bloom period was similar for the two cultivars in both years.

Since floral budbreak and fruit set overlapped with each other and fruit density (fruit·cm^{-1} cane length) was not adjusted in this study, it was not possible to separate the effects of FBD from the effects of fruit density. Fruit density increased as FBD increased in both cultivars (Fig. 4-1). Fruit

density was similar for 'Misty' and 'Sharpblue' in 1995, but in 1996, fruit density was higher in 'Sharpblue' than in 'Misty'. In 1995, a number of plants were infected with *Botryosphaeria dothidea* and were removed from the experiment. Both 'Misty' and 'Sharpblue' were infected and at all treatment levels. However, more 'Misty' plants were affected, thus no 'Misty' plants were harvested 4 weeks after bloom and few plants remained at fruit ripening. In 1996, *Botryosphaeria dothidea* was again a problem but only in 'Misty', which began showing decline approximately 4-5 weeks after bloom. Over 80% of the affected plants were in the FBD > 0.17 treatment range. 'Sharpblue' plants did not show symptoms of the disease in 1996.

Vegetative Development and Biomass Allocation

The number of vegetative buds that broke and grew per unit cane length decreased as FBD increased (Fig. 4-2 and 4-3). Although the decrease in vegetative budbreak as FBD increased was significant, FBD only explained a small proportion of the total variability in vegetative budbreak. The trend was consistent in both cultivars and in both years, although vegetative budbreak was always greater in 'Sharpblue' than in 'Misty'. Although reduction in vegetative growth due to fruiting has been reported in different species (Hurd et al., 1979; Maggs, 1963; Schechter et al., 1994), there have been no reports on the effect of flower or fruit density on initial vegetative budbreak. Vegetative budbreak was delayed as FBD increased in

'Misty' ($p = .0059$) and 'Sharpblue' ($p = .0212$) in 1995 but not in 1996. In 1995, vegetative budbreak was over 80% complete by 28 DAB, but in 1996, vegetative budbreak was only 55% complete by 28 DAB. The overall delay in vegetative budbreak in 1996 may be related to higher fruit densities in 1996 compared to 1995 (Fig. 4-1). Higher fruit densities in 1996 could be caused by higher fruit set due to increased cross-pollination (El-Agamy et al., 1981; Lyrene, 1989) or more favorable temperature and/or other environmental conditions (Williamson and Lyrene, 1995).

Total leaf area, leaf dry weight, new stem length, and new stem dry weight were highly correlated at all sampling dates ($r > 0.85$) and responses to FBD were similar, therefore only the relationship between FBD and leaf area is presented (Fig. 4-4). In 1995, leaf area decreased with increasing FBD in 'Sharpblue' but not in 'Misty'. The lack of significant response in 'Misty' may be partially a result of the small sample number, since the incidence of *Botryosphaeria dothidea* was severe. In 1996, leaf area decreased with increasing FBD in both 'Misty' and 'Sharpblue'. The decrease in leaf area as FBD increased was evident by 14 DAB in 1995 and 28 DAB in 1996 and the trend continued to fruit harvest, suggesting that early vegetative budbreak and canopy development are critical in determining further development. The reduction in leaf area with increased FBD also resulted in decreases in leaf area:fruit ratios in both cultivars (Fig. 4-5).

The reduction in leaf area development with increased FBD is similar to that in other crops, including tomato (Hurd et al., 1979), apple (Maggs, 1963; Schechter et al., 1994), and strawberry (Schaffer et al., 1986c) where the rate of leaf production was slower and final leaf area was less on fruiting plants compared to nonfruiting plants. In sweet cherry, where floral and vegetative budbreak occur simultaneously, leaf area at fruit harvest was reduced 13% on fruiting trees vs nonfruiting trees (Kappel, 1991). In the present study, leaf area at high FBDs was approximately 20-40% lower than at low FBDs in 1996. The greater reduction in leaf area in SHB compared to sweet cherry may be caused in part by later vegetative budbreak relative to floral budbreak in SHB.

Flower bud density did not affect root and cane dry weights. However, root and cane dry weights differed with various developmental stages. In 1995, root and cane dry weights decreased between dormancy and 14 DAB in 'Misty' before increasing by fruit harvest (Table 4-1). In 'Sharpblue', root and cane dry weights remained constant from dormancy until 42 DAB before increasing by fruit harvest. In 1996, root and cane dry weights in 'Sharpblue' remained the same from dormancy until fruit harvest, while in 'Misty', root and cane dry weights decreased between dormancy and 28 DAB (Table 4-2). 'Misty' root dry weights continued to decrease until fruit harvest.

The reduction in root and cane dry weight in 'Misty' between dormancy and 14 DAB or 28 DAB is similar to the pattern found in rabbiteye blueberry. In 'Climax' rabbiteye blueberry, a cultivar that is very similar to 'Misty' in patterns of vegetative and floral budbreak, root dry weight declined continuously from dormancy to fruit maturity while shoot dry weight declined from dormancy to 51 days after anthesis, before increasing by fruit maturity (Birkhold and Darnell, 1993). The decrease in root and cane dry weight in 'Misty' probably reflects carbohydrate mobilization for respiration and fruit growth as the decrease in total root and cane carbohydrate content accounted for >55% of the decrease in root and cane dry weights in 1996 (data not shown). Similarly, the decline in root carbohydrate content accounted for >70% of the root dry weight decline in rabbiteye blueberry (Darnell and Birkhold, 1996).

In 1995, biomass allocation to the flowers or fruit was low, probably due to low fruit set and density. Fruit accounted for only 17.6% and 3.5% of the dry weight increase between dormancy and fruit harvest in 'Misty' and 'Sharpblue', respectively (Table 4-1). In 1995, fruit on 'Misty' accounted for most of the dry weight increase between dormancy and 14 DAB, while the leaves were the major sink for dry weight allocation between 14 DAB and fruit harvest. In 'Sharpblue', the leaves were the major sink for dry weight gain throughout fruit development.

Dry weight allocation to the fruit was much greater in 1996 than in 1995, with fruit accounting for 69% and 44% of the dry weight increase between dormancy and fruit harvest in 'Misty' and 'Sharpblue', respectively (Table 4-2). In comparison, fruit accounted for 35-70% of the total annual dry weight increase in apple (Forshey et al., 1983; Hansen, 1970; Heim et al., 1979; Heinicke, 1937; Maggs, 1963; Schechter et al., 1994), 37-50% in peach (Miller and Walsh, 1988), 16% in sweet cherry (Kappel, 1991), and 4-86% in wild blueberry (Pritts and Hancock, 1985). In 1996, biomass allocation to 'Misty' fruit was greater than to any other plant part from dormancy to fruit harvest, while in 'Sharpblue', the fruit was the main sink between dormancy and bloom and between 28 DAB and fruit harvest. The leaves were the main sink during the early fruit development period between bloom and 28 DAB. The roots and canes always exhibited the least dry weight gain during fruit development in both years. Similarly, dry weight partitioning to the roots is low in fruiting apple (Heim et al., 1979) and coffee (Cannell, 1971; 1985). Fruit is a dominant sink in SHB, reducing dry weight allocation to vegetative plant parts, however, when fruit growth is low, as in 1995, then leaves may become the predominant sink.

Carbohydrates

Cane sugar concentrations were similar at all FBD in both 'Misty' and 'Sharpblue' at each sampling date in 1996 (Fig 4-6 and 4-7). Cane starch, root sugar, and root starch concentrations decreased with increased FBD at

bloom, 28 DAB, and at fruit harvest in 'Misty' (Fig. 4-6 and 4-8). In 'Sharpblue', the effect of FBD on carbohydrate concentrations depended on stage of development. Cane starch concentration decreased with increased FBD at bloom and fruit harvest (Fig 4-7). Root sugar concentrations decreased with increased FBD at bloom, but were unaffected by FBD at later stages of development (Fig 4-9). Root starch concentrations decreased with increased FBD at bloom, 28 DAB, and fruit harvest. The effect of FBD on root and cane carbohydrate concentrations in 'Misty' and 'Sharpblue' was apparent by bloom, indicating that competition for carbohydrates begins early in the spring and could also affect floral development, although this was not measured in the present study. The decrease in carbohydrate concentrations with increased FBD follows a similar pattern to that found in citrus, where starch concentrations in girdled twigs decreased with increased fruit load (Fishler et al., 1983), but contrary to that found in apple (Ferree and Cahoun, 1987) and sweet cherry (Roper et al., 1988) where no differences were seen in root or shoot carbohydrate levels at different crop loads. Discrepancies between the studies may be due to differences in plant species and size or the number of alternative sinks.

Root and cane carbohydrate concentrations changed with development. Root starch was the main carbohydrate reserve form during dormancy in 'Sharpblue', as it is in rabbiteye blueberry (Darnell and Birkhold, 1996) and many fruit trees (Loescher et al., 1990). Root starch

concentrations decreased rapidly between dormancy (-17 and -20 DAB) and bloom (0 DAB), reaching 63% and 37% of dormancy levels by bloom in 'Misty' and 'Sharpblue', respectively (Fig. 4-8 and 4-9). Root starch concentrations continued to decrease with development and by 28 DAB concentrations were 25% and 9% of dormancy concentrations in 'Misty' and Sharpblue', respectively. Root starch concentrations in 'Sharpblue' increased between 28 DAB and fruit harvest, although total root carbohydrates exhibited no change. In 'Misty', root starch concentrations continued to decrease until fruit harvest. Cane sugar and starch concentrations decreased until 28 DAB in both cultivars before exhibiting a slight increase by fruit harvest (Fig. 4-6 and 4-7). The reduction in root starch, but not cane carbohydrates throughout fruit development in 'Misty' suggests that root carbohydrate reserves continued to be used for root respiration, possibly for ion uptake and maintenance. The absence of substantial carbohydrate reserve buildup prior to fruit harvest is similar to rabbiteye blueberry and supports the contention that in blueberry, concomitant fruit and vegetative growth requires most of the current photoassimilates during fruit development (Darnell and Birkhold, 1996).

