

Apple Tree Physiology— Implications for Orchard and Tree Management

Jens N Wünsche¹ and Alan N. Lakso²

¹HortResearch, Nelson Research Center, Motueka, New Zealand

²Department of Horticultural Sciences, New York State Agricultural Experiment Station, Cornell University, Geneva, New York, USA

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Apple yield and fruit quality are the end result of myriad cultural practices (e.g., pruning, thinning, spraying), environmental inputs (e.g., light, carbon dioxide, water, nutrient supply) and physiological processes (e.g., leaf area development, light interception, photosynthesis, respiration). All of them are truly essential contributors to fruit production. That does not mean, however, that any one resource or process is necessarily controlling the variation in yield and fruit quality of apple orchards. There are only two possible means to improve crop performance: 1) increase total dry matter yield and/or 2) increase the magnitude of partitioning of dry matter toward the fruits. This review will emphasize the key processes of tree canopy light interception/distribution and carbon partitioning

in limiting apple yields and discuss the implications of these processes for grower practices of orchard/tree design and canopy management. Although factors such as frost, drought, nutrient deficiencies and incidence of diseases can limit fruit yields, in a healthy, well-maintained and supplied orchard system these factors are less critical in determining overall yield and fruit quality.

LIMITS OF APPLE ORCHARD PRODUCTIVITY

The production of dry matter (DM) of plant crops including apple is a function of four key factors (Scurlock et al., 1985):

$DM = (RAD \times \%INT \times PH) - RESP$
where RAD is the quantity of incident photosynthetically active radiation (PAR),

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1) increase total dry matter yield and/or
2) increase the magnitude of partitioning of dry matter toward the fruits.

%INT is the percent of light intercepted by the crop, PH is the photosynthetic conversion of light energy into biomass and RESP is the respiratory carbon loss (Table 1).

The amount of incident solar radiation varies primarily with latitude and cloud cover and is thus independent of the crop or its management. A growing region with high light energy input and a long season is essential for setting a high potential yield. Within the climatic limits, the total amount of light intercepted by an apple orchard system depends, however, on orchard design and canopy display, an important and manageable process for obtaining potential productivity. The conversion of absorbed light by the leaves into biomass is only 5 to 10% due to the inefficiency of the photosynthetic process. Although respiration of biomass provides energy for growth of new cell structure and maintenance of existing tissue it constitutes an important reduction in potential productivity. The possibilities for decreasing these losses are limited under field conditions. Fortunately, apple

TABLE 1

Reductive pathway of annual total solar radiation (100%) and factors limiting the efficiency of light conversion into fruit yield (<0.5%). Limiting factors and processes in bold indicate major effects on orchard productivity.

Limitations on total utilization of solar energy	Relative importance of factors limiting efficiency of light conversion into fruit yield
50% of total solar radiation is PAR (photosynthetically active radiation)	50% climate
75% of growing season (9 months) is used	37.5% region
40% is typical light interception by orchard systems	15% orchard design, leaf area
5% is photosynthetic conversion efficiency	0.75% photosynthesis
15% is whole-tree respiration loss	0.64% climate (temperatures)
60% is typical harvest index	<u>0.38%</u> partitioning
	100%

trees appear to have very efficient respiration, so the losses are relatively small compared to most crops.

Three factors appear to control the actual fruit yield of apple: 1) the quantity of light energy that is intercepted by an orchard system, 2) the proportion of that energy which is converted into available carbohydrate for partitioning and 3) the amount of assimilates allocated into fruits. Therefore, these factors will be considered next and evaluated closely from a grower's perspective.

ORCHARD LIGHT INTERCEPTION

Biological yield has been increased in many crops due to an enhancement in the amount of seasonal total light interception, and this generally is attributable to improved cultural practices that affect leaf growth, leaf duration and/or canopy display (Gifford and Jenkins, 1982).

The total amount of light intercepted by an apple orchard system depends primarily on orchard design factors such as planting system, tree spacing, tree shape, tree height, alley width, row orientation as well as leaf area index (ratio between the total area of all leaves per tree to the land area allocated to the tree) and the length of the growing season (Table 2). These various factors have been well researched over the past 20 to 25 years (see reviews by Jackson, 1980; Lakso, 1994; Palmer, 1989; Wagenmakers, 1991).

Monteith (1977) has demonstrated a fundamental relationship, a landmark in modern crop physiology, between crop dry matter production and seasonal accumulated light interception by the crop. This relationship was confirmed for apple production systems by Palmer (1989). Apple yields, which are of greater interest to the orchardist, are also well related to the total amount of sunlight intercepted by the orchard (Fig. 1). This summarized relationship from the literature covers a wide range of light environments, planting systems and scion/rootstock combinations. Below about 50% light interception yield is linearly related to light interception. Such orchards frequently have open and well-exposed canopies. In contrast, fruit yields vary considerably when light interception is over 50%, indicating that factors other than total light interception may become limiting.

