Seasonal patterns of nonstructural carbohydrates of apple (*Malus pumila* Mill.) fruits: Relationship with relative growth rates and contribution to solute potential

By E. W. PAVEL[1] and T. M. DEJONG[2]*

[1]Institut für Obstbau und Gemüsebau der Rheinischen Friedrich-Wilhelms-Universität, Auf dem Hügel 6, D-53121 Bonn, F.R. Germany

[2]Department of Pomology, University of California, Davis, CA 95616, USA

SUMMARY

The seasonal dry-weight accumulation of midseason (cv. Cox's Orange Pippin) and late-maturing (cv. Golden Delicious) apple (*Malus pumila* Mill.) fruits, followed the characteristic sigmoid growth pattern. Similar to patterns reported for peach fruits, apple fruit relative growth rates of dry-matter accumulation, calculated on a degree-day basis, declined rapidly in an exponential fashion early in the season, then decreased slowly taking an asymptotic course later in the season. Unlike peach, the relative growth rate curve of apple fruits did not exhibit a distinct phase shift between two physiological phases of growth. However, seasonal changes of the relative nonstructural carbohydrate composition of apple fleshy tissue, in particular, the rapid increase of sucrose later in the season, indicated that there may be two phases of fruit sink activity in both cultivars. Seasonal patterns of nonstructural carbohydrates of the two apple cultivars were different if expressed on a dry weight basis. In 'Cox's Orange Pippin', sucrose was the main soluble carbohydrate later in the season, whereas 'Golden Delicious' accumulated high fructose concentrations. Estimated contribution of soluble carbohydrates to fruit solute potential declined over the growing season in both apple cultivars. Fructose contributed the largest amount to the solute potential, followed by sucrose.

THE growth curve of apple (*Malus pumila* Mill.) fruits is sigmoid in shape like those of pears, oranges, and kiwifruits (Bain, 1958, 1961; Bain and Robertson, 1951; Walton and DeJong, 1990). The growth of apples can be divided into one short postanthesis stage and two major subsequent stages (Denne, 1960). During the postanthesis stage, lasting about 6–12 d after pollination, there is a slow increase in fruitlet weight due mainly to cell division. The first major stage is characterized by a rapid exponential increase of fruitlet weight. The cells also elongate and continue to expand at a diminishing rate during the second major stage until harvest. Bain and Robertson (1951) measured the growth of apple fruit compartments by studying transverse sections of the fruit at the equator and determining the areas of cortex,

pith, and carpel tissues. The growth curves of all three fruit compartments follow a sigmoid pattern over the season, and the cortex contributes the largest part to the total area.

The seasonal sigmoid growth pattern of apple fruits has been described in terms of relative growth rates by Lakso *et al.* (1989) and Skene (1966). However, those studies were not focused on relationships between the relative growth rate pattern and physiological changes of sink activities in apple fruits. Recently, Schechter *et al.* (1993a, b) related the seasonal pattern of apple fruit relative growth rates to dry matter concentration and cell division. DeJong and Goudriaan (1989) used relative growth rate analysis techniques to model the double sigmoid growth of peach fruits in two distinct phases. These two phases have been shown to be related to changes in growth pat-

*Corresponding author.

terns of the individual peach fruit compartments and to patterns of nonstructural carbohydrate concentrations in the mesocarp (Pavel and DeJong, 1993a, b).

During their development, apple fruits accumulate large amounts of soluble carbohydrates reaching about 65–75% of dry matter at harvest (Buchloh and Neubeller, 1969). Fructose is the main soluble carbohydrate for most apple cultivars, but high accumulations of sucrose occur in comparison to glucose and sorbitol (Berüter, 1985; Buchloh and Neubeller, 1969). The relative nonstructural carbohydrate composition of apple fruits varies with the cultivar (Berüter, 1985; Chan *et al.*, 1972; Yamaki and Ishikawa, 1986) as it has been also reported for Asian pears (Moriguchi *et al.*, 1992).