Leaf and Whole-Canopy NCER

In 1996, leaf NCER at fruit ripening increased with increased FBD in 'Sharpblue' ($y = 10.27 + 2.42 \ln FBD$) but not in 'Misty'. The increase in leaf NCER observed in 'Sharpblue' is similar to that found in fruiting vs

nonfruiting apple (Fujii and Kennedy, 1985; Hansen, 1970; 1971b; Kazaryan et al., 1965), citrus (Lenz, 1979), grape (Edson et al., 1993), and strawberry (Schaffer 1986b; 1986c). The lack of response in 'Misty' may be due to the fact that all the 'Misty' plants had low leaf area:fruit ratios and so sink demand was always high. Lower leaf area:fruit ratios in 'Misty' compared to 'Sharpblue' (Fig. 4-5) may be part of the explanation why leaf NCER was higher in 'Misty' (7.94 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) than in 'Sharpblue' (5.65 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$).

FBD did not affect whole-canopy NCER between dormancy and 28 DAB. Respiration was greater than photosynthesis during dormancy and at 50% bloom with whole-canopy NCER averaging -0.17 μmol $CO_2 \cdot plant^{-1} \cdot s^{-1}$ during both measurement periods. By 14 DAB, whole-canopy NCER was positive (0.25 μmol $CO_2 \cdot plant^{-1} \cdot s^{-1}$), indicating net carbon gain during daylight hours under the experimental conditions used. Whole-canopy NCER decreased with increased FBD at 42 DAB ($y = 0.67 - 3.99 \ln FBD + .004 length$) in 'Sharpblue' in 1995. In both years and for both cultivars, whole-canopy NCER decreased with increased FBD at fruit ripening (Fig 4-10). The decreased whole-canopy NCER with increased FBD is similar to that found in fruiting vs nonfruiting strawberry (Schaffer et al., 1986c), but contrary to results found in grape (Edson et al., 1993) and apple (Francesconi et al., 1996), where no differences in whole-canopy NCER were detected due to crop load variation, and in coffee, where whole-branch NCER increased with

increased fruit load (Cannell, 1985). This indicates that unlike grape, apple, and coffee, SHB plants are not able to compensate for the reduction in leaf area development through increases in leaf NCER at increased FBD levels.

Reproductive Development

The reduction in the leaf area:fruit ratios and whole-canopy NCER with increased FBD significantly affected fruit development. Average fruit fresh weight of both cultivars increased as leaf area:fruit ratio increased in both years (Fig. 4-11 and 4-12). This observation is consistent with patterns found in apple (Ferree and Cahoon, 1987; Haller and Magness, 1925), peach (Overholser and Claypool, 1931; Weinberger, 1931), cherry, (Facteau et al., 1983; Flore, 1985; Roper and Loescher, 1987), and northern highbush blueberry (Ballinger et al., 1963). Average fruit fresh weight also increased as whole-canopy NCER:fruit ratio increased (Fig. 4-13 and 4-14). The increase in fruit fresh weight as whole-canopy NCER:fruit ratio increased is similar to results found in apple (Lakso et al., 1996).

Leaf area:fruit and whole-canopy NCER:fruit ratios also affected the rate of fruit development. The FDP increased with decreased leaf area:fruit and whole-canopy NCER:fruit ratios (data not shown). Thus, the decrease in canopy development and carbohydrate supply as FBD increased resulted in a delay in fruit harvest. In a similar manner, fruit harvest was delayed as fruit load increased in 'Wolcott' blueberry (Ballinger et al., 1963).

In conclusion, FBD in SHB affected vegetative budbreak, canopy development, and whole-canopy NCER, which in turn affected fruit development. Vegetative budbreak, total leaf area, and leaf area:fruit ratios decreased as FBD increased. Although leaf NCER increased with increased FBD, whole-canopy NCER decreased as FBD increased. Fruit fresh weight decreased and fruit ripening was delayed as leaf area:fruit and whole-canopy NCER:fruit ratios decreased. These results suggest that flower bud thinning can increase fruit size by advancing and increasing vegetative budbreak, which in turn increases the photosynthetic leaf area and canopy NCER for increased carbohydrate availability to the fruit. Other factors such as greater carbohydrate reserve levels or cultivars that break vegetative bud earlier relative to floral budbreak (thus, potentially leading to increased leaf area, whole-canopy NCER, and carbohydrate production), may also result in larger, earlier ripening fruit.

Table 4-1. Organ dry weights (g) of 'Misty' and 'Sharpblue' SHB at various stages of development in 1995.

	'Misty'	'Sharpblue'
Root dry weight		
Dormancy	16.9 a[z]	12.8 b
14 DAB	12.3 b	11.6 b
42 DAB	-[y]	14.0 b
Fruit harvest	15.1 a	19.5 a
Cane dry weight		
Dormancy	17.2 ab	13.0 b
14 DAB	14.7 b	14.8 b
42 DAB	-	16.2 b
Fruit harvest	20.0 a	19.8 a
Flower or fruit dry weight		
Dormancy	0.32 b	0.97 b
14 DAB	1.36 b	1.35 b
42 DAB	-	1.36 b
Fruit harvest	5.89 a	3.31 a
Stem dry weight		
Dormancy	0	0
14 DAB	0.01 b	0.24 b
42 DAB	-	1.85 b
Fruit harvest	4.27 a	10.2 a
Leaf dry weight		
Dormancy	0	0
14 DAB	0.12 b	2.98 c
42 DAB	-	13.7 b
Fruit harvest	18.9 a	41.3 a

[z]Mean separation within groups within columns by LSD at P=0.05. Values are means adjusted using flower bud density and cane length as covariates.
[y]Missing data.

Table 4-2. Organ dry weights (g) of 'Misty' and 'Sharpblue' SHB at various stages of development in 1996.

	'Misty'	'Sharpblue'
Root dry weight		
Dormancy	23.5 a[z]	52.0 a
0 DAB	20.3 ab	44.2 a
28 DAB	19.3 bc	45.2 a
Fruit harvest	16.6 c	45.2 a
Cane dry weight		
Dormancy	50.7 a	71.0 a
0 DAB	45.3 ab	63.8 a
28 DAB	42.1 b	65.9 a
Fruit harvest	41.2 b	73.7 a
Flower or fruit dry weight		
Dormancy	3.36 c	4.16 c
0 DAB	6.17 bc	6.83 bc
28 DAB	9.31 b	14.5 b
Fruit harvest	33.9 a	54.5 a
Stem dry weight		
Dormancy	0	0
0 DAB	0.01 b	0.05 b
28 DAB	0.07 b	1.52 b
Fruit harvest	1.93 a	12.4 a
Leaf dry weight		
Dormancy	0	0
0 DAB	0.34 b	0.74 c
28 DAB	0.74 b	12.0 b
Fruit harvest	12.0 a	49.4 a

[z]Mean separation within groups within columns by LSD at P=0.05. Values are means adjusted using flower bud density and cane length as covariates.

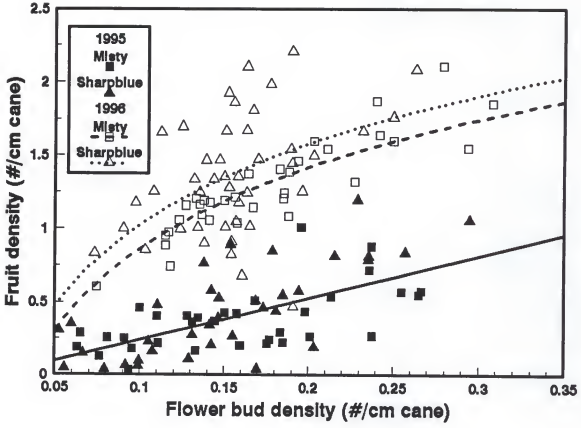

Figure 4-1. Relationship between fruit density and flower bud density in 'Misty' and 'Sharpblue' SHB: 1995: ($y = -0.05 + 2.88\ln x$; $r^2 = 0.41$, $P < .001$); 1996: ('Misty' $y = 2.71 + 0.80\ln x$; 'Sharpblue' $y = 2.88 + 0.80\ln x$; overall $r^2 = 0.36$, $P < .001$).

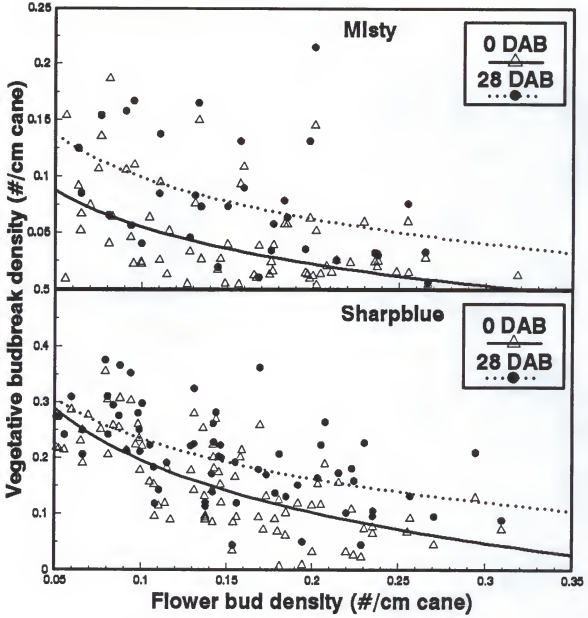

Figure 4-2. Relationship between vegetative budbreak and flower bud density in 'Misty' and 'Sharpblue' SHB in 1995: 'Misty': (0 DAB $y=-0.05-0.05\ln x$, $r^2=0.24$, $P<0.001$; 28 DAB $y=-0.03-0.05\ln x$, $r^2=0.18$, $P<0.05$); 'Sharpblue': (0 DAB $y=-0.11-0.14\ln x$, $r^2=0.57$, $P<0.001$; 28 DAB $y=-0.01-0.10\ln x$, $r^2=0.42$, $P<0.001$).

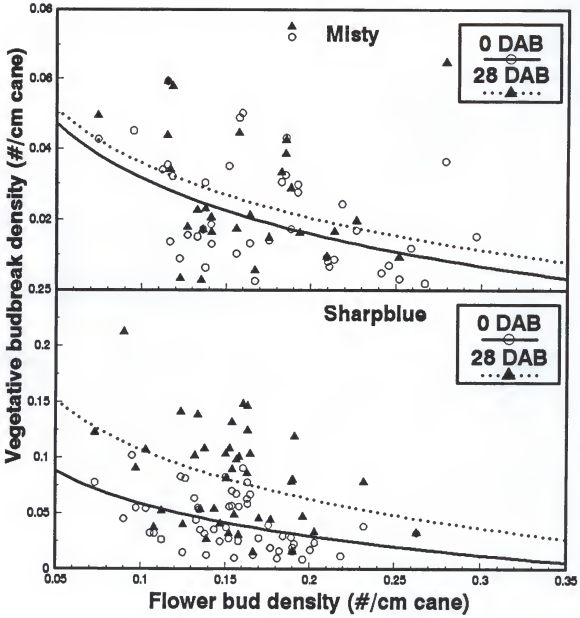

Figure 4-3. Relationship between vegetative budbreak and flower bud density in 'Misty' and 'Sharpblue' SHB in 1996: 'Misty': (0 DAB y=-0.02-0.02lnx, r^2=0.17, P <0.01; 28 DAB y=-0.02-0.02lnx, r^2=0.12, P <0.05); 'Sharpblue': (0 DAB y=-0.04-0.04lnx, r^2=0.18, P <0.01; 28 DAB y=-0.04-0.06lnx, r^2=0.13, P <0.05).

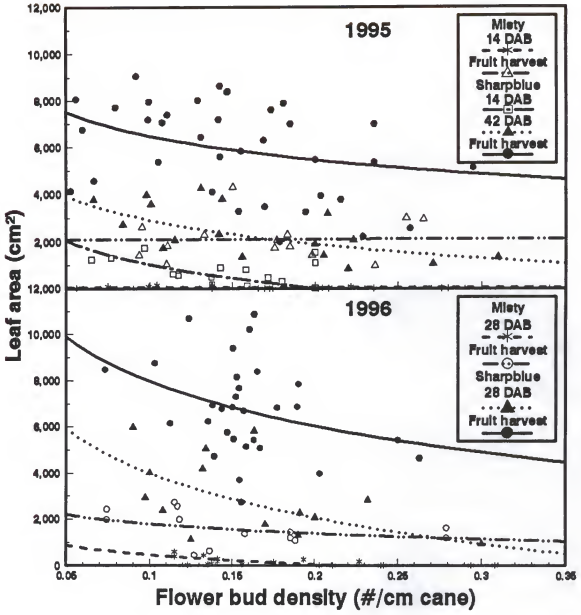

Figure 4-4. Relationship between leaf area and flower bud density in 'Misty' and 'Sharpblue' SHB: 1995: ('Misty' 14 DAB $y = 25$; fruit harvest $y = 2115$; $P =$ n.s.; 'Sharpblue' 14 DAB $y = 4581 - 1474\ln x + 12.5\text{length}$; 42DAB $y = -2704 - 1471\ln x + 12.5\text{length}$; fruit harvest $y = -870 - 1474\ln x + 12.5\text{length}$; $r^2 = 0.75$, $P < 0.01$); 1996: ('Misty' 28 DAB $y = -892 - 593\ln x$; fruit harvest $y = 442 - 593\ln x$; $r^2 = 0.74$, $P < 0.05$; 'Sharpblue' 28 DAB $y = -1971 - 2790\ln x + 6.5\text{length}$; fruit harvest $y = -2001 - 2790\ln x + 6.5\text{length}$; $r^2 = 0.56$, $P < 0.05$). The regression lines and data points shown indicate adjustment at the average value of the cane length covariate.

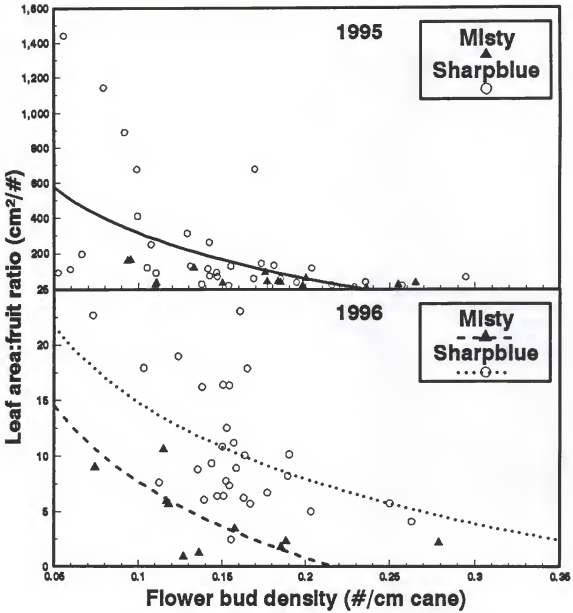

Figure 4-5. Relationship between leaf area:fruit ratio and flower bud density in 'Misty' and 'Sharpblue' SHB: 1995: ($y = -537 - 371 \ln x$; $r^2 = 0.28$, $P < 0.001$); 1996: ('Misty' $y = -15.2 - 10.0 \ln x$; 'Sharpblue' $y = -8.1 - 10.0 \ln x$; overall $r^2 = 0.44$, $P < 0.01$).

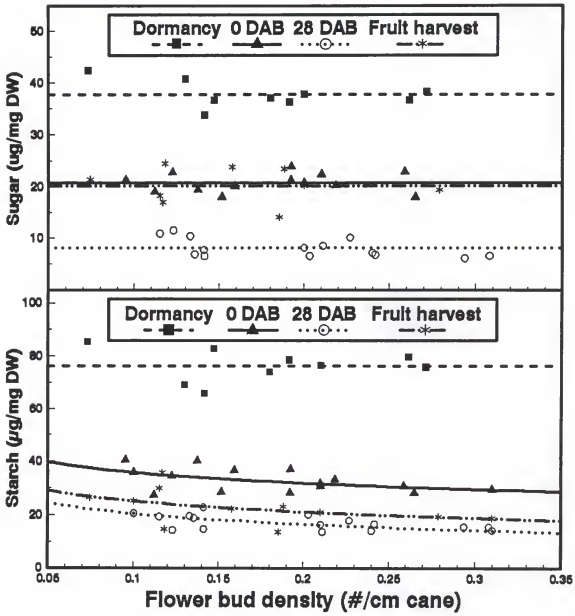

Figure 4-6. Cane sugar and starch concentrations of 'Misty' SHB as related to flower bud density in 1996: sugar: (dormancy $y = 37.7$, P = n.s.; 0 DAB $y = 20.9$, P = n.s.; 28 DAB $y = 8.1$, P = n.s.; fruit harvest $y = 20.3$, P = n.s.); starch: (dormancy $y = 76.4$, P = n.s.; 0 DAB $y = 22.7 - 5.7\ln x$; 28 DAB $y = 7.4 - 5.7\ln x$; fruit harvest $y = 12.0 - 5.7\ln x$; overall $r^2 = 0.74$, $P < 0.001$).

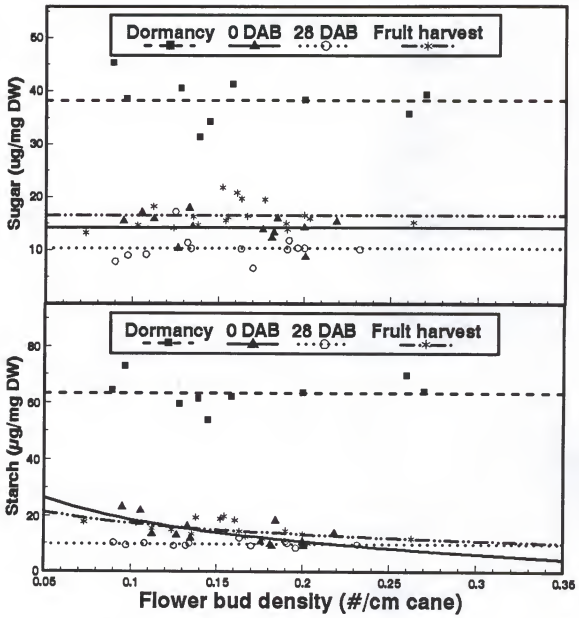

Figure 4-7. Cane sugar and starch concentrations of 'Sharpblue' SHB as related to flower bud density in 1996: sugar: (dormancy y = 38.3, P = n.s.; 0 DAB y = 14.2, P = n.s.; 28 DAB y = 10.3, P = n.s.; fruit harvest y = 16.5, P = n.s.); starch: (dormancy y = 63.5, P = n.s.; 0 DAB y = 3.8-11.4lnx, r^2 = 0.43, P < 0.05; 28 DAB y = 9.8, P = n.s.; fruit harvest y = 3.9-5.9lnx, r^2 = 0.30, P < 0.05).