The erratic relationship between yield and high light interception suggests that, although total light interception may provide the potential for high yields, other factors such as light distribution within apple

TABLE 2

Factors increasing the percentage of tree canopy light interception and light distribution.

Interception	<ul style="list-style-type: none"> • increasing tree density per area of land • high ratio of leaf area per tree to land area allocated per tree • reducing distance between rows • increasing height of the trees • orienting rows in north-south direction
Distribution	<ul style="list-style-type: none"> • light dormant pruning, avoiding heading cuts • spreading or tying down branches to a horizontal position • summer pruning

FIGURE 1

Summarized relationship between apple fruit yield and mid-season percent total orchard light interception from several reports in the literature.

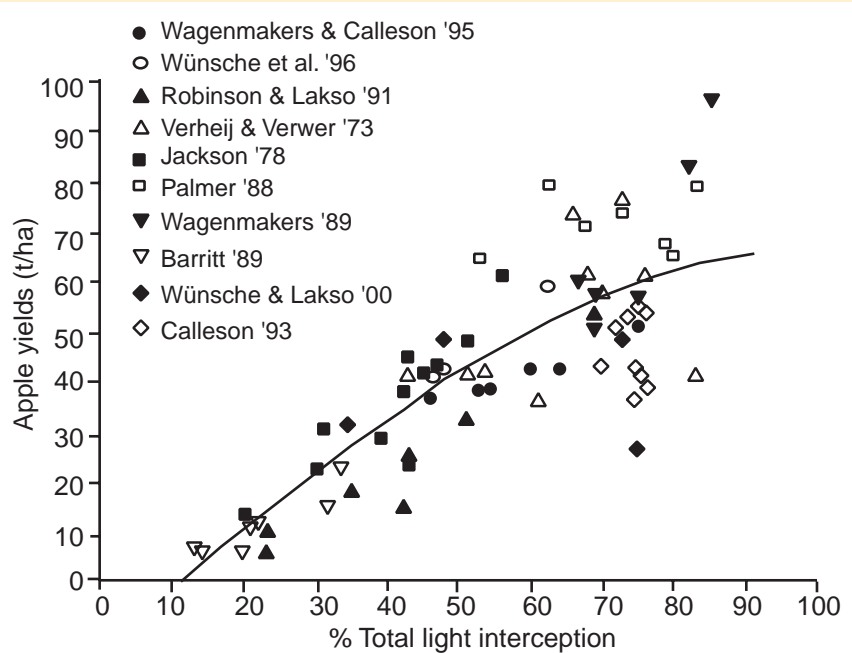


FIGURE 2

Effect of photosynthetic photon flux (PPF) (light level) on the rate of leaf and whole-canopy carbon dioxide exchange (photosynthesis) of Braeburn apple trees.

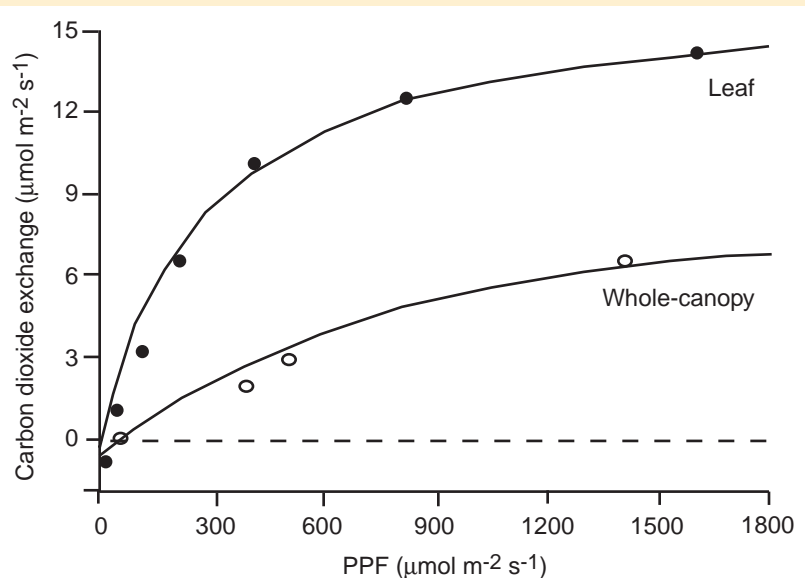


TABLE 3

Positive effects of increased tree canopy light interception and light distribution on plant processes, growth and development, yield and fruit quality.

Interception	<ul style="list-style-type: none"> • whole-canopy photosynthesis • yield
Distribution	<ul style="list-style-type: none"> • flowering, fruit set • carbohydrate partitioning to fruit • fruit growth, fruit weight • nutrient supply of xylem-derived solutes • fruit firmness, fruit soluble solids • fruit color

FIGURE 3

Effect of crop load (kg fruit per cm² of trunk cross-sectional area) on mid-season leaf and whole canopy carbon dioxide exchange rate (photosynthesis) of Braeburn apple trees.

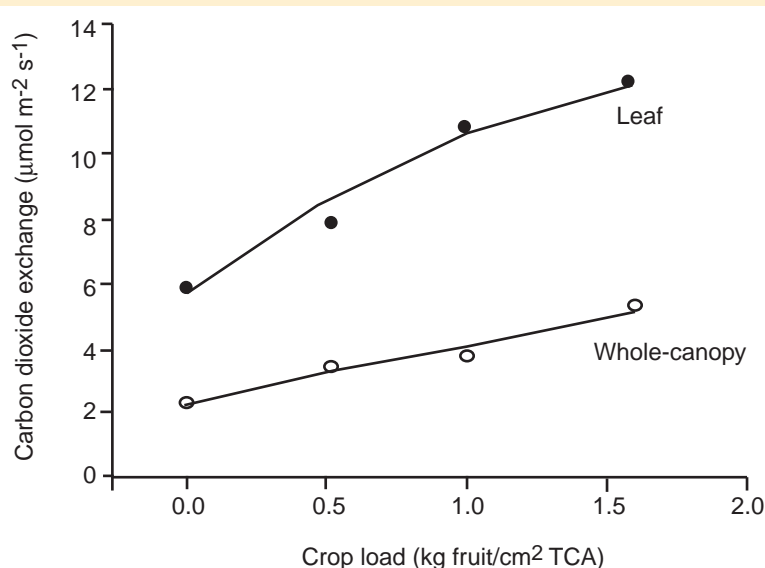
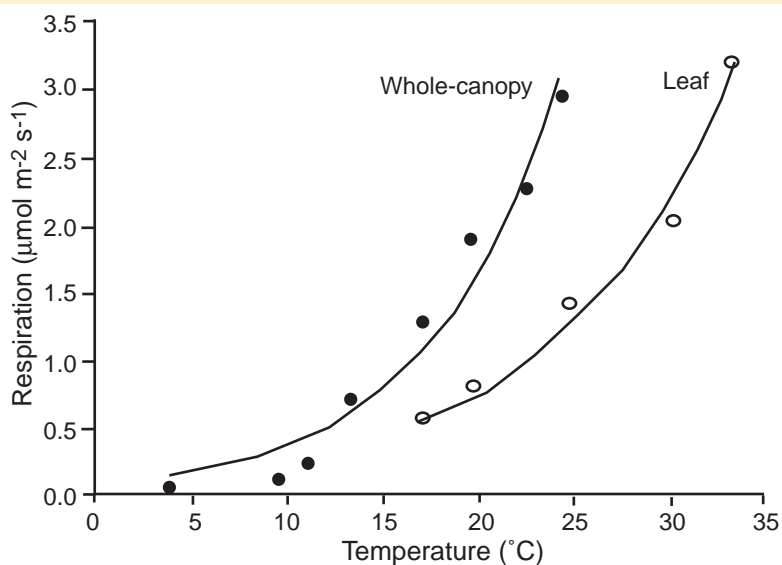


FIGURE 4

Effect of temperature on leaf and whole-canopy respiration of Braeburn apple trees.



tree canopies are critical to actual yield (Table 3). Due to the deleterious effects of canopy shading, optimum apple yields are obtained at about 60 to 70% light interception. Yield performance at higher light interception can be reduced due to a multiple year effect of overly dense, shaded tree canopies and carryover effects on flowering and/or fruit development. The relationship between yield and light interception is expected to show a curvilinear response (Wünsche and Lakso, 2000), corresponding to the curvilinear pattern between yield and leaf area (Wünsche et al., 1996). As leaf area increases excessively, therefore, the increases in light interception or potential yield become not only less but in many cases decrease due to increases in mutual shading among the leaves and internal shading of fruiting sites that require good exposure for high productivity and quality.

Adequate light distribution within the tree canopy is further important to secure high fruit quality since shade causes a reduction in fruit weight and symptoms of fruit immaturity such as decreased fruit color, fruit dry matter, fruit soluble solids and increased fruit firmness (Table 3; Jackson, 1980; Lakso, 1994; Robinson et al., 1983). Shade does, however, reduce the incidence of apple skin blemishes such as russet and sunburn.

LEAF- AND WHOLE-CANOPY CARBON EXCHANGE

Light is the single most important factor controlling the fixation of atmospheric carbon dioxide by the leaves of healthy trees. This photosynthetic process is important since more than 90% of the total dry matter produced by apple trees originates from photosynthesis by leaves (Hansen, 1977). Whole-canopy photosynthesis depends on leaf photosynthetic rates, whole-canopy light interception and leaf area. These factors are in turn influenced by crop characteristics (genetics, stage of development), environment (light, temperature, water relation, carbon dioxide concentration) and cultural practices (nutrition, irrigation, pest management).

Increased light interception offers the best method to increase leaf and whole-canopy photosynthesis (Fig. 2). Apple leaf photosynthesis has a hyperbolic response to increasing irradiance and saturates under the environmental conditions in New Zealand at about 45% of full sunlight. The light-saturated photosynthetic rates of single leaves are not expected to differ dramatically among healthy, well-maintained apple orchard systems. The photosynthetic light

response of the whole-canopy is similar to that of an individual leaf, but the curve is shallower with a lower maximum. This difference in the curves is due primarily to poor within-canopy light distribution with only a small proportion of leaves being exposed to saturating incident light level at any time and the inclusion of non-photosynthetic components (e.g., fruit, wood). Whole-canopy carbon fixation can be improved under diffuse, i.e., bright, hazy conditions when light is omnidirectional leading to a more uniformly illuminated leaf canopy and, by means of canopy management where leaf area is displayed, to maximize the interception of incoming sunlight. On the contrary, the photosynthetic response of apple trees to temperature is relatively small over the typically encountered range of ambient temperatures in temperate environments.

Leaf and whole-canopy photosynthesis increase curvilinearly with higher apple crop loads a few weeks after fruit removal (Fig. 3; Palmer et al., 1997, Wünsche et al., 2000). The reduction of photosynthesis in trees with lower fruit numbers frequently occurs after shoots have terminated vegetative growth although there is typically a significant increase of extension shoot growth, leaf area and trunk thickening when compared to high-cropping trees (Wünsche et al., 2000).

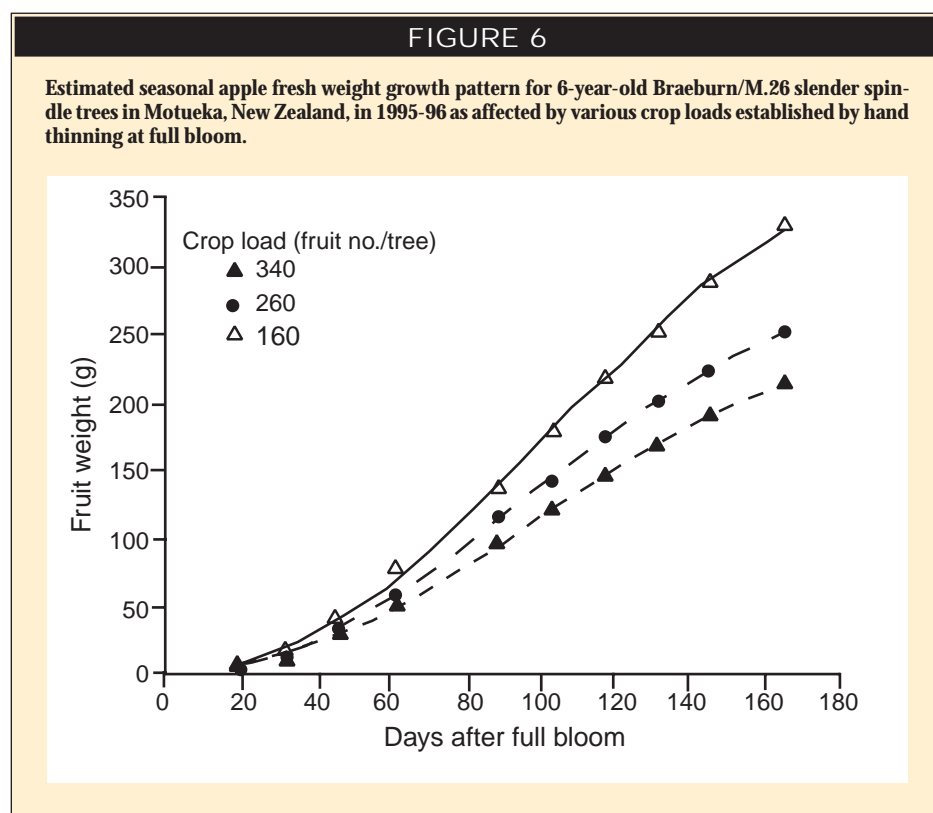
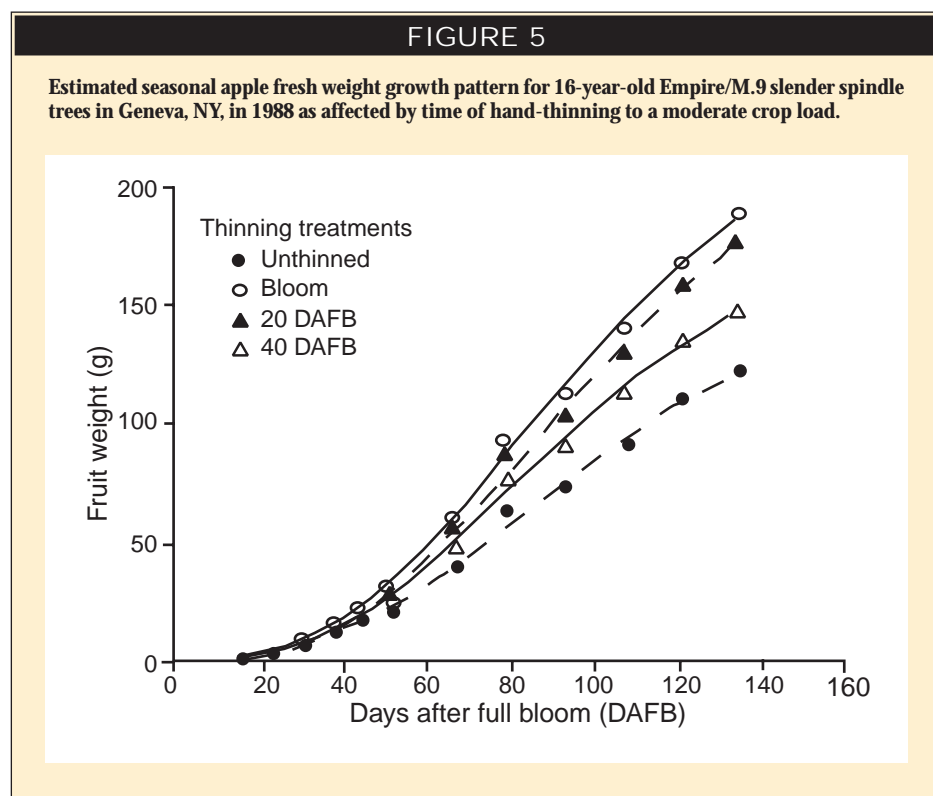
Trees with low or no crop load can be rejuvenated to relatively high photosynthetic capacity in late season when presumably carbohydrate demand increases due to bud development and root growth. Leaves that are long-term shaded, however, show little photosynthetic recovery if re-exposed by canopy opening through tree training (e.g., branch positioning) or summer pruning (Lakso et al., 1989; Li and Lakso, unpublished).

Total respiration of healthy, well-supplied apple trees requires about 15% of the fixed carbon (Wünsche and Palmer, unpublished data). Respiration rates differ with type of tissue (e.g., leaf, fruit, wood) and depend on time of year as temperature is a key driver for the substantial yet unavoidable carbon loss. Leaf and whole-canopy respiration typically shows an exponential temperature dependence with a more than 2.5-fold increase from 15 to 25°C (Fig. 4). At any given temperature, whole-canopy respiration is about two times higher than leaf respiration, again due to the inclusion of fruit and wood respiration along with the leaves.

SEASONAL LEAF AND FRUIT GROWTH PATTERN

The apple tree canopy is comprised of several shoot types that develop concurrently in the spring with a distinct growth pattern: a slight increase until about bloom, then a rapid rise up to 2 months after bud break and then termination of growth in mid-season (Wünsche et al., 1996). "Spurs" refer to short shoot complexes that devel-

op a rosette of primary leaves unfolding at bloom, followed by the development of typically one lateral "bourse" shoot that differs in length depending on growing conditions. Long "extension shoots" (>5 cm in length) and "short shoots" (<5 cm in length) develop from terminal or lateral buds on last year's extension shoots. The short shoots become either the spurs or extend to extension shoots in the following



season. Fruit typically develop on all shoot types. Spur-fruit, however, is often of greater size and improved quality than fruit borne directly on new axillary structures, e.g., one-year wood. The spur:shoot ratio depends mainly on rootstock/scion combination, pruning regime and growing conditions and has significant implications for light distribution within the canopy and carbohydrate partitioning patterns (see section on "Seasonal carbohydrate partitioning").

Fruit yield is a function of two components, fruit number and fruit size. Fruit number, as the primary factor, is mainly affected by flower bud formation and final fruit set. The growth of apple fruits occurs generally in two phases, the phase of cell division and cell expansion for approximately 4 to 5 weeks after full bloom, followed by the phase of only cell expansion for the remaining growing season (Bain and Robertson, 1951). In fruit growth studies on Empire it was found that different thinning times led to differences in final fruit size that was closely associated with variation in cell numbers in the cortex rather than cell volume (Goffinet et al., 1995; Fig. 5). Flower thinning of Braeburn trees at different severities resulted in 50% heavier fruit in the low-cropping trees compared to the high cropping trees (Fig. 6).

It appears that short-term shade conditions at about 3 to 5 weeks after bloom may cause a deficit in the carbon availability to the fruits compared to the stronger

vegetative sinks (Lakso and Corelli Grappadelli, 1993; Bepete and Lakso, 1998). Ultimately the sink demand may be adjusted downward resulting from a reduction in fruit growth rate and cell division followed by either fruit abscission or reduced final fruit size at harvest (Byers et al., 1991, Ferree and Palmer, 1982; Lakso et al., 1989). At this time, maintaining the fruit growth rate at its potential by improved carbon availability to the fruits seems to be an important aspect to canopy management. Although mid- or late-season shade due to canopy closure can be, depending on crop load and severity of shade, still detrimental, carbon deficits at that time seem to be relatively less significant to final fruit size (Lakso et al., 1989; 1995).

The fruit growth pattern suggests that 1) from the end of the cell division period until fruit harvest the fruit growth rate or the carbohydrate demand of the fruit (weight gain per day) remains essentially constant and 2) the slope of the linear phase depends on accumulation of cell numbers during the earlier exponential phase.

These results indicate that practices that increase the fruit's ability to produce cells after bloom have a much greater relative effect on final fruit size than practices later in the season. The challenge for the grower remains to adjust the crop load of the trees during the early cell division period so that an optimum distribution of commercially acceptable fruit sizes can be produced.

SEASONAL CARBOHYDRATE PARTITIONING

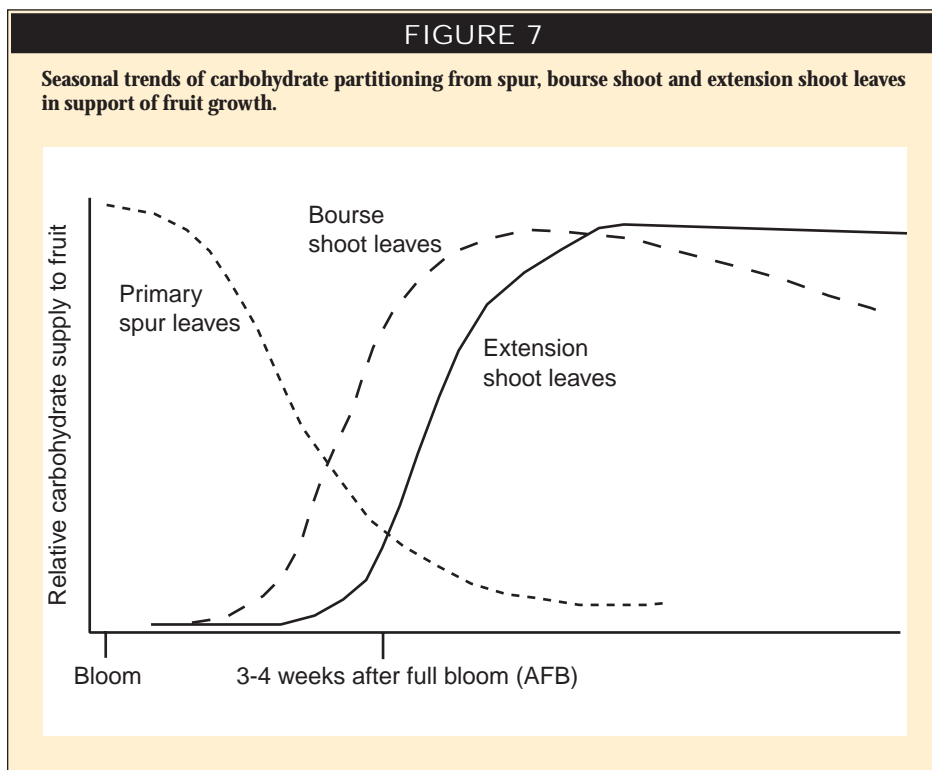
We have seen that apple yield depends on tree light interception, carbon fixation and early fruit growth which, in turn, depends on the partitioning of available carbohydrates into fruit versus vegetative tissues. The seasonal trend of carbohydrate partitioning from spurs, bourse shoots and extension shoot leaves in support of fruit growth is shown in Figure 7.

At about bloom time a shift occurs from the dependence on storage materials to current year's photosynthates. Thus the primary spur leaf area becomes the primary source of carbohydrates for fruit growth (Hansen, 1971).

Fruit development in the first 3 to 5 weeks after full bloom, which is critical in determining potential fruit size and final fruit set, appears to be essentially supported by carbohydrate supply from spur leaves, whereas actively growing extension shoots utilize the synthesized carbohydrates for their own development (Corelli Grappadelli et al., 1994; Hansen, 1971; Lakso, 1994; Lakso et al., 1989). Limiting incident light due to either cloudiness or shade at that time period alters the carbohydrates distribution, resulting in a greater relative retention of assimilates in vegetative sinks and thus a reduction in carbohydrate availability to the fruitlets. Furthermore, the carbohydrate export pattern of spurs supporting fruit growth seems to be relatively localized at that stage. If fruit demand for carbohydrates exceeds spur carbohydrate production (e.g., under high-cropping situation), fruit growth will be decreased due to the limited carbohydrate supply resulting in fewer fruit cells and/or increased fruit drop. Thus the carbohydrate availability to the developing fruit sinks, before export from extension shoots occurs, depends on the total photosynthetic production of the spur leaves, a function of spur number, spur leaf area and their photosynthetic rate (Tustin et al., 1992).

Mid-season and late-season carbohydrate supply is less likely to limit fruit growth due to reduced fruit numbers after final set, maximum light availability and interception by full canopies, carbohydrate export from terminated extension shoots and a more general carbohydrate distribution pattern. Final fruit growth before harvest may be limited by total tree carbohydrate production in climates with shorter seasons due to reduced light and temperature (Lakso and Corelli Grappadelli, 1993) and canopy management practices such as summer pruning (Li and Lakso, unpublished).

The lowered productivity at high total



light interception (Fig. 1; Wünsche and Lakso, 2000) then must be due to excessive extension shoot growth on the outside of the tree canopy which captures a disproportionate amount of sunlight. The fruit-bearing spurs on 2-year and older wood inside the tree canopy are shaded under these circumstances and consequently this leads to less carbohydrate partitioning toward the fruits, followed by smaller fruit growth rates, fruit abscission, and poor flower bud formation and fruit set (Lakso et al., 1989; Wünsche et al., 1996).

Fruit yields are positively related to spur leaf light interception (Fig. 8) and this emphasizes the importance of exposure of the spur leaf area to the efficiency of conversion of intercepted light into fruit yield. Canopy management should emphasize the development and maintenance of open, spur-rich tree canopies that intercept a high percentage of the light with the spur canopy.

In comparison, yields are negatively or curvilinearly correlated to extension shoot light interception (Fig. 8; Wünsche and Lakso, 2000). The importance of extension shoots for canopy development in young orchards and for late season support of fruit growth, especially in heavily cropping trees, should not be ignored.

IMPORTANCE TO TREE DESIGN AND CANOPY MANAGEMENT

A better understanding of the role of light interception/distribution in the variation in yield and fruit quality is needed to optimize orchard and tree design and canopy management. Knowledge of how and when to manipulate sunlight exposure to support optimal fruit development will allow the fruit grower to target his/her canopy management strategy to produce the desired canopy exposure patterns at the proper time.

Canopy management practices for maximizing yield and fruit quality should focus on several approaches:

1. Open, well-exposed canopies with high amounts of sunlight captured by spur leaves are needed early in the growing season since it appears that fruit yield depends primarily on early spur canopy light microclimate.

2. Avoid canopy closure until at least 4 to 6 weeks after full bloom to prevent a shade-induced reduction of fruit growth.

3. Continuous exposure appears to be needed for the development of vigorous and productive spur complexes and to allow good exposure of spurs for flower

bud development. Opening up closed canopies by late summer pruning may help fruit color but will not reverse detrimental effects on fruit growth and internal fruit quality of excessively dense early-season canopies.

Implications for pruning and training for establishing open, well-exposed tree canopies are as follows:

1. Pruning and training should be done each year, because it appears that fruit yield differences are a multiple season effect, yet fruit quality differences are due to current season growing conditions. Dormant pruning should ensure open canopies in early season.

2. Limit the number and vigor of competing extension shoots by a) thinning cuts rather than excessive heading cuts, b) pruning lightly and c) using more horizontal branch positioning by spreading or tying down branches.

3. Summer pruning with thinning cuts or branch removal into older wood is useful to create gaps for light penetration in overly dense canopies.

4. Well-spaced branches or geometric tree forms that help ensure open canopies

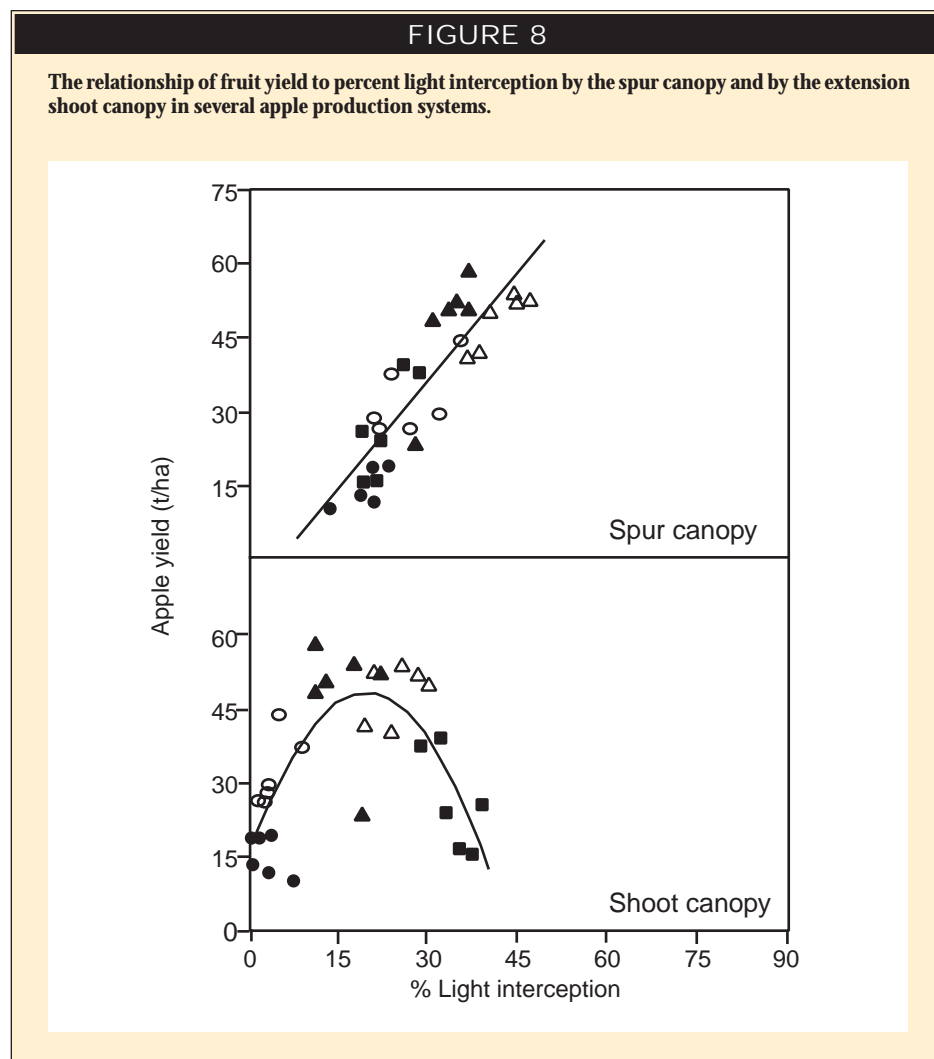
with improved light distribution (Y-, V-trellis, vertical Palmette, Palmette Leader, etc.) are useful.

CONCLUSIONS

Open tree canopies with the fruit-bearing spurs well exposed throughout the growing season provide not only the basis for high fruit numbers and large fruit sizes but also for good fruit color and quality. By comparison, dense tree canopies appear to be detrimental to both fruit yield and quality due to poor interior light distribution, especially if the canopy closes early in the growing season. Canopy management practices have to optimize tree canopy light interception/distribution and carbohydrate partitioning in support of potential fruit growth.

REFERENCES

- Bain, J.M. and R.N. Robertson. 1951. The physiology of growth in apple fruits. I. Cell size, cell number, and fruit development. *Austral. J. Sci. Res. Ser. B.* 4:75-91.
- Barritt, B.H. 1989. Influence of orchard system on canopy development, light interception and production of third-year Granny Smith apple trees. *Acta Hort.* 243:121-130.



- Bepete, M. and A.N. Lakso. 1998. Differential effects of shade on early season fruit and shoot growth rates in 'Empire' apple branches. *HortScience* 33:823-825.
- Byers, R.E., D.H. Carbaugh, C.N. Presley and T.K. Wolf. 1991. The influence of low light on apple fruit abscission. *J. Hort. Sci.* 66:7-17.
- Calleson, O. 1993. Influence of apple tree height on yield and fruit quality. *Acta Hort.* 349:111-115.
- Corelli Grappadelli, L., A.N. Lakso and J.A. Flore. 1994. Early season patterns of carbohydrate partitioning in exposed and shaded apple branches. *J. Amer. Soc. Hort. Sci.* 119:596-603.
- Faust, M. 1989. *Physiology of Temperate Zone Fruit Trees*. Wiley-Interscience, New York.
- Ferree, D.C. and J.W. Palmer. 1982. Effect of spur defoliation and ringing during bloom on fruiting, fruit mineral level, and net photosynthesