HortScience 35(1):55–59. 2000.

Seasonal Patterns of Photosynthesis and Stomatal Conductance in Lowbush Blueberry Plants Managed in a Two-year Production Cycle

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Additional index words. CO_2 assimilation, light response, leaf water potential, soil moisture, fruiting, pruning, *Vaccinium angustifolium*

Abstract. **Seasonal patterns of CO_2 assimilation (A_{CO2}), leaf water potential (ψ_l) and stomatal conductance (g_l) were studied in three clones ('Augusta', 'Brunswick', and 'Chignecto') of lowbush blueberry (*Vaccinium angustifolium* Ait.) over two growing seasons. Plants were managed in a 2-year cycle of fruiting (year 1) and burn-prune (year 2). In the fruiting year, A_{CO2} was lowest in mid-June and early September. Rates peaked between 10 and 31 July and declined after fruit removal in late August. Compared with the fruiting year, A_{CO2} in the prune year was between 50% and 130% higher in the early season, and between 80% and 300% higher in mid-September. In both years, however, mid-season maximum A_{CO2} for each clone was between 9 and 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2. Assimilation of CO_2 increased with increasing photosynthetic photon flux *(PPF)* to between 500 and 600 $\mu mol \cdot s^{-1} \cdot m^{-2}$ in 'Augusta' and 'Brunswick', and to between 700 and 800 $\mu mol \cdot s^{-1} \cdot m^{-2}$ in 'Chignecto'. Midday ψ_l was generally lower in the prune year than in the fruiting year, reflecting year-to-year differences in soil water content. Stomatal conductance (g_l), however, was generally higher in the prune year than in the fruiting year over similar vapor pressure deficit (VPD) ranges, especially in June and September when prune year g_l was often twice that observed in the fruiting year. In the fruiting year, g_l declined through the day in response to increasing VPD in June, but was quite constant in mid-season. It tended to be higher in 'Augusta' than in the other two clones. Stomatal closure imposes limitations on A_{CO2} in lowbush blueberries, but not all seasonal change in C-assimilative capacity can be explained by changes in g_l.**

The wild lowbush blueberry is farmed on >26,000 ha in Maine and the Canadian Maritime Provinces. Total berry production in 1997 exceeded 137 million pounds with a crop value of about U.S. $45 million. The crop is typically managed in a biennial production system in which plants are mowed or burned in alternate years to force regrowth of fruiting shoots (Ismail and Hanson, 1982). Plants grow vegetatively for 1 year following pruning. Flower buds are formed toward the end of the year; flowering and pollination occur during the following spring, and the crop is harvested in July and August.

Despite the importance of the crop, very little is known of its ecophysiology. This has hampered both our understanding of the environmental limitations to productivity and attempts to improve production through changes in crop management. The effect of environment on CO_2 assimilation has been extensively studied in many small fruit crops (Fernandez and Pritts, 1994; Moon et al., 1987; Percival et al., 1996) but has received very little attention in lowbush blueberry. Study of environmental physiology in lowbush blueberry is complicated by the genetic heterogeneity among plants. Commercial blueberry fields, generally developed on abandoned pasture or cleared woodland, consist of a mixed, wild population of seedlings. Seedlings spread vegetatively by rhizomes (Trevett, 1956) to create large clumps that can be identified in the field as individual clones (Kender and Eggert, 1966). The clones may differ considerably in form (Vander Kloet, 1978), fruiting potential (Sanderson and Cutcliffe, 1991) and physiology (Forsyth and Hall, 1965), but there has thus far been no attempt to identify baseline information on physiological responses of lowbush blueberries under field conditions.

The present study was conducted using three lowbush blueberry clones to investigate: 1) the light saturation ranges for photosynthesis in the field; and 2) the seasonal variation in net CO_2 assimilation and stomatal conductance over the course of two growing seasons ("fruiting" year and "prune" year), with an overall aim of improving our knowledge of fundamental factors governing assimilative capacity.

Materials and Methods

Plant material and location. Three 15-year old clones of lowbush blueberry growing at the Agriculture and Agri-Food Canada Experimental Farm, Sheffield Mills, N.S. (45°N, 64.5°W) were chosen for study. 'Augusta' and 'Chignecto' are characterized by a branched, low-mounding, growth form and small leaves, ≈3.3 cm long × 1.7 cm wide (Aalders et al., 1975; Hall et al., 1977); 'Brunswick' has a more vertical growth habit and larger leaves, 4.3 cm × 1.7 cm (Aalders et al., 1977). The clones were growing in a well-drained loamy-sand soil of the Cornwallis series (Cann et al., 1954) and had been managed in a biennial system with burn-pruning for 14 years before the study began. Experiments were conducted over a 2-year (1996 and 1997) period and began with plants in the fruiting year.

Environmental measurements. Air temperature and relative humidity (RH) were measured continuously through each season using a model CS500 combined temperature/Vaisala RH sensor (Campbell Scientific, Logan, Utah) in association with a model CR10 datalogger. The sensors were scanned every minute and readings were averaged each hour. Growing degree-days (GDD; 10 °C base) and VPD were calculated from the measurements. Volumetric soil water content was monitored using the time domain reflectometry (TDR) technique (Topp et al., 1980). Measurements were made each hour using 30-cm TDR sensors (Campbell Scientific Model CS615-L) inserted at an angle under blueberry plants to provide average volumetric soil water content for the top 15 cm of the soil profile. Equipment failure resulted in loss of soil water content data between 24 June and 18 July 1996.

Photosynthesis, stomatal conductance, and leaf water potential measurements. Photosynthesis was measured on nine dates between 12 June and 19 Sept. 1996 and on eight dates between 19 June and 15 Sept. 1997. Earlier measurements in 1997 were not possible due to the slower leaf expansion in prune-year plants. Field measurements of CO_2 uptake were estimated using an open-flow gas-exchange system consisting of a portable infrared gas analyzer (LCA-2; ADC Ltd., Hoddesdon, U.K.) and a temperature-controlled leaf chamber (PLC 2A). Measurements of chamber flow rate, CO_2 exchange, leaf and

Received for publication 25 Jan. 1999. Accepted for publication 16 June 1999. Research supported in part by grants from the Nova Scotia Wild Blueberry Institute and the Matching Investment Initiative Program of Agriculture and Agri-Food Canada. Contribution no. 2196, Atlantic Food and Horticulture Research Centre. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

air temperature, and chamber RH were recorded and used to calculate net photosynthesis (von Caemmerer and Farquhar, 1981). All measurements were conducted between 1000 and 1500 HR on leaves which had reached >80% full lamina expansion. Chamber air temperature was maintained between 24 and 28 °C and, except for the light response determinations, photosynthetic photon flux *(PPF)* incident on the chamber was always between 900 and 2000 $\mu mol \cdot s^{-1} \cdot m^{-2}$. The ambient atmospheric CO_2 concentration was between 340 and 350 $\mu L \cdot L^{-1}$. Light response curves were constructed from data obtained by placing neutral density filters directly over the chamber to progressively reduce the *PPF*. These data were collected on several dates between 10 and 31 July on fruiting-year plants only.

Stomatal conductance (g_l) was measured with a LI-1600 steady state porometer (LI-COR Inc., Lincoln, Nebr.) according to standard protocols (McDermitt, 1990). Measurements were made in full sun between 0800 and 1700 HR on the abaxial surface of leaves adjacent to those used for measuring photosynthesis.

Leaf water potential (ψ_l) was measured using a pressure chamber (PMS Instrument Co. Ltd., Corvallis, Ore.) at the same time as g_l. Leaves with a short length of attached stem tissue were removed from the upper canopy, placed immediately in a plastic bag, and inserted into the pressure chamber with the stem tip protruding through a rubber stopper. The chamber was pressurized with nitrogen at a rate not exceeding 0.03 $MPa \cdot s^{-1}$ and the endpoint (when sap just returns to the cut surface of the xylem) was recorded.

Experimental design and data analysis. Measurements were conducted on five plants of each clone arranged in a randomized complete block. Three leaves were measured on each plant on each date to determine the seasonal pattern of CO_2 assimilation. Seasonal response curves were fitted by least squares polynomial regression. Light response curves were constructed from measurements on a minimum of seven leaves per plant. Curves were fitted by nonlinear regression using an asymptotic function:

$$Y = B(1) * [1 - B(2)] * e^{[-B(3) * X]}$$

and the Marquardt compromise method of successive approximations. The g_l was measured on one tagged leaf from each replicate plant throughout each measurement day. A new leaf was selected whenever a leaf was damaged or showed signs of cuvette-induced stomatal closure, and at the start of each day.

The ψ_l was measured on successive single samples from each replicate plant. Analysis of ψ_l data revealed no significant differences between clones at any single measurement time, so these data were pooled for presentation.

Results and Discussion

Light saturation of A_{CO2} occurred between 500 and 600 $\mu mol \cdot s^{-1} \cdot m^{-2}$ for 'Augusta' and 'Brunswick' clones (Fig. 1 a and b). For 'Chignecto' (Fig. 1c) the range was higher (between 700 and 800 $\mu mol \cdot s^{-1} \cdot m^{-2}$) although the A_{CO2}/*PPF* curve failed to reach a clear asymptote. Light saturation was between three and four times as high as previously inferred from laboratory studies (Forsyth and Hall, 1965). Both 'Augusta' and 'Brunswick' showed lower light saturation than highbush (*V. corymbosum* L.) (Moon et al., 1987), and rabbiteye (*V. ashei* Reade) blueberry (Teramura et al., 1979). The response of 'Chignecto', however, was similar to that of those other species. *Vaccinium angustifolium* has been classified as a shade-tolerant plant and is frequently found in heavily shaded, forest floor habitats (Hall, 1955). However, much higher light intensities are required to realize maximum growth and fruiting potential (Hall, 1958, Hall and Ludwig, 1961) and it is clear from the present data that, even under full-sun conditions, whole-plant A_{CO2} is unlikely to be saturated, given the often dense and interleaved branch structure.

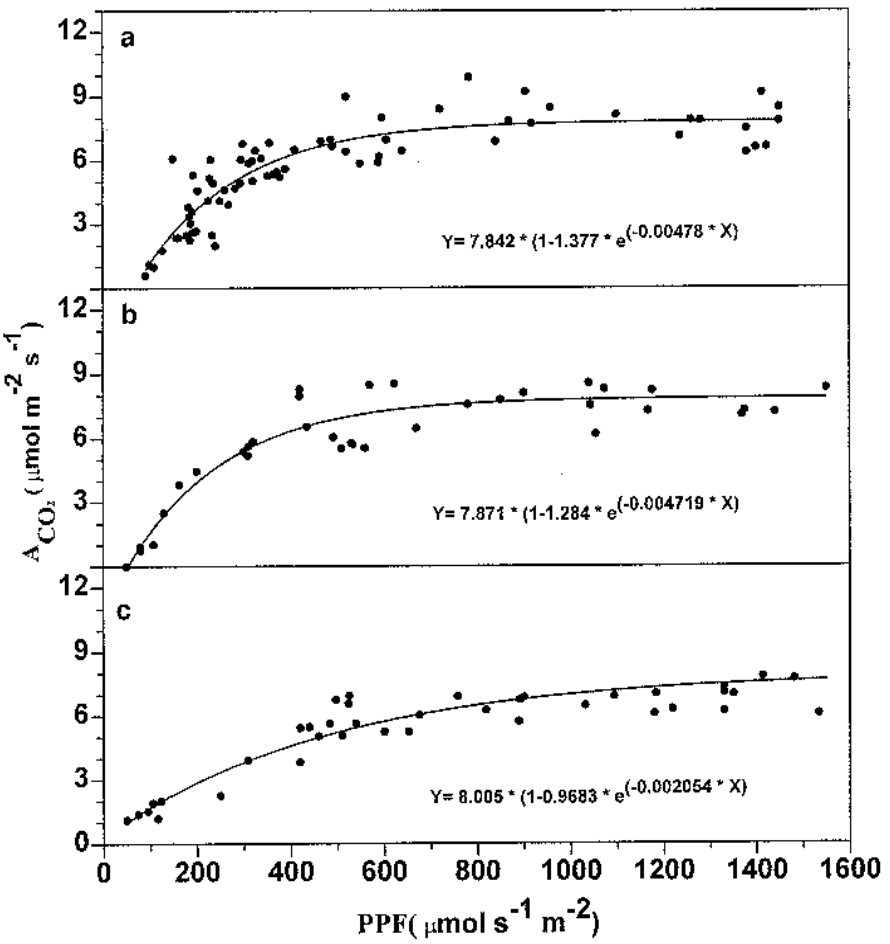

Fig. 1. The response of (**a**) 'Augusta', (**b**) 'Brunswick', and (**c**) 'Chignecto' lowbush blueberry to photosynthetic photon flux (*PPF*). Measurements were made at 24 to 28 °C. Points are derived from measurement on at least seven leaves of five individual plants.

For both fruiting and prune years, leaf A_{CO2} varied through the season (Fig. 2). Maximum rates for all clones were similar in both years, averaging between 9 and 10 $\mu mol \cdot m^{-2} \cdot s^{-1} CO_2$, ≈20% lower than those reported for cultivars of the highbush blueberry (Moon et al., 1987) but 40% higher than those for rabbiteye blueberry (Teramura et al., 1979). Early season A_{CO2} (on 19 June) was lower in the fruiting year than in the prune year despite a 15% greater GDD accumulation to that date. Epicormic shoots arise vigorously from latent buds in below-ground crowns and rhizomes following pruning, and our data suggest that the early photosynthetic potential is greater in these shoots than in those that have overwintered above ground. Similar effects have been described in new shoots formed following grazing in grasses where A_{CO2} may be as much as 39% higher than in nongrazed plants (Dyer et al., 1991). The higher rates may be due to enhanced sink strength in the new shoots, since apical meristems are stronger sinks than existing shoot tissues and adventitious buds of some species (Chapman et al., 1991), although developing flower buds in fruiting-year plants are probably also strong sinks. A_{CO2} peaked in the fruiting year between 10 July and 31 July 1996 but there were some differences among clones (Fig. 2). 'Brunswick' showed highest rates on 31 July, when both 'Augusta' and 'Chignecto' had declined from their 10 July peak. In the prune year there was a closer similarity among the clones. Peak A_{CO2} occurred over a broader time period (from mid-July until mid-August), and higher GDD range,

compared with the fruiting year. There were no differences in the maximum A_{CO2} among clones in either year. By 4 Sept. in the fruiting year, rates had declined to levels equivalent to those in early June, except in 'Augusta' in which higher rates were sustained through 18 Sept. The late season decline occurred after the fruit was removed from the plants in late August and resembled similar seasonal patterns following fruit removal in cherry (*Prunus avium* L.) (Gucci et al., 1991a), plum (*Prunus domestica* L.) (Gucci et al., 1991b), and peach (*Prunus persica* L.) (Mandre et al., 1995). In prune year plants there was no equivalent decline, and by mid-September, shortly before leaf senescence, A_{CO2} remained ≈65% of that in early August. The strong late season assimilative capacity in prune-year plants may reflect the sink strength of developing fruit and vegetative buds, roots, and rhizomes, which continue growth late into the fall (Kender and Abdalla, 1966). Similar sinks are present in fruiting-year plants, but fruit harvest represents the loss of a major sink, which may lead to a reduction in A_{CO2}. Still, some reduction in A_{CO2} occurred in fruiting-year plants before fruit harvest, suggesting that factors other than fruit sink strength may also play a role in late season decline in A_{CO2}. From a practical standpoint, the low assimilative capacity in September suggests that growers can prune plants after harvest with relatively little loss of potential C gain.

Throughout much of the season, volumetric soil moisture content was lower in the prune year as compared with the fruiting year, reflecting the much lower June to September precipitation in 1997 (Fig. 3). Excluding September, the study site received just 132 mm of rain in 1997, but 232 mm in the 1996 fruiting year, compared with a 35-year average of 237 mm. The lower soil moisture levels were reflected in reduced daytime ψ_l from late June until early September in prune-year plants (Fig. 4). For similar dates, in July and August, midday ψ_l was between 20% and 60% lower in plants sampled in the prune year as compared with the fruiting year. Only for plants sampled in mid-June and mid-September were ψ_l values similar throughout much of the day.

Diurnal g_l patterns changed through the season in both prune-year and fruiting-year plants. In the fruiting year, early season (19 and 26 June) g_l in each clone declined over the day (Fig. 5). On 19 June the decline mirrored the increase in VPD from 0.2 KPa at 0800 HR to 2.0 KPa at 1700 HR, but on 26 June the decline occurred despite a relatively low and constant VPD. In highbush blueberries, declines in g_l of between 0.1 and 0.2 $mol \cdot m^{-2} \cdot s^{-1}$ were associated with a decline in A_{CO2} of ≈20% (Moon et al., 1987). Similar declines in g_l observed on 19 and 26 June in the present study may have contributed to the rather low values for A_{CO2} recorded on these dates in each clone. On mid-season sampling dates (10 and 31 July), g_l was quite constant despite daytime increases in VPD of 0.6 and 1.3 KPa, respectively. On 4 Sept., early morning g_l in each clone had declined by between 11% ('Augusta') and 39% ('Chignecto' and 'Brunswick')

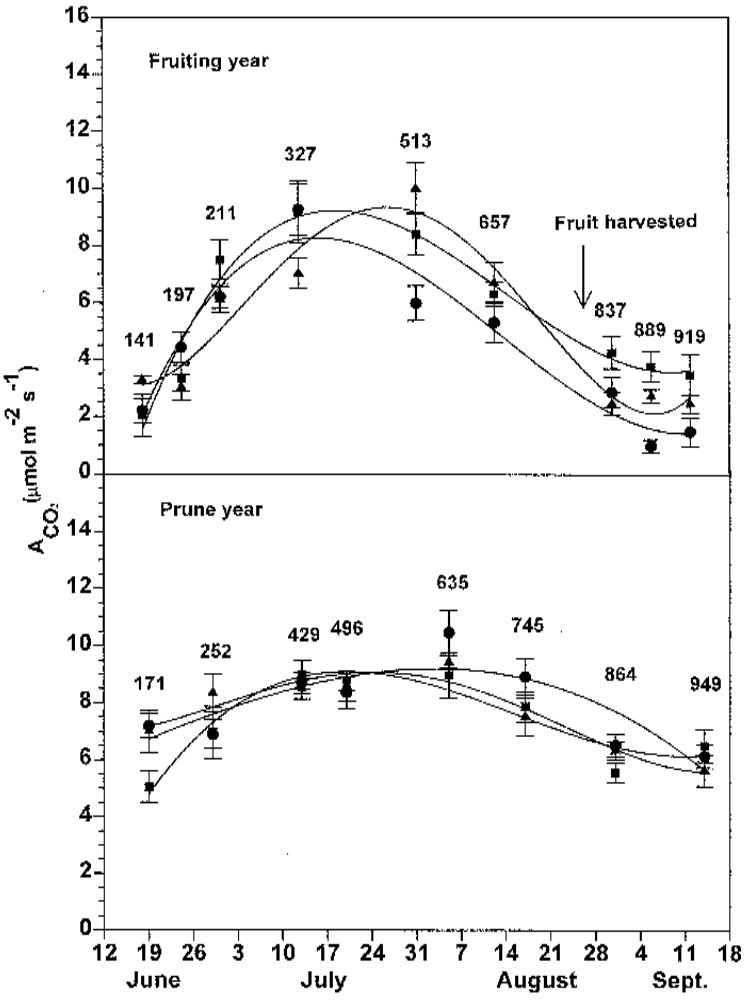

Fig. 2. Seasonal response of net CO_2 assimilation in (■) 'Augusta', (▲) 'Brunswick', and (●) 'Chignecto' lowbush blueberry for the fruiting year (1996) and in the prune year (1997). Numbers above each set of points indicate accumulated degree-days (10 °C base). Each point is the mean of three determination on each of five replicate plants. Bars indicate ±1 SEM.

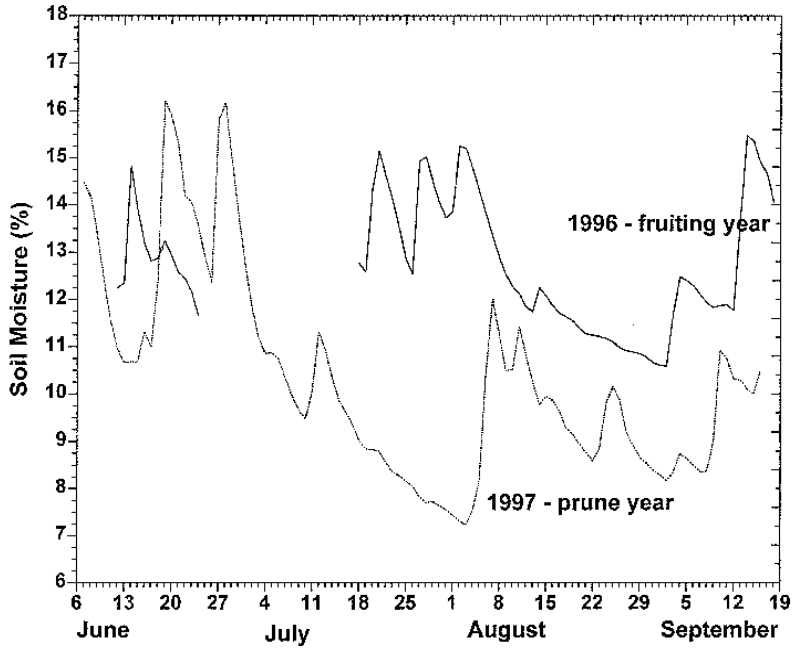

Fig. 3. Average daily volumetric soil moisture content for the top 15 cm of the soil profile under blueberry plants for the fruiting (1996) and prune (1997) years. Data not available between 24 June and 18 July 1996.

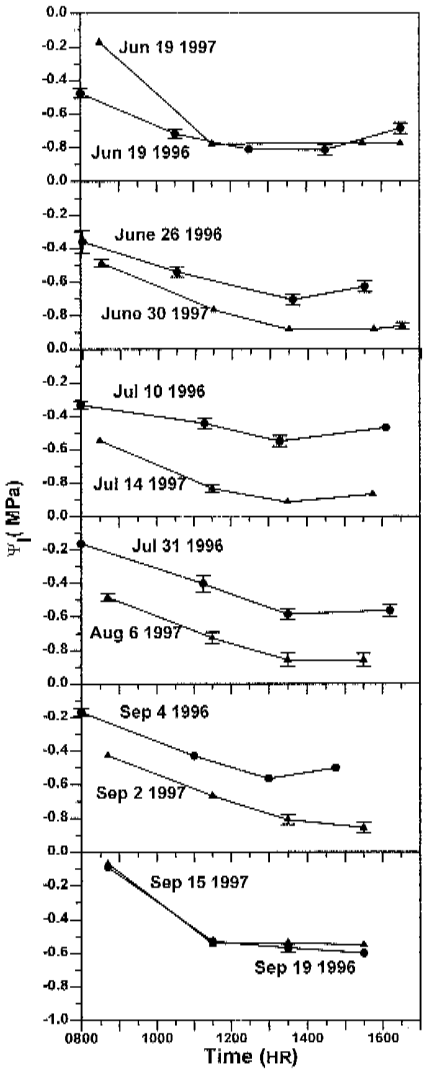

Fig. 4. Diurnal variation in leaf water potential (2_1) of lowbush blueberry in the fruiting (1996) and prune (1997) years. Each point is the mean of 15 measurements (five each for 'Augusta', 'Brunswick', and 'Chignecto'). Bars as for Fig. 2.

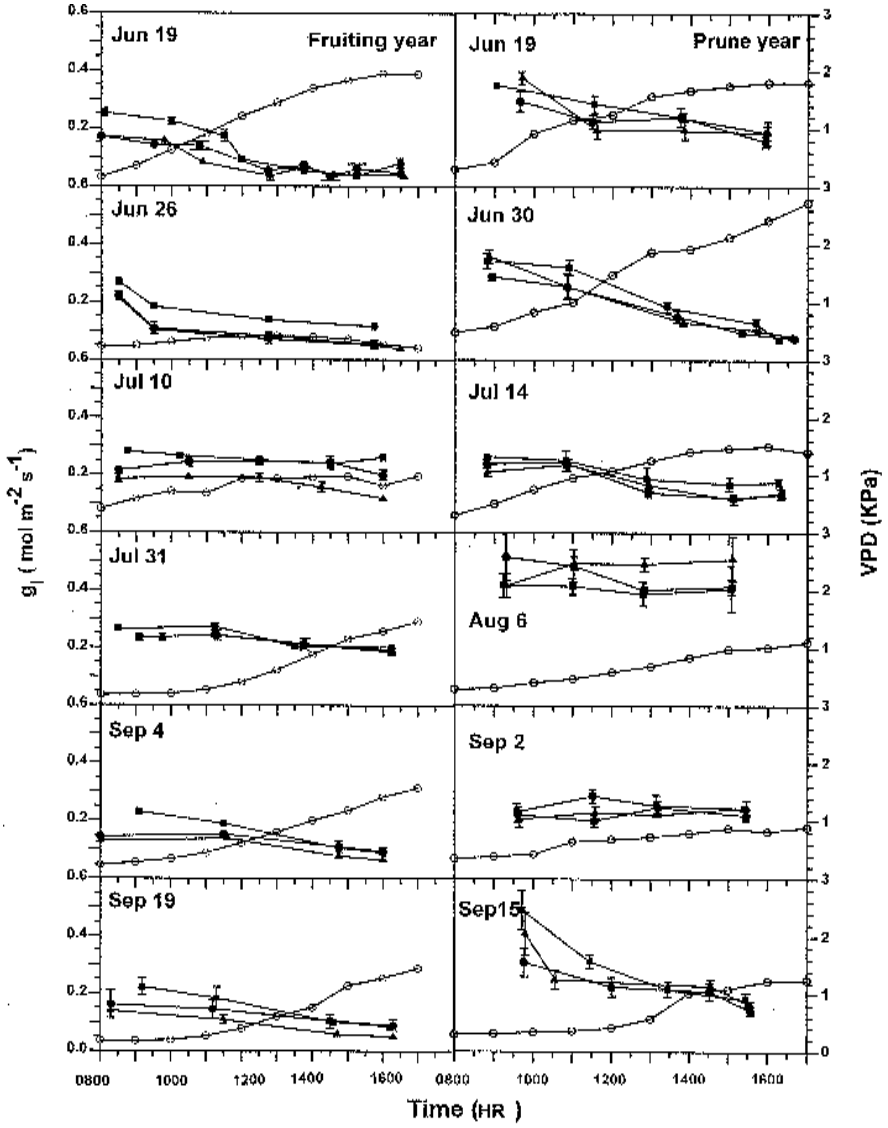

Fig. 5. Diurnal variation in stomatal conductance (g_l) and vapor pressure deficit (VPD) for 'Augusta', 'Brunswick', and 'Chignecto' lowbush blueberry in the fruiting year (1996) and in the prune year (1997). Each point is the mean of five measurements on individual plants. Symbols and bars as for Fig. 2. VPD is represented by open symbols.

from their seasonal maxima. The late season decline in g_l coincided with low A_{CO2} in fruiting year plants suggesting that lowered g_l contributes to a reduced assimilative capacity at this time of year. There were few differences between fruiting-year g_l in 'Chignecto' and 'Brunswick', but g_l was often higher in 'Augusta'. Through most of the year these differences were not reflected in higher A_{CO2}, except in September when 'Augusta' showed a more gradual seasonal decline in A_{CO2}.

In the prune year, diurnal changes in g_l in June were similar to those of the fruit year although values were generally higher for each clone than those for fruiting-year plants (Fig. 5). This was surprising in view of the relatively large year-to-year differences in soil and plant water status (Figs. 3 and 4). Higher g_l coincided with higher prune year A_{CO2} early in the season. Similarly, in September, g_l values were often twice as high in the prune year as in the fruiting year over a similar VPD range. In mid-July (14 July), when A_{CO2} in each clone was similar to that in the fruiting year, g_l was also similar. However, on 6 Aug., under relatively low VPD, soil moisture, and ψ_l, g_l were higher than on any other occasion in the 2-year crop cycle. This also coincided with maximal A_{CO2} in the prune year. Stomata are sensitive to light, temperature, atmospheric humidity, internal and external CO_2 concentrations, and plant water status. There is a tendency for stomata to close as ψ_l declines (Jarvis 1980), but in some species even moderate water deficits have no direct effect on g_l until a critical level is reached (Ehlig and Gardner, 1964), whereas in others, notably apple (*Malus*×*domestica* Borkh.), ψ_l is closely controlled by changes in g_l over a range of soil water contents (Jones et al., 1983). Our data, which actually show higher g_l under lower soil water contents and ψ_l (in the prune year), suggest a weaker linkage between ψ_l and g_l in lowbush blueberry, although further work under controlled conditions is necessary for confirmation.

The factors responsible for observed within- and between-season differences in g_l are not clear from the present results, and it may be that g_l is just one of several factors that influence seasonal C-assimilative capacity in lowbush blueberries. Thus, higher A_{CO2} during June in the prune year compared with the fruiting year may be partly explained by higher g_l and hence a reduced stomatal limitation. In the prune year, however, g_l values were as high throughout the day on 19 June (when A_{CO2} was between 50% and 70% of seasonal maxima) as on 14 July when rates were maximal. In many cases, leaves reach their maximum photosynthetic potential at 80% of full leaf expansion (Besford et al., 1985; Roper and Kennedy, 1986), but changes in internal resistances to CO_2 transfer, chloroplast structure, and relationships between photosynthesis and respiration change progressively through development (Šesták et al., 1985) and can lead to further alteration in photosynthetic potential. In lowbush blueberry, early formed leaves are

apparently not fully photosynthetically competent, so that plant C-assimilative capacity may not peak until mid-season.

Forsyth and Hall (1965) have reported significant differences in photosynthetic capacity between plants of different clonal origin. Our data do not indicate major differences between three other clones, but we cannot extrapolate from this small sample size to understand the range of photosynthetic variation in a diverse seedling population. We have barely begun to uncover the complex interactions between environment, genotype, C-acquisition, and distribution patterns that underpin growth and development in all woody perennial species. The unique 2-year management system employed in commercial lowbush blueberry production provides an opportunity to investigate many aspects of C-cycling and growth in a plant forced into a biennial cropping cycle. The results of the present study provide a baseline of information from which we may begin to investigate these more complex interactions.

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