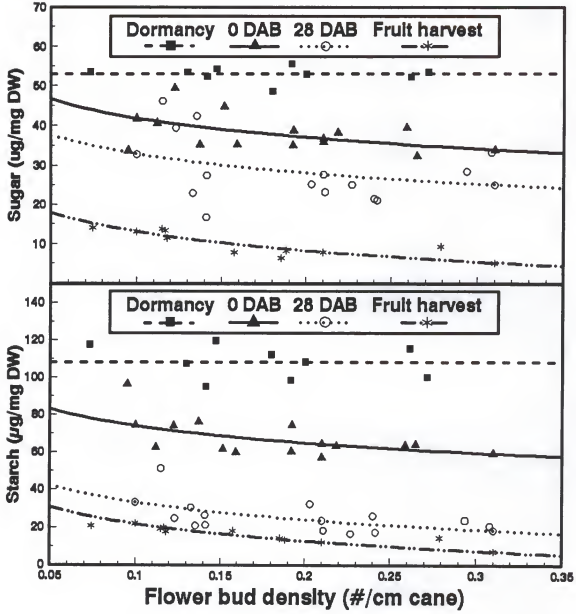

Figure 4-8. Root sugar and starch concentrations of 'Misty' SHB as related to flower bud density in 1996: sugar: (dormancy $y = 53.0$, P = n.s.; 0 DAB $y = -25.8\text{-}7.0\ln x$; 28 DAB $y = 16.9\text{-}7.0\ln x$; fruit harvest $y = -3.0\text{-}7.0\ln x$; overall $r^2 = 0.78$, $P < 0.001$); starch: (dormancy $y = 108.4$, P = n.s.; 0 DAB $y = 44.3\text{-}13.2\ln x$; 28 DAB $y = 3.1\text{-}13.2\ln x$; fruit harvest $y = -8.2\text{-}13.2\ln x$; overall $r^2 = 0.91$, $P < 0.001$).

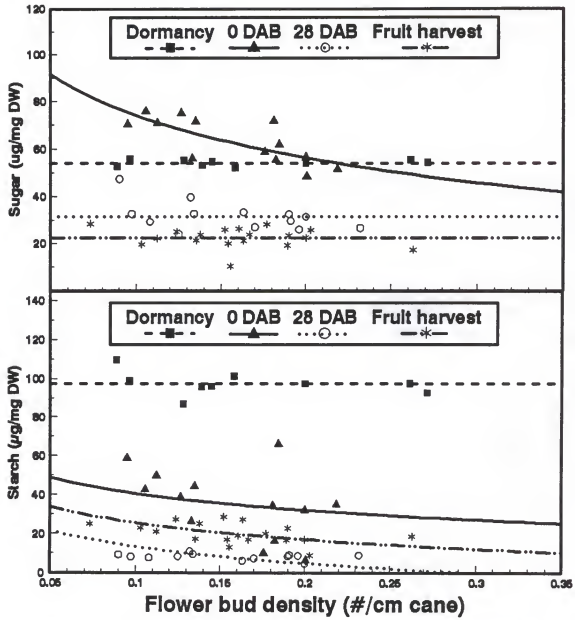

Figure 4-9. Root sugar and starch concentrations of 'Sharpblue' SHB as related to flower bud density in 1996: sugar: (dormancy y=54.2, P =n.s.; 0 DAB y=15.3-25.6lnx, r^2=0.53, P <0.01; 28 DAB y=22.4, P =n.s.; fruit harvest y=22.4, P =n.s.); starch: (dormancy y=101.8, P =n.s.; 0 DAB y=12.5-12.3lnx; 28 DAB y=-15.0-12.3lnx; fruit harvest y=-2.7-12.3lnx; overall r^2=0.57, P <0.001).

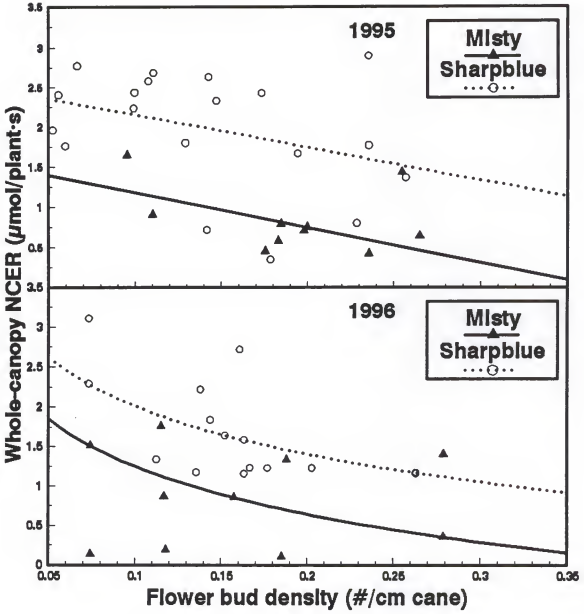

Figure 4-10. Relationship between whole-canopy NCER at fruit ripening and flower bud density in 'Misty' and 'Sharpblue' SHB: 1995: ('Misty' $y = 0.09 - 4.35x + 0.009length$; 'Sharpblue' $y = 1.07 - 4.35x + 0.009length$; overall $r^2 = 0.58$, $P < 0.03$); 1996: ('Misty' $y = -2.85 - 0.88lnx + 0.004length$; 'Sharpblue' $y = -2.09 - 0.88lnx + 0.004length$; $r^2 = 0.69$, $P < 0.05$). The regression lines and data points shown indicate adjustment at the average value of the cane length covariate.

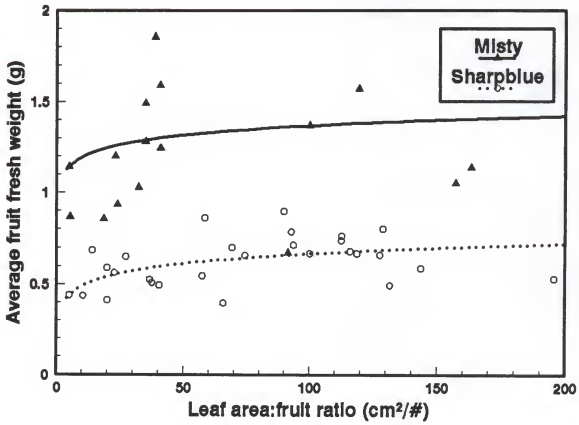

Figure 4-11. Relationship between fruit fresh weight and leaf area:fruit ratio in 'Misty' and 'Sharpblue' SHB in 1995: 'Misty' ($y = 1.02 + 0.08\ln x$); 'Sharpblue' ($y = 0.32 + 0.08\ln x$); overall $r^2 = 0.66$, $P < 0.01$).

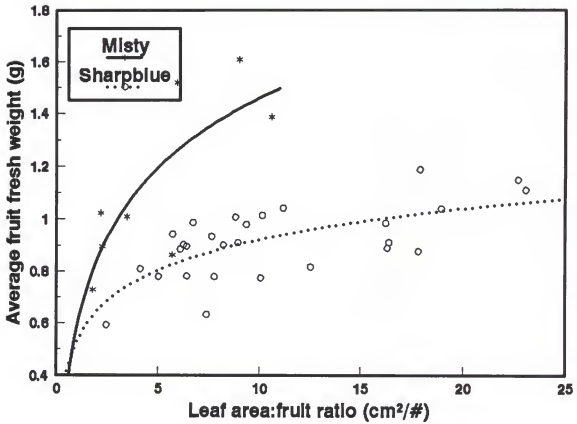

Figure 4-12. Relationship between fruit fresh weight and leaf area:fruit ratio in 'Misty' and 'Sharpblue' SHB in 1996: 'Misty' ($y = 0.58 + 0.38\ln x$, $r^2 = 0.62$, $P < 0.05$); 'Sharpblue' ($y = 0.53 + 0.17\ln x$, $r^2 = 0.45$, $P < 0.001$).

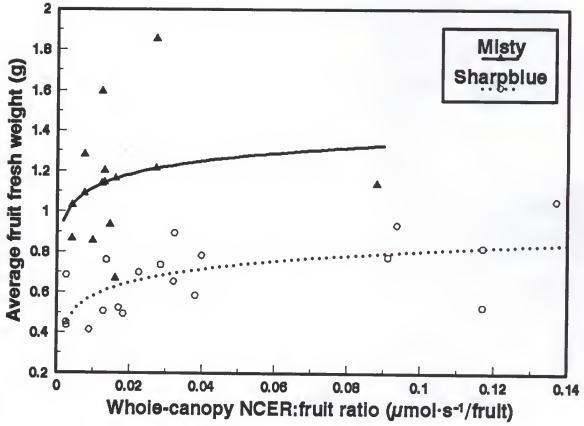

Figure 4-13. Relationship between fruit fresh weight and whole-canopy NCER:fruit ratio at fruit ripening in 'Misty' and 'Sharpblue' SHB in 1995: 'Misty' ($y = 1.56 + 0.10 \ln x$); 'Sharpblue' ($y = 1.03 + 0.10 \ln x$); overall $r^2 = 0.65$, $P < 0.02$.

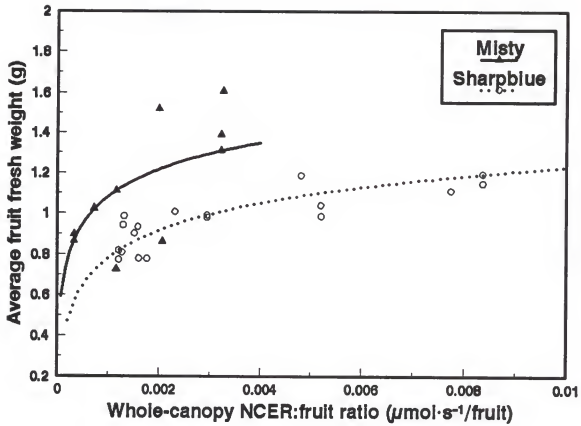

Figure 4-14. Relationship between fruit fresh weight and whole-canopy NCER:fruit ratio in 'Misty' and 'Sharpblue' SHB in 1996: 'Misty' ($y = 2.42 + 0.03\ln x$); 'Sharpblue' ($y = 2.12 + 0.03\ln x$); overall $r^2 = 0.51$, $P < 0.001$.

CHAPTER 5
CARBOHYDRATE RESERVE LEVELS AND FLOWER BUD DENSITY INFLUENCE VEGETATIVE AND REPRODUCTIVE DEVELOPMENT IN SOUTHERN HIGHBUSH BLUEBERRY PLANTS

Introduction

Flowering and fruit set begin prior to vegetative budbreak in many southern highbush blueberry (SHB) (*Vaccinium corymbosum* L.) cultivars. Flower bud density (FBD) (flower buds·cm^{-1} cane length) affects the amount of vegetative budbreak and new shoot development (see chapters 3 and 4), suggesting that there is competition between reproductive and vegetative growth for carbohydrate reserves. Carbohydrate reserves clearly occupy a key role in supporting new spring growth in deciduous species. Numerous studies have documented the mobilization of reserve carbohydrates into new spring growth (Davis and Sparks, 1974; Hansen, 1971a; Lockwood and Sparks, 1978; Quinlan, 1969) and changes in carbohydrate reserve levels during flowering and fruiting in the spring have been extensively investigated in several deciduous fruit crops (see Loescher et al., 1990). The relationship between carbohydrate reserve levels and fruiting has also been studied in alternate bearing trees (Crane et al., 1976; Goldschmidt and Golomb, 1982; Jones et al., 1975; Weinbaum et al., 1994; Wood, 1989).

There are few studies, however, that document the affect of carbohydrate reserves levels on the amount of spring vegetative growth in woody species (Loescher et al., 1990; Wilcox, 1937). There is some evidence in forage crops that carbohydrate reserve concentrations affect new vegetative growth. In rhizoma perennial peanut (*Arachis glabrata* Benth.), increased carbohydrate levels in the rhizome planting material increased new shoot number and biomass accumulation 180 days after planting (Rice et al., 1996). Similarly, increased carbohydrate reserve levels increased tiller initiation and growth in alfalfa (*Medicago sativa* L.) (Chatterton et al., 1974). This suggests that carbohydrate reserve levels may influence vegetative budbreak and subsequent shoot development in other species, such as SHB. Increased shoot development should also increase fruit development as leaf area:fruit and whole-canopy net CO_2 exchange rates (NCER):fruit ratios increase (Ballinger et al., 1963; Facteau et al., 1983; Ferree and Cahoon, 1987; Haller and Magness, 1925; Lakso et al., 1996; Roper and Loescher, 1987; Overholser and Claypool, 1931; Weinberger, 1931). Therefore, this study investigated the hypothesis that increased carbohydrate reserve concentrations would increase vegetative budbreak and subsequent shoot and reproductive development in SHB.

Materials and Methods

Two-year-old 'Misty' and 'Sharpblue' SHB plants were obtained from a commercial grower in July, 1995 and transplanted into 12L containers using a 1:1 (v/v) peat:perlite mix. Plants were maintained outside on a gravel bed in Gainesville, FL. Plants were fertigated with a 20N-8.8P-16.6K water-soluble fertilizer (Peters, Grace-Sierra Horticultural Products Co., Milpitas, CA) at 200 mg N·liter^{-1} twice a week until the middle of September. Plants were sprayed with either propiconazole or a mixture of benomyl and captan every two to three weeks throughout the course of the experiment. In order to increase carbohydrate reserve concentrations in half of the plants, plants of each cultivar were randomly separated into two equal groups. On 15 December, 1996, while still fully foliated, the plants were placed inside open-ended plastic tunnel greenhouses described by Sinclair et al. (1995) and grown under natural light conditions (PPF >1450 μmol·m^{-2}·s^{-1} on clear days). One half of the plants of each cultivar were placed inside a tunnel greenhouse with ambient CO_2 concentrations ($\approx$360 μmol·mol^{-1}), while the other half was placed in a corresponding location in a similar tunnel greenhouse with CO_2 concentrations maintained at $\approx$700 μmol·mol^{-1} during the daytime by a computer-controlled injection system. Temperatures were maintained at ambient temperatures $\pm$1.5C except when ambient temperatures were below 0C, then greenhouse temperatures were maintained above 0C. All plants were removed from the greenhouses on 22

January, 1996, hand-defoliated, and grown out-of-doors for the remainder of the experiment except during freezes, which necessitated moving the plants into a heated fiberglass greenhouse. Total chill hour (≤7C) accumulation was >950 h (Ag Weather Information Services, Auburn, AL). The total numbers of flower buds per plant were counted, the total lengths of all canes and stems per plant were measured, and FBDs were calculated for each plant. FBDs were adjusted into two treatment levels as follows:

1. FBD 0.07 - 0.16
2. FBD > 0.17

FBDs were adjusted by removing flower buds along the canes to decrease FBDs or small stems with very low FBDs were removed to increase overall plant FBDs. Plants were fertigated weekly with 20N-8.8P-16.6K water-soluble fertilizer at 200 mg N·liter^{-1}.

Plant Measurements

Floral and vegetative budbreak was measured on a weekly basis and ripe fruit was harvested every 3-5 days until 50% of the fruit was ripe. Bloom for a particular flower bud was when the majority of the florets had open corollas. Fifty percent bloom was when 50% of the flower buds were at bloom. Fruit development periods (FDP) were calculated as the number of days from 50% bloom to 50% ripe fruit. Vegetative buds were considered breaking when they were extended at least 0.5 cm. Whole plants were randomly harvested from within each cultivar, CO_2 treatment,

and FBD range at the following times: 1) removal from the greenhouse (dormancy), 2) 50% bloom (0 DAB), 3) four weeks after 50% bloom (28 DAB), and 4) 50% ripe fruit (fruit harvest). At each plant harvest, plants were divided into roots, previous years' canes, new stems, leaves, and flowers or fruit. Leaf area was measured using a LI-COR Model LI-3000 portable leaf area meter (LI-COR, Lincoln, NE) and the leaves and current year's stems were dried to a constant weight at 70C to determine dry weights. The roots and canes were frozen and held at -30C until lyophilized and dry weights measured. Lyophilized roots and canes were ground in a Wiley mill to pass a 20-mesh screen, and subsamples were analyzed for sugar and starch levels.

Carbohydrate Analysis

Root and cane soluble sugars were extracted from 50 mg of tissue by boiling in 80% ethanol (1:100 w/v) for 2 min. Extracts were shaken for 20 min and centrifuged, the supernatant decanted, and the pellet re-extracted twice. The supernatants were combined, and final volumes were measured. Sample pigment was removed by adding 35 mg activated charcoal, and soluble sugars were assayed using the phenol-sulfuric acid method (Buysse and Merckx, 1993; Dubois et al., 1956). Tissue starch content was determined by suspending the insoluble fraction from the 80% ethanol extraction in 2.0 ml 0.2 N KOH and boiling for 30 min. After cooling, pH was adjusted to 4.5 with 1.0 ml 1.0 M acetic acid, and 1.0 ml of *Rhizopus*

amyloglucosidase (10 $mg \cdot ml^{-1}$) (Sigma Chemical Co., St. Louis, MO) in 0.2 M calcium acetate buffer (pH 4.5) was added. Samples were incubated in a shaking water bath for 24 h at 37C. After incubation, samples were centrifuged and the supernatant decanted. Sample pigment was removed by adding 35 mg activated charcoal, and glucose liberated from starch hydrolysis was quantified by the phenol-sulfuric acid method.

Net CO_2 Exchange Rate Measurements

Net CO_2 exchange rates (NCER) of whole blueberry plant canopies were determined at the beginning of fruit ripening. Whole-canopy NCER was measured using an open flow system with an Anarad AR600R infrared gas analyzer (IRGA) (Anarad Inc., Santa Barbara, CA). Plants were enclosed in a 1 m x 1 m x 1 m plexiglass chamber covered on the inside with Propafilm C (ICI Films, Wilmington, DE). Roots were enclosed in a Tedlar gas sampling bag (Fisher Scientific) sealed at the base of the canes. Photosynthetic photon flux (PPF), provided by a 400W metal halide lamp (Sylvania Lumalux Lu400), was 1750-2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of the canopy. CO_2 concentrations of incoming ambient air, pumped from outside the building to the chamber, were 373 ± 10 $\mu mol \cdot mol^{-1}$. Vapor pressure was measured with a General Eastern 1100DP dew point hygrometer (General Eastern Corp., Watertown, MA). Vapor pressure deficit was maintained at <1 kPa (Moon et al., 1987a). Air flow into the chamber was regulated using Manostat 36-546-305 flow meters (Manostat, New York, NY). Fans

built into the chamber circulated the air and the temperature was held at 25 ± 1C using a water-filled reservoir below the light source and a water-cooled heat sink inside the chamber. Leaf and chamber temperatures were monitored using copper-constantan thermocouples and a digital thermometer (Model AD2036, Analog Devices, Norwood, MA). Reference and sample gas subsamples were pulled from the gas entering and leaving the chamber, respectively, and dried by passing through magnesium perchlorate before entering the IRGA for analysis. Differential CO_2 concentrations were recorded after they stabilized for at least 15 min.

Statistical Analysis

Although FBD was targeted into 2 different levels, a range of FBD resulted, therefore differences were examined with respect to CO_2, FBD, and cultivar with regression analysis. Total cane length was used as a covariate to account for differences in plant size. SAS (SAS Institute, Cary, NC) was used for statistical analyses. PROC GLM was used for analysis of variance and regression analysis and PROC CORR was used to test correlations.

Results

There was no visible shoot growth on any plants while in the CO_2 treatments. Flower bud densities after treatment application ranged from 0.07 to 0.40 flower buds·cm^{-1} cane length in 'Misty' and from 0.07 to 0.27 flower buds·cm^{-1} cane length in 'Sharpblue'.

Carbohydrates

Root starch and whole plant carbohydrate concentrations at the end of dormancy were increased in plants exposed to enriched (ENR) CO_2 conditions compared to plants exposed to ambient (AMB) CO_2 conditions in both 'Misty' and 'Sharpblue' (Fig. 5-1 and 5-2). In 'Sharpblue', cane sugar concentrations were also higher in ENR plants compared to AMB plants at the end of dormancy. No differences in reserve carbohydrate concentration between ENR and AMB plants were observed from bloom (0 DAB) to fruit ripening (82 DAB), with the exception that root starch concentrations in 'Misty' were higher in ENR than in AMB plants at bloom. In general, root and cane carbohydrate concentrations decreased steadily between dormancy and 28 DAB, then plateaued or increased slightly by fruit harvest in both AMB and ENR plants. Cane and root starch concentrations in 'Sharpblue' increased between 28 DAB and fruit harvest. However, in 'Misty', only cane carbohydrate concentrations increased before fruit harvest, while root carbohydrate concentrations continued to decrease and remained low.

In AMB 'Misty' and 'Sharpblue' plants, cane and root starch concentrations at bloom, 28 DAB, and fruit harvest decreased 40-60% as FBD increased from 0.05 to 0.35 flower buds·cm^{-1} cane length (data not shown). However, CO_2 enrichment altered this pattern of reserve carbohydrate depletion. In ENR 'Misty' plants, cane and root starch

concentrations decreased as FBD increased only at bloom. In ENR 'Sharpblue' plants, carbohydrate concentrations were similar across the range of FBDs.

Plant Development

AMB and ENR cane and root dry weights were similar within cultivars (Table 5-1) and were not affected by FBD. However, root and cane dry weights changed during development. Root dry weight decreased between dormancy and bloom for both cultivars, then remained constant between bloom and fruit harvest. Cane dry weight decreased between dormancy and 28 DAB in both cultivars. Cane dry weight increased in AMB and ENR 'Sharpblue' plants at fruit harvest but not in 'Misty'.

In 'Sharpblue', the number of vegetative buds that broke dormancy and grew per cm cane length was greater in ENR plants than in AMB plants (Table 5-1 and Fig. 5-3). However, in 'Misty', vegetative budbreak was similar in AMB and ENR plants. Vegetative budbreak decreased as FBD increased in both AMB and ENR plants of both cultivars (Fig 5-3).

Leaf area and leaf area:fruit ratios were greater in ENR than in AMB plants (Fig. 5-4 and 5-5). Leaf dry weight and new stem dry weight were also greater in ENR compared to AMB plants but since leaf area, leaf dry weight, and stem dry weight were always highly correlated ($r > 0.97$), only leaf area is presented. Leaf area and leaf area:fruit ratios decreased as FBD increased in AMB and ENR plants of both cultivars.

Whole-canopy NCER at fruit ripening was greater in ENR compared to AMB plants (Fig. 5-6). Whole-canopy NCER also decreased as FBD increased. Whole-canopy NCER:fruit ratios followed a pattern similar to whole-canopy NCER (data not shown).

Reproductive Development

The timing of bloom was similar between plants from the AMB and ENR CO_2 treatments and was not affected by FBD in 'Sharpblue'. However, bloom was delayed up to 5 days as FBD increased in 'Misty' (data not shown). Fruit density (fruit·cm^{-1} cane length) was similar between AMB and ENR plants. Fruit density increased as FBD increased in 'Misty' and 'Sharpblue', with fruit density slightly higher in 'Sharpblue' ($y = 2.95 + 0.88 \ln FBD$) than in 'Misty' ($y = 2.84 + 0.88 \ln FBD$).

Average fruit fresh weights were higher in ENR plants compared to AMB plants in 'Sharpblue', but fruit fresh weights were similar between ENR and AMB plants in 'Misty' (Table 5-1). Fruit fresh weights increased as leaf area:fruit or whole-canopy NCER:fruit ratios increased (Fig. 5-7 and 5-8). The FDP was similar between AMB and ENR plants in both 'Misty' and 'Sharpblue' (Table 5-1) and the FDP decreased as leaf area:fruit ratio and whole-canopy NCER:fruit ratio increased (data not shown).

Discussion

The decrease in root dry weight between dormancy and bloom (0 DAB) probably reflects carbohydrate mobilization for respiration and fruit growth, as the decrease in total root carbohydrate content accounted for about 50% of the decrease in root dry weight. Similar decreases in root dry weight at budbreak have been observed in apple (*Malus domestica* Borkh.) (Kandiah, 1979) and rabbiteye blueberry (Birkhold and Darnell, 1993). In rabbiteye blueberry, the decline in root carbohydrate content between dormancy and anthesis accounts for >70% of the root dry weight decline (Darnell and Birkhold, 1996). Root starch concentrations in 'Sharpblue' decreased 63-78% between dormancy and 0 DAB while root sugar concentrations increased 23% indicating a strong mobilization of starch reserves into a more readily available form in the roots of 'Sharpblue' prior to vegetative budbreak. In 'Misty', root starch concentrations decreased only 35% between dormancy and 0 DAB, and root sugar concentrations exhibited a 26% decrease, suggesting an inability to rapidly access starch in the roots. The decrease in cane dry weight between dormancy and 28 DAB probably also indicates carbohydrate reserve usage during the period of early fruit and vegetative development. Although cane carbohydrate concentrations increased in both cultivars between 28 DAB and fruit harvest, indicating that replenishment of carbohydrate reserves was beginning, root carbohydrate concentrations increased only in 'Sharpblue'

before fruit harvest. Root carbohydrate concentrations continued to decrease in 'Misty', suggesting that carbohydrate production and availability were lower in 'Misty' and replenishment of carbohydrate reserves in the cane was taking precedence over root carbohydrate demands.

Starch was the major form of carbohydrate reserves in both cultivars during dormancy, as reported in rabbiteye blueberry (*V. ashei* Reade) (Darnell and Birkhold, 1996) and many other deciduous fruit species (Loescher et al., 1990). Root carbohydrate concentrations exceeded cane carbohydrate concentrations in both cultivars, which is similar to rabbiteye blueberry (Darnell and Birkhold, 1996), but contrary to that reported in cranberry (*Vaccinium macrocarpon* Ait.) (Hagidimitriou and Roper, 1994). However, in 'Misty', total cane carbohydrate content was greater than the total root carbohydrate content due to the high cane:root dry weight ratio.

'Sharpblue' plants were able to use the higher concentrations of carbohydrate reserves in ENR plants at dormancy to increase vegetative budbreak and overcome some of the competition from flower and fruit development, but 'Misty' plants were not able to take equal advantage of their increased carbohydrate reserves under ENR conditions to increase vegetative budbreak. The decrease in root starch between dormancy and 0 DAB in 'Misty' was much less than the decrease observed in 'Sharpblue'. This suggests that starch degradation and/or reserve remobilization is reduced, possibly by reduction in the activities of enzymes involved in these

processes (Goldschmidt and Golomb, 1982; Volenec et al., 1991). For example, the specific activity of endoamylase is highly correlated with periods of increased starch utilization in alfalfa (*Medicago sativa* L.) taproots (Volenec et al., 1991) suggesting their importance in starch degradation. Similar increases in endoamylase activity is exhibited during rapid starch degradation in *Verbascum thapsus* roots (Glier and Caruso, 1974). Additionally, the regulation of starch degradation in some crops may depend on location. In mandarin (*Citrus reticulata* Blanco), Goldschmidt and Golomb (1982) found that there was little change in the starch content in the trunk of bearing vs non-bearing trees. However, starch content in the roots of bearing trees was much less than that of nonbearing trees, indicating differences in availability of reserves for remobilization. Cane starch was the primary carbohydrate reserve form in 'Misty', which may be less easily mobilized than root starch.

The increased shoot growth and leaf area in SHB plants containing higher carbohydrate reserves compared to plants with lower reserves is parallel to findings in other fruit species. In sweet cherry (*Prunus avium* L.), trees defoliated early in the fall had reduced reserve carbohydrate concentrations and smaller leaves and less overall growth the following spring compared to control trees allowed to defoliate naturally (Loescher et al., 1990). Similarly, in apple, new shoot length was greater following a nonbearing year which had allowed carbohydrate levels to build up than

following a bearing year which had depleted carbohydrate levels (Wilcox, 1937). Thus, in certain fruit crops, practices that can elevate carbohydrate reserve levels may enhance canopy development the following year.

Since carbohydrate concentrations were not affected by FBD in ENR 'Sharpblue' plants and vegetative budbreak was greater in ENR compared to AMB 'Sharpblue' plants, this would support the hypothesis that increased carbohydrate reserve levels can help compensate for the competition from early flower and fruit development in some SHB cultivars. However, increased carbohydrate reserves were unable to completely overcome the effects of competition between reproductive and vegetative development since vegetative budbreak and leaf area decreased as FBD increased.

Greater whole-canopy NCER in ENR compared to AMB plants indicates that increased carbohydrate reserve concentrations through their effect on vegetative budbreak and leaf development can increase carbohydrate production. The increases in whole-canopy NCER and carbohydrate production in ENR plants compared to AMB plants were reflected in fruit fresh weights in 'Sharpblue' but not in 'Misty'. Thus, increased carbohydrate reserve concentrations can indirectly contribute to increased fruit fresh weight, although the effect is cultivar-specific.

In conclusion, AMB and ENR CO_2 treatments resulted in differences in root starch and whole plant carbohydrate concentrations in 'Misty' and 'Sharpblue' SHB. Vegetative budbreak was higher in ENR plants compared

to AMB plants in 'Sharpblue' but not in 'Misty'. However, leaf area development and whole-canopy NCER were higher in ENR plants than in AMB plants in both cultivars, although only in 'Sharpblue' was fruit fresh weight greater in ENR plants compared to AMB plants. 'Sharpblue' plants were able to use the extra carbohydrate reserves to increase vegetative development, which in turn increased reproductive development. However, 'Misty' plants were not able to respond similarly. It appears that although carbohydrate reserve levels play a role in vegetative budbreak and development in species where floral budbreak precedes vegetative budbreak, an additional component or components are needed in order to increase the response in some plants.

Table 5-1. Reproductive and vegetative development of 'Misty' and 'Sharpblue' SHB as affected by CO_2 treatment or date.

	'Misty'		'Sharpblue'	
	AMB	ENR	AMB	ENR
Root dry weight (g)				
Dormancy	23.5[z]a[y]A[x]	26.9 aA	52.0 aA	57.3 aA
0 DAB	20.3 aB	26.1 aB	44.2 aB	46.9 aB
28 DAB	19.3 aB	20.3 aB	45.2 aB	42.9 aB
Fruit harvest	16.6 aB	19.6 aB	45.2 aB	48.9 aB
Cane dry weight (g)				
Dormancy	50.7 aA	51.6 aA	71.0 aA	76.7 aA
0 DAB	45.3 aA	54.6 aA	63.8 aAB	67.9 aAB
28 DAB	42.1 aB	45.0 bB	65.9 aB	59.5 bB
Fruit harvest	41.2 aB	45.6 aB	73.7 aA	72.2 aA
Vegetative budbreak density (#·cm^{-1} cane)				
0 DAB	0.019 a	0.025 a	0.041 b	0.067 a
14 DAB	0.022 a	0.030 a	0.069 b	0.088 a
28 DAB	0.024 a	0.031 a	0.081 b	0.104 a
Fruit FW (g)	1.13 a	1.03 a	0.90 b	1.02 a
FDP (days)	86.5 a	89.3 a	81.5 a	78.6 a

[z]Values are means adjusted using flower bud density as a covariate within each cultivar.
[y]Lower case letters indicate mean separation between AMB and ENR plants within cultivar and whole plant harvest date by LSD at P=0.05.
[x]Upper case letters indicate mean separation between whole plant harvest dates within columns and plant parts by LSD at P=0.05

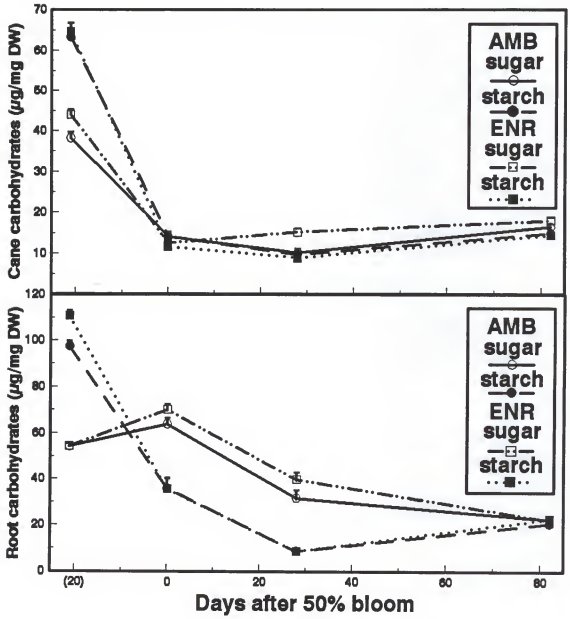

Figure 5-1. Cane sugar and starch concentrations of 'Sharpblue' SHB between dormancy [-21 d after 50% bloom (DAB)] and fruit harvest (82 DAB) (means ±SE, SE bars present only when larger than symbol).

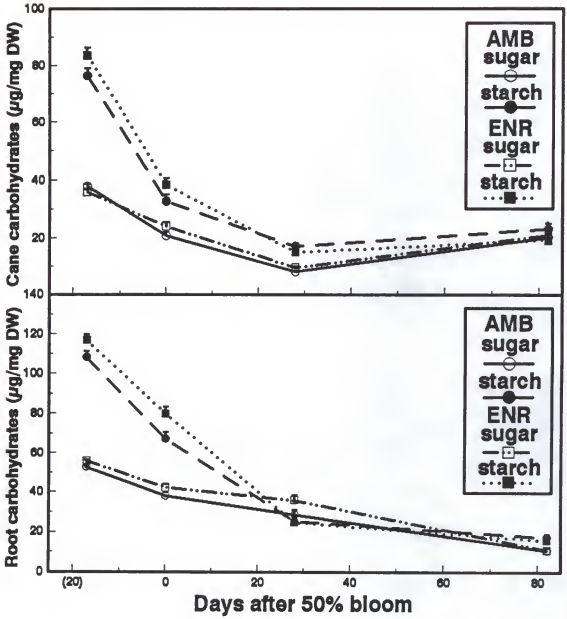

Figure 5-2. Cane sugar and starch concentrations of 'Misty' SHB between dormancy [-17 d after 50% bloom (DAB)] and fruit harvest (82 DAB) (means ±SE, SE bars present only when larger than symbol).

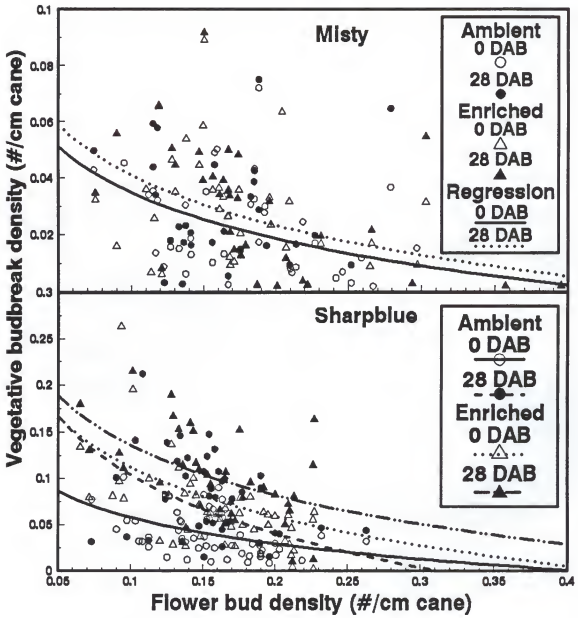

Figure 5-3. Relationship between vegetative budbreak and flower bud density and CO_2 treatment in 'Misty' and 'Sharpblue' SHB: 'Misty': AMB and ENR (0 DAB $y = -0.019 - 0.023 \ln x$, $r^2 = 0.17$, $P < 0.01$; 28 DAB $y = -0.018 - 0.026 \ln x$, $r^2 = 0.14$, $P < 0.01$); 'Sharpblue': AMB (0 DAB $y = -0.037 - 0.041 \ln x$, $r^2 = 0.18$, $P < 0.01$; 28 DAB $y = -0.018 - 0.077 \ln x$, $r^2 = 0.26$, $P < 0.001$); ENR (0 DAB $y = -0.106 - 0.091 \ln x$, $r^2 = 0.36$, $P < 0.001$; 28 DAB $y = -0.042 - 0.077 \ln x$, $r^2 = 0.26$, $P < 0.001$).

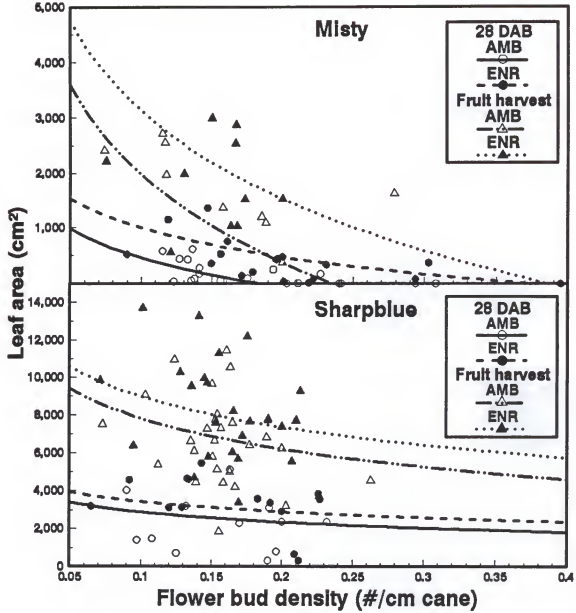

Figure 5-4. Relationship between leaf area and flower bud density and CO_2 treatment in 'Misty' and 'Sharpblue' SHB: 'Misty' 28 DAB (AMB y=-1299-765lnx, ENR y=-1144-765lnx); fruit harvest (AMB y=-3373-2328lnx, ENR y=-2217-2328lnx), overall $r^2=0.66$; 'Sharpblue' 28 DAB (AMB y=-756-765lnx, ENR y=1687-765lnx); fruit harvest (AMB y=2481-2328lnx, ENR y=3636-2328lnx), overall $r^2=0.61$.

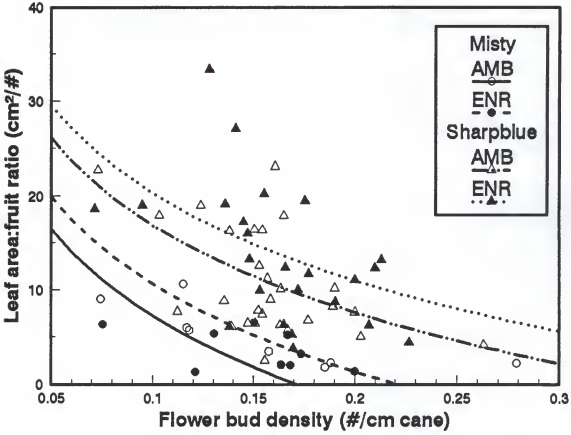

Figure 5-5. Relationship between leaf area:fruit ratio and flower bud density and CO_2 treatment in 'Misty' and 'Sharpblue' SHB: 'Misty' (AMB y=-23.6-13.4lnx, ENR y=-20.2-13.4lnx); 'Sharpblue' (AMB y=-14.0-13.4lnx, ENR y=-10.6-13.4lnx); overall r^2=0.42.

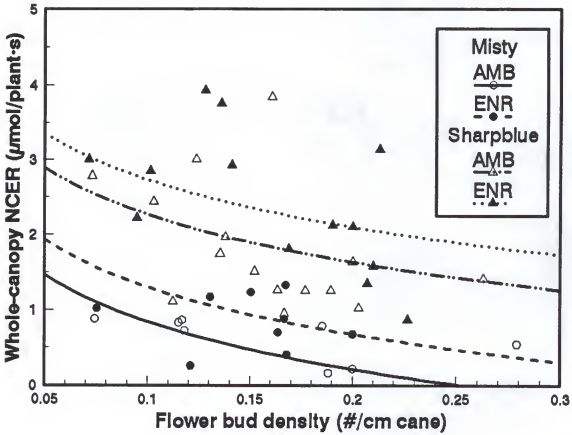

Figure 5-6. Relationship between whole-canopy NCER at fruit ripening and flower bud density and CO_2 treatment in 'Misty' and 'Sharpblue' SHB: 'Misty' (AMB y=-1.25-0.91lnx, ENR y=-0.79-0.91lnx); 'Sharpblue' (AMB y=0.17-0.91lnx, ENR y=0.63-0.91lnx); overall r^2=0.56.

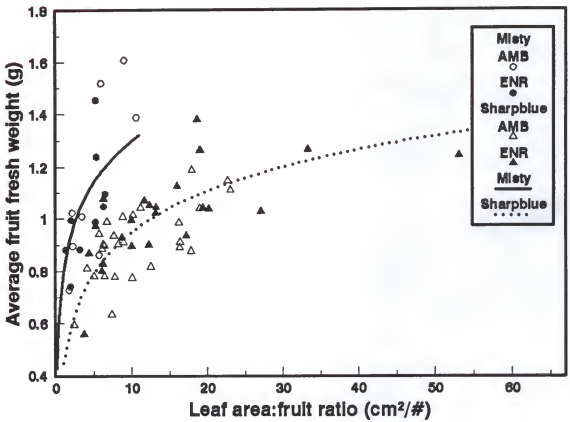

Figure 5-7. Relationship between fruit fresh weight and leaf area:fruit ratio and CO_2 treatment in 'Misty' and 'Sharpblue' SHB: 'Misty': AMB and ENR ($y = 0.77 + 0.23\ln x$); 'Sharpblue': AMB and ENR ($y = 0.42 + 0.23\ln x$); overall $r^2 = 0.54$.

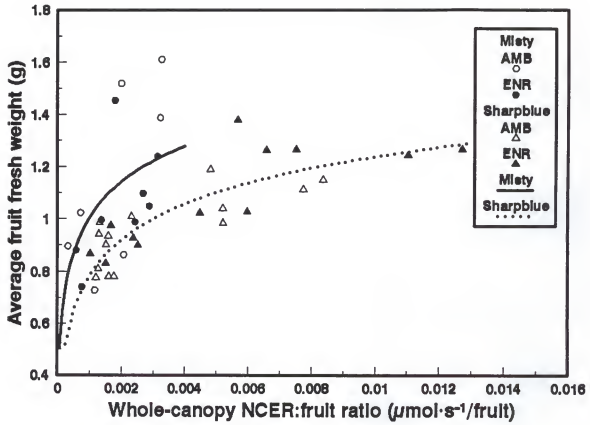

Figure 5-8. Relationship between fruit fresh weight and whole-canopy NCER:fruit ratio and CO_2 treatment in 'Misty' and 'Sharpblue' SHB: 'Misty': AMB and ENR ($y = 2.37 + 0.20\ln x$); 'Sharpblue': AMB and ENR ($y = 2.15 + 0.20\ln x$); overall $r^2 = 0.50$.

CHAPTER 6
SUMMARY AND CONCLUSIONS

Plants contain many meristems that compete for resources such as carbohydrates, nutrients, and water. Carbohydrate competition between reproductive and vegetative growth occurs when the demands from these sinks exceed the supply from carbohydrate sources, either stored reserves or current photosynthesis. Sink demands come from the need for carbohydrates for C-skeletons for new growth and from respiration for growth, maintenance, or ion uptake. A sink's strength is determined by its capacity (number of cells and cell size) and activity (ability to unload and use carbohydrate from the transport stream) (Hansen, 1989).

In southern highbush blueberry (SHB) (*Vaccinium corymbosum* L.), floral budbreak and fruit set in the spring begin prior to vegetative budbreak and canopy development. Thus, early reproductive and vegetative development must rely on carbohydrate reserves until the canopy is sufficiently established to supply carbohydrates from current photosynthesis. However, since both reproductive and new vegetative growth occur simultaneously, carbohydrate reserves may be insufficient to meet the demands of both reproductive and vegetative sinks, creating

competition and a reduction in growth of one or both types of sinks, unless the carbohydrate supply can be increased. In support of this, field observations indicate that heavy flower and fruit load may delay and reduce vegetative budbreak and development in some SHB.

This research was undertaken to examine the manner and extent of the competition between the reproductive and vegetative sinks in 'Misty' and 'Sharpblue' SHB and the role carbohydrate reserves might play.

Reserves are an important source of carbohydrates during early fruit and new shoot development (Birkhold *et al.*, 1992; Darnell and Birkhold, 1996). Plants placed in a greenhouse with enriched (ENR) levels of CO_2 ($\approx$700 μmol·mol^{-1}) for 38 days had elevated root starch and whole plant carbohydrate concentrations at the end of dormancy compared to plants placed in a greenhouse with ambient (AMB) levels of CO_2 ($\approx$360 μmol·mol^{-1}). The numbers of vegetative buds that broke dormancy and grew were higher in ENR plants compared to AMB plants in 'Sharpblue' SHB. ENR plants had increased canopy development and whole-canopy NCER compared to AMB plants in both 'Misty' and 'Sharpblue' SHB. However, only in 'Sharpblue' was fruit fresh weight increased in ENR plants compared to AMB plants. Thus, increased carbohydrate reserve concentrations increased vegetative budbreak and canopy development in SHB, but the effect on subsequent reproductive development was cultivar-specific.

Vegetative budbreak, new shoot development, and leaf area:fruit ratio decreased as flower bud density (FBD) (flower buds·cm^{-1} cane length) increased, indicating the strong competition from the reproductive sinks on vegetative sinks. This was further supported by the finding that the roots only increased in dry weight during the fruit development period in the one year (1995) when fruit set was low. In 1996, reproductive growth was the major sink for biomass accumulation during all stages of fruit development in 'Misty' and during the early and late stages of reproductive development in 'Sharpblue'.

Fruit fresh weight increased and the fruit development period was shortened as leaf area:fruit ratios increased. Leaf net CO_2 exchange rates (NCER) increased as FBD increased and leaf area:fruit ratios decreased in 'Sharpblue' indicating that at least in some SHB, sink demand can increase source supply. However, whole-canopy NCER in both cultivars decreased as FBD increased suggesting that the reproductive sinks' overall effect on the development of the source of current photosynthesis (leaf area) was greater than the reproductive sinks' effect on the leaves' photosynthetic rate. Fruit fresh weight increased and the fruit development period was shortened as whole-canopy NCER:fruit ratios increased, indicating the importance of establishing the photosynthetic canopy.

Reproductive sinks compete strongly with vegetative sinks for carbohydrates during the flowering and fruiting period in SHB and reduction

in the number of reproductive sinks or increasing carbohydrate reserve levels can increase vegetative shoot and canopy development resulting in the production of larger and faster maturing fruit.

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Brian Eugene Maust was born September 20, 1953, in Goshen, Indiana. In August 1980, he received a Bachelor of Science degree from Eastern Mennonite College in Harrisonburg, Virginia. He graduated summa cum laude with a major in biology: agriculture development. He worked as a volunteer for the Mennonite Central Committee in Bolivia from 1982 to 1989, first as an agriculture extension agent with subsistence farmers and then as manager of an appropriate technology training center in Santa Cruz. In August 1989, he entered the University of Florida and graduated with a Master of Science degree in Horticultural Sciences in 1992. In 1993, he began work on a Ph.D. degree, working with southern highbush blueberry. He worked as a graduate assistant during this time to help support his family. He is married and has two daughters and one son. He plans to work at the Centro de Investigacion Cientifica de Yucatan in Merida, Mexico, upon graduation.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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