The two major stages, following the postanthesis stage, of apple fruit growth are characterized by cell elongation and increase of fruit weight (Denne, 1960). The enlargement of plants is mainly attributable to increasing cell water contents by simultaneous uptake of water, extension of the cell walls, and accumulation of solutes (Boyer, 1985). When the cell walls are loosened by metabolic events followed by a turgor-driven extension, the cell turgor decreases creating a lower water potential within the cells. This low water potential causes water to enter the cells, enlarging them. To prevent a dilution of the cell solution during this process, solutes must continually accumulate. Solutes maintain the necessary osmotic potential to generate the cell turgor for wall extension and the water potential for water uptake (Boyer, 1985). Over the season, solute and water potentials of apple and tomato fruits and grape berries decrease whereas the turgor potential remains fairly constant (Berüter, 1989; Ho *et al.*, 1987; Matthews *et al.*, 1987). Matthews *et al.* (1987) found a strong negative correlation between soluble solids and solute potential in grape berries. Except for the tomato fruit (Ho *et al.*, 1987), the relative contribution of soluble carbohydrates to fruit solute potential has not yet been estimated.

The following investigations were designed to analyze the seasonal sigmoid growth of apple fruits with relative growth rates and to determine relationships between the relative growth rate pattern and the accumulation and composition of nonstructural carbohydrates in the apple fruit flesh. Composition of nonstructural carbohydrates were compared in two differently maturing apple cultivars and the contribution of soluble carbohydrates to fruit solute potential was estimated.

MATERIALS AND METHODS

Apple (*Malus pumila* Mill.) fruit samples were collected from a midseason (Cox's Orange Pippin) and late-maturing (Golden Delicious—Schweiz) cultivar during the 1988 growing season in the orchard of the Institut für Obstbau und Gemüsebau der Rheinischen Friedrich-Wilhelms-Universität in Bonn, Federal Republic of Germany. The six year old trees growing on M.9 rootstock were planted and trained to a high density-central leader (flat spindle) system (1.25 × 4.0 m). Cultural management practices such as fertilization, pruning, and thinning were conducted as in a commercial orchard.
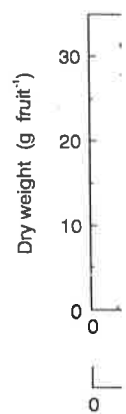
Apple fruits, excluding stems, were randomly sampled from 20 trees per cultivar at weekly intervals from about six weeks after flowering until harvest. Initially, 20 fruits, and later in the season ten fruits, were collected on each sampling date and separated into groups of four and two, respectively. Each group was weighed, sliced, frozen, and freeze-dried; the dry weight was then determined. Mean dry-weight accumulations over the season were used to calculate relative growth rates according to the method of Hunt (1982). Degree-day accumulations were integrated into the equations instead of daily time intervals. Ambient air temperatures were monitored at the weather station of the Deutscher Wetterdienst located in Bonn (within 5 km of the study site). Degree-day accumulations were calculated from daily minimum and maximum temperatures by the single-sine method (Zalom *et al.*, 1983) with lower and upper temperature thresholds at 7°C and 30°C. The relative growth rate curve was fitted by regression analysis using the function $y = ax^b$ [$<=>$ $\ln y = b\ln x + \ln a$ $<=>$ $y = e^{b\ln x + \ln a}$] requiring a double-log transformation of the data.

The freeze-dried fruit samples were analyzed for nonstructural carbohydrates. Soluble carbohydrates (sucrose, fructose, glucose, sorbitol) were determined by HPLC and starch enzymatically as described previously (Pavel and DeJong, 1993a).

Contribu
fruit solute
Hoff relat
number of
ume V (m
mol⁻¹), and
(Baker, 19
ble carbol
sorbitol) o
osmolal co
water con
weight).

Seasona
ion of the
and late-m
were quite
moid grov
Robertson
exhibit the
two major
sampling i
Apple f
exponentia
describing
and indica
fruit relati
mulation
Golden D
functions

Patterns of
('Cox's Oran
cious') apple
points repres

Contribution of soluble carbohydrates to fruit solute potential was estimated by the van't Hoff relationship $\varphi_s = \frac{n}{v} R T$, where $\frac{n}{v}$ is the number of solute molecules in solution of volume V (mol l^{-1}), R the gas constant (8.31 J °K^{-1} mol^{-1}), and T the absolute temperature (298°K) (Baker, 1984). Concentration (mg g^{-1}) of soluble carbohydrates (sucrose, glucose, fructose, sorbitol) of fruit tissue were converted into osmolal concentrations (osmolal l^{-1}) using fruit water content (difference of fresh and dry weight).

RESULTS AND DISCUSSION

Seasonal patterns of dry weight accumulation of the midseason ('Cox's Orange Pippin') and late-maturing ('Golden Delicious') apples were quite similar (Figure 1) and followed a sigmoid growth pattern as reported by Bain and Robertson (1951). The growth curves did not exhibit the postanthesis stage followed by the two major stages because of a late beginning of sampling in spring.

Apple fruit relative growth rates declined exponentially over the season (Figure 2A, 2B), describing a 'Richards function' (Hunt, 1982) and indicating a negative relationship between fruit relative growth rate and degree-day accumulation (Cox's Orange Pippin: $r^2 = 0.74$; Golden Delicious: $r^2 = -0.86$). The exponential functions were $y = e^{-1.63\ln x + 4.76}$ and $y = e^{-1.56\ln x + 4.45}$
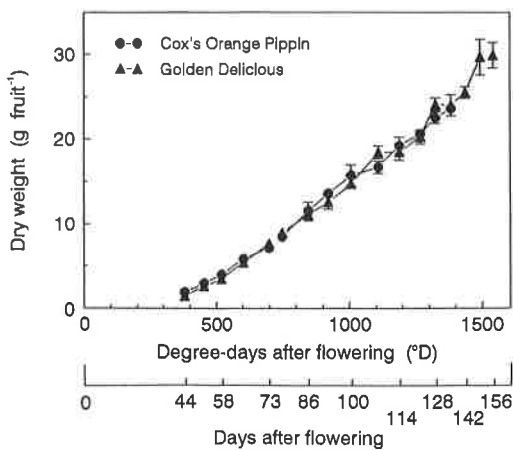

FIG. 1

Patterns of fruit dry weight accumulation of midseason ('Cox's Orange Pippin') and late-maturing ('Golden Delicious') apple cultivars during the 1988 growing season. Data points represent means ± SE of five replicate fruit samples harvested on each date.

for 'Cox's Orange Pippin' and 'Golden Delicious, respectvely. In 'Golden Delicious', only the first nine data points were included for the regression analysis because the last seven data points were too variable. The pattern is similar to those reported for tomato (Monselise et al., 1978) and apple (Lakso et al., 1989; Schechter et al., 1993a,b; Skene, 1966). However, Lakso et al. (1989) and Skene (1966) used fruit fresh weight or fruit diameter instead of dry weight for their calculation of relative growth rates. Seasonal relative growth rate patterns were quite similar for both cultivars, but the slope of the relative growth rate curve was slightly lower for 'Cox's Orange Pippin' (−1.63) than for 'Golden Delicious' (−1.56) indicating lower growth increases. Recently, Schechter et al. (1993a,b) showed that the relative growth rate curve of apple fruits displays three phases. During phase I (postanthesis stage, lasting about two weeks after full bloom), relative growth rates as well as percent cell division increased rapidly in 'Idared' apples. By the end of phase I, 85% of the cell division had occurred (Schechter et al., 1993b). In 'Miller's Seedling' and 'Cox's Orange Pippin', rapid cell division takes place during the first three weeks and 6–7 weeks after full bloom, respectively (Denne, 1960; Skene, 1966). Since in the present study the first fruit sampling started at 44 d after flowering (382°DAF, degree-days after flowering), the postanthesis phase (Phase I) characterized by rapidly increasing relative growth rates (Schechter et al., 1993a,b) could not be included. Therefore, the two phases of relative growth rates in 'Cox's Orange Pippin' (Figure 2A) and 'Golden Delicious' (Figure 2B) represent phase II and III according to Schechter et al. (1993a,b). Although distinct shifts between the phases are not clear, in phase II, fruit relative growth rates declined rapidly, whereas in phase III they decreased slightly taking an asymptotic course. Phase III was shorter for the midseason 'Cox's Orange Pippin' cultivar than for 'Golden Delicious' because of a shorter time to fruit maturity. In peach fruits, those two phases of the relative growth rate curve were more distinctly displayed in the late-maturing cultivars and mean relative growth rates remained relatively constant in the second phase (Pavel and DeJong, 1993a). The peach fruit relative growth rate curve also exhibited only the two
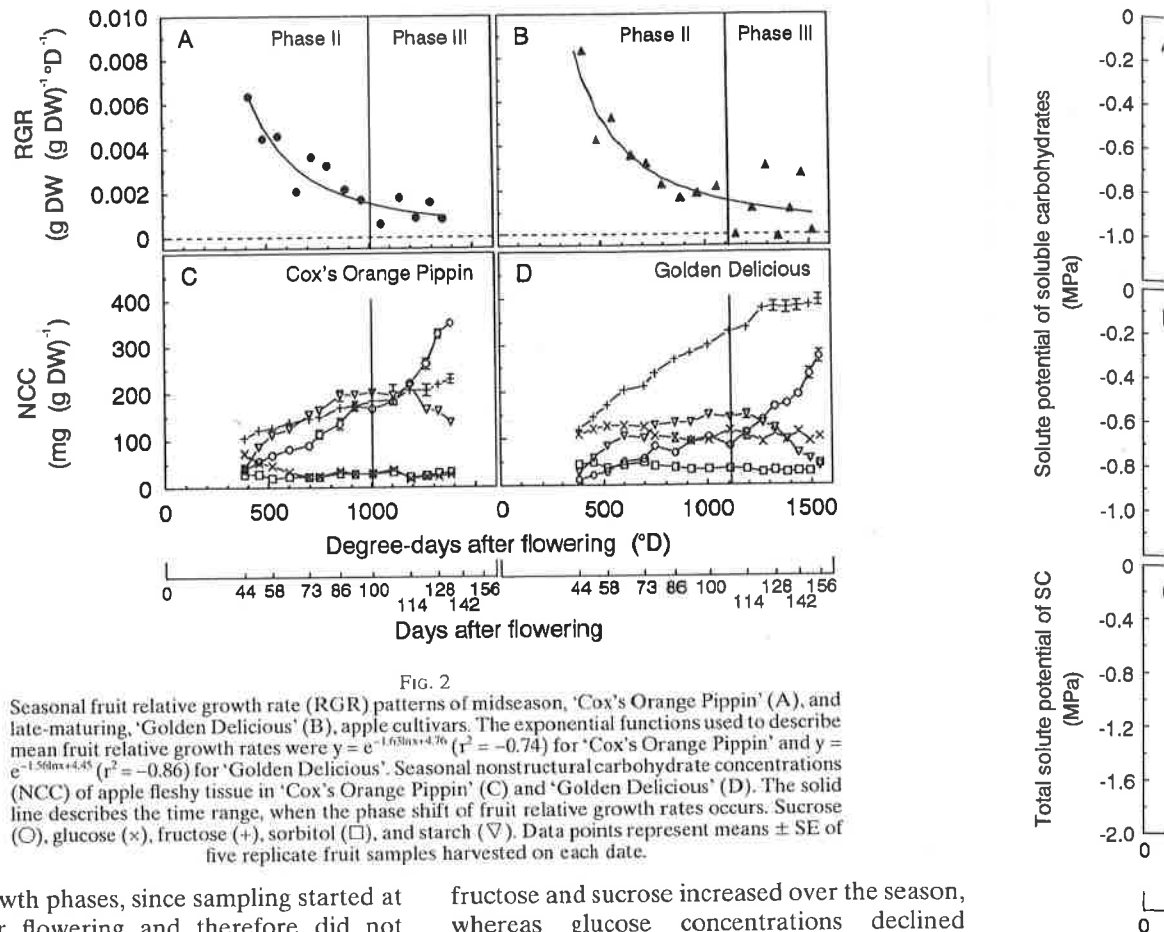
Fig. 2

Seasonal fruit relative growth rate (RGR) patterns of midseason, 'Cox's Orange Pippin' (A), and late-maturing, 'Golden Delicious' (B), apple cultivars. The exponential functions used to describe mean fruit relative growth rates were $y = e^{-1.63\ln x + 4.76}$ ($r^2 = -0.74$) for 'Cox's Orange Pippin' and $y = e^{-1.56\ln x + 4.45}$ ($r^2 = -0.86$) for 'Golden Delicious'. Seasonal nonstructural carbohydrate concentrations (NCC) of apple fleshy tissue in 'Cox's Orange Pippin' (C) and 'Golden Delicious' (D). The solid line describes the time range, when the phase shift of fruit relative growth rates occurs. Sucrose (O), glucose (×), fructose (+), sorbitol (□), and starch (∇). Data points represent means ± SE of five replicate fruit samples harvested on each date.

major growth phases, since sampling started at 21 d after flowering and therefore did not include the postanthesis phase characterized by rapid cell division and increasing fruit relative growth rates (Addoms *et al.*, 1930; Pavel and DeJong, 1993a; DeJong, unpublished). Seasonal growth curves of cortex, pith, and carpels follow a sigmoid pattern (Bain and Robertson, 1951; Tukey and Young, 1942). The carpels reach their maximum size early in the season, whereas the pith and cortex are still growing. The cortex represents the major growth component of the whole apple fruit in a manner similar to that of the peach mesocarp. In peach fruits, the shift between the two major phases of the relative growth rate curve has been related to changes in growth patterns of the mesocarp and endocarp in later maturing cultivars (Pavel and DeJong, 1993a).

Seasonal patterns of nonstructural carbohydrates of the two apple cultivars were slightly different (Figure 2C, 2D). Concentrations of fructose and sucrose increased over the season, whereas glucose concentrations declined slightly in young fruits and remained fairly consistent in maturing fruits. Fructose dominated in fruits of 'Golden Delicious' as reported by Berüter (1985) and Latché *et al.* (1975), but in 'Cox's Orange Pippin' sucrose was the main carbohydrate later in the season. Similar to 'Cox's Orange Pippin' and 'Golden Delicious', 'Jonagold', another apple cultivar, and European and Asian pears also accumulate high amounts of sucrose during fruit ripening (Latché *et al.*, 1975; Moriguchi *et al.*, 1992; Yamaki and Ishikawa, 1986). Starch concentrations increased early in the season and declined towards fruit maturation, when sucrose concentrations increased rapidly in both cultivars. Starch is probably converted to sucrose during that period (Latché *et al.*, 1975). Latché *et al.* (1975) and Moriguchi *et al.* (1992) found that during fruit ripening, the metabolic shift between starch and sucrose coincided with

low and constant in both apple cultivars over the season.

DeJong and Goudriaan (1989) suggest that the two major phases of fruit relative growth rates are related to changes in physiological sink activities of peach fruits. Compositional nonstructural carbohydrate changes of peach mesocarp have been related to those two phases of fruit relative growth rates in later maturing peach cultivars (Pavel and DeJong, 1993a). Seasonal changes of nonstructural carbohydrate composition of apple fleshy tissue appear to be related to the two major phases of fruit relative growth rate curves (Figure 2). The shift from phase II to phase III of apple fruit relative growth rate curves apparently coincides with rapid increases of sucrose concentrations similar to late maturing peaches (Pavel and DeJong, 1993a).

Fructose made the greatest contribution to calculated fruit solute potential in both apple cultivars followed by sucrose in 'Cox's Orange Pippin' (Figure 3A) and by glucose and sucrose in 'Golden Delicious' (Figure 3B). Although, sucrose was the major soluble carbohydrate on a dry weight basis in 'Cox's Orange Pippin' apples towards fruit maturation (Figure 2C), fructose dominated when its concentration was expressed on a osmolal basis (data not shown).

Solute potential attributed to soluble carbohydrates decreased over the growing season in both apple cultivars (Figure 3C). Osmometer measurements of total solute potential have a
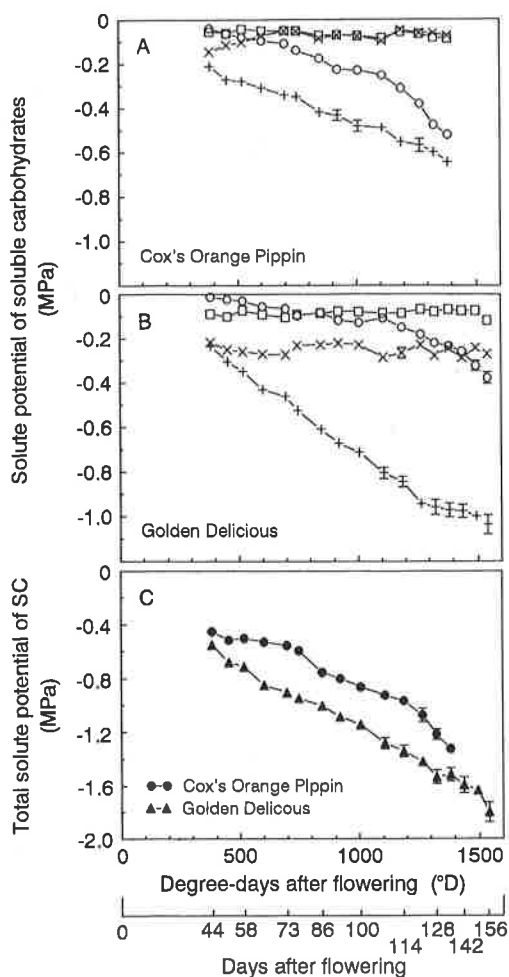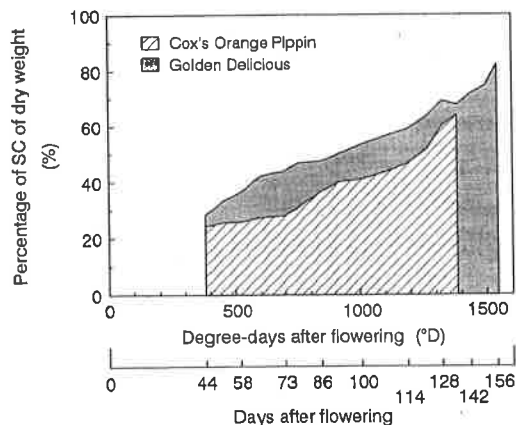
FIG. 3
Seasonal fruit solute potential of soluble carbohydrates of midseason 'Cox's Orange Pippin' (A) and late-maturing 'Golden Delicious' (B) apple cultivars. Sucrose (O), glucose (×), fructose (+), and sorbitol (□). Seasonal pattern of the total fruit solute potential of soluble carbohydrates (SC) in 'Cox's Orange Pippin' and 'Golden Delicious' (C). Data points represent means ± SE of five replicate fruit samples harvested on each date.

increasing activities of the enzymes sucrose synthase and sucrose-phosphate synthase in apples and pears. The concentrations of sucrose and starch were higher in fruits of the midseason 'Cox's Orange Pippin' than of the late-maturing 'Golden Delicious' cultivar. Sorbitol, the main photosynthate translocated from leaves to fruits in the Rosaceae, is metabolized to other sugars after uptake into the fruit (Berüter, 1985; Bieleski, 1969; Hansen, 1970, 1979). Its concentration remained relatively

FIG. 4
Percentage of soluble carbohydrates (SC) of fruit dry weight of midseason (Cox's Orange Pippin) and late-maturing (Golden Delicious) apple cultivars during the 1988 growing season.

similar pattern in apples (Berüter, 1989) and grape berries (Matthews *et al.*, 1987). Based on Berüter's (1989) osmometer data, soluble carbohydrates apparently contribute about 46% early in the season and about 86% at harvest to the total fruit solute potential in 'Golden Delicious'. The contribution of organic acids and ions, in particular potassium, to fruit solute potential (Ho *et al.*, 1987) may account for the difference. There was no difference in measured relative water content of fresh weight between the two apple cultivars that could offset differences in solute potential attributable to soluble carbohydrates. The relative water content of fresh weight remained fairly constant over the season in 'Cox's Orange Pippin' and 'Golden Delicious' fruits and accounted for 87% in young and for 83–84% in mature fruits.

The percentage of fruit dry weight consisting of soluble carbohydrates increased over the season (Figure 4) to 64% and 82% in 'Cox's Orange Pippin' and 'Golden Delicious', respectively, at harvest. In young fruits, the soluble carbohydrate percentage of fruit dry weight was low, accounting for 24% in 'Cox's Orange Pippin' and 28% in 'Golden Delicious'.

Concentrations of organic acids and ions, in particular potassium, are high early in the season and decrease then towards fruit maturity in apples (Askew *et al.*, 1959; Hulme, 1958; Rogers and Batjer, 1954). In young apples, the percentage of dry matter accounted for by potassium is about 1.8–2.2%, in 'Cox's Orange Pippin' and 'Golden Delicious' (Askew *et al.*, 1959; Rogers and Batjer, 1954) and decreases towards fruit maturity (0.8–1.1%). Matthews *et al.* (1987) found a strong negative correlation between soluble solids and solute potential in grape berries throughout the growing season. However, the correlation was less strong early in the berry development. Although the total fruit solute potential was not determined in the present research, soluble carbohydrates apparently contributed substantially to the solute potential later in the growing season in both apple cultivars but not early in the season.

REFERENCES

ADDOMS, R. M., NIGHTINGALE, G. T. and BLAKE, M. A. (1930). Development and ripening of peaches as correlated with physical characteristics, chemical composition, and histological structure of the fruit flesh: II. Histology and microchemistry. *New Jersey Agricultural Experiment Station Bulletin*, **507**, 1–19.

ASKEW, H. O., CHITTENDEN, E. T., MONK, R. J. and WATSON, J. (1959). Chemical investigation on bitter pit of apples. I. Physical and chemical changes in leaves and fruits of Cox's Orange variety during the season. *New Zealand Journal of Agricultural Research*, **2**, 1167–86.

BAIN, J. M. (1958). Morphological, anatomical, and physiological changes in the developing fruit of the Valencia orange. *Citrus sinensis* (L.) Osbeck. *Australian Journal of Botany*, **6**, 1–24.

BAIN, J. M. (1961). Some morphological, anatomical, and physiological changes in the pear fruit (*Pyrus communis* var. William Bon Chrétien) during development and following harvest. *Australian Journal of Botany*, **9**, 99–123.

BAIN, J. M. and ROBERTSON, R. N. (1951). The physiology of growth in apple fruits. I. Cell size, cell number, and fruit development. *Australian Journal of Scientific Research. Series B, Biological Sciences*, **4**, 75–91.

BAKER, D. A. (1984). Water relations. In: *Advanced plant physiology*. (Wilkins, M. B., Ed.). Longman Scientific & Technical, Harlow, UK, 297–318.

BERÜTER, J. (1985). Sugar accumulation and changes in the activities of related enzymes during development of the apple fruit. *Journal of Plant Physiology*, **121**, 331–41.

BERÜTER, J. (1989). Carbohydrate partitioning and changes of water relations of growing apple fruit. *Journal of Plant Physiology*, **135**, 583–7.

BIELESKI, R. L. (1969). Accumulation and translocation of sorbitol in apple phloem. *Australian Journal of Biological Sciences*, **22**, 611–20.

acids and ions, in
high early in the
towards fruit matu-
1959; Hulme, 1958;
n young apples, the
:counted for by pot-
ı 'Cox's Orange Pip-
' (Askew *et al.*, 1959;
i4) and decreases
-1.1%). Matthews *et*
ıegative correlation
J solute potential in
the growing season.
ₐvas less strong early
Although the total
ot determined in the
arbohydrates appar-
ıtially to the solute
ₐving season in both
ly in the season.

hackel for his advise
technical assistance.
Heinrich Hertz-Stif-
edged.

d ripening of peaches
histological structure
·icultural *Experiment*

ıical investigation on
uits of Cox's Orange
rch, **2**, 1167–86.
he developing fruit of
f Botany, **6**, 1–24.
nges in the pear fruit
nd following harvest.

fruits. I. Cell size, cell
·h. *Series B, Biological*

Wilkins, M. B., Ed.).

lated enzymes during
–41.
of growing apple fruit.

le phloem. *Australian*

BOYER, J. S. (1985). Water transport. *Annual Review of Plant Physiology*, **36**, 473–516.

BUCHLOH, G. and NEUBELLER, J. (1969). Zur qualitativen und quantitativen Bestimmung von Zuckern und Zuckeralkoholen in einigen Obstfrüchten mittels Gaschromatographie. *Erwerbsobstbau*, **11**, 22–7.

CHAN, W. W., CHONG, C. and TAPER, C. P. (1972). Sorbitol and other carbohydrate variation during growth and cold storage of McIntosh apple fruits. *Canadian Journal of Plant Science*, **52**, 743–50.

DeJONG, T. M. and GOUDRIAAN, J. (1989). Modeling peach fruit growth and carbohydrate requirements: reevaluation of the double-sigmoid growth pattern. *Journal of the American Society for Horticultural Science*, **114**, 800–4.

DENNE, M. P. (1960). The growth of apple fruitlets, and the effect of early thinning on fruit development. *Annals of Botany*, **24**, 397–406.

HANSEN, P. (1970). ^{14}C-studies on apple trees. V. Translocation of labeled compounds from leaves to fruit and their conversion within the fruit. *Physiologia Plantarum*, **23**, 564–73.

HANSEN, P. (1979). ^{14}C-studies on apple trees. IX. Seasonal changes in the formation of fruit constituents and their subsequent conversions. *Physiologia Plantarum*, **47**, 190–4.

HO, L. C., GRANGE, R. I. and PICKEN, A. J. (1987). An analysis of the accumulation of water and dry matter in tomato fruit. *Plant, Cell and Environment*, **10**, 157–62.

HULME, A. C. (1958). Some aspects of the biochemistry of apple and pear fruits. *Advances in Food Research*, **8**, 297–413.

HUNT, R. (1982). *Plant growth curves*. E. Arnold, London, UK.

LAKSO, A. N., ROBINSON, T. L. and POOL, R. M. (1989). Canopy microclimate effects on patterns of fruiting and fruit development in apples and grapes. In: *Manipulation of fruiting*. (Wright, C. J., Ed.) Butterworths, London, UK, 263–74.

LATCHÉ, A., PECH, J.-C. and FALLOT, J. (1975). Amylolyse et maturation chez la pomme et la poire. *Physiologie Vegetale*, **13**, 637–49.

MATTHEWS, M. A., CHENG, G. and WEINBAUM, S. A. (1987). Changes in water potential and dermal extensibility during grape berry development. *Journal of the American Society for Horticultural Science*, **112**, 314–9.

MONSELISE, S. P., VARGA, A. and BRUINSMA, J. (1978). Growth analysis of the tomato fruit, *Lycopersicum esculentum* Mill. *Annals of Botany*, **42**, 1245–7.

MORIGUCHI, T. M., ABE, K., SANADA, T. and YAMAKI, S. (1992). Levels and role of sucrose synthase, sucrose-phosphate synthase, and acid invertase in sucrose accumulation in fruit of Asian pear. *Journal of the American Society for Horticultural Science*, **117**, 274–8.

PAVEL, E. W. and DeJONG, T. M. (1993a). Relative growth rate and its relationship to compositional changes of nonstructural carbohydrates in the mesocarp of developing peach fruits. *Journal of the American Society for Horticultural Science*, **118**, 503–8.

PAVEL, E. W. and DeJONG, T. M. (1993b). Source- and sink-limited growth periods of developing peach fruits indicated by relative growth rate analysis. *Journal of the American Society for Horticultural Science*, **118**, 820–4.

ROGERS, B. L. and BATJER, L. P. (1954). Seasonal trend of six nutrient elements in the flesh of Winesap and Delicious apple fruits. *Proceedings of the American Society for Horticultural Science*, **63**, 67–73.

SCHECHTER, I., PROCTOR, J. T. A. and ELFVING, D. C. (1993a). Reappraisal of seasonal apple fruit growth. *Canadian Journal of Plant Science*, **73**, 549–56.

SCHECHTER, I., PROCTOR, J. T. A. and ELFVING, D. C. (1993b). Characterization of seasonal fruit growth of 'Idared' apple. *Scientia Horticulturae*, **54**, 203–10.

SKENE, D. S. (1966). The distribution of growth and cell division in the fruit of Cox's Orange Pippin. *Annals of Botany*, **30**, 493–512.

TUKEY, H. B. and YOUNG, J. O. (1942). Gross morphology and histology of developing fruit of the apple. *Botanical Gazette*, **104**, 3–25.

WALTON, E. F. and DeJONG, T. M. (1990). Growth and compositional changes in kiwifruit berries from three Californian locations. *Annals of Botany*, **66**, 285–98.

YAMAKI, S. and ISHIKAWA, K. (1986). Roles of four sorbitol related enzymes and invertase in the seasonal alteration of sugar metabolism in apple tissue. *Journal of the American Society for Horticultural Science*, **111,** 134–7.

ZALOM, F. G., GOODELL, P. B., WILSON, L. T., BARNETT, W. W. and BENTLEY, W. J. (1983). Degree-days: The calculation and use of heat units in pest management. *Division of Agriculture and Natural Resources, University of California*, Leaflet no. 21373,1–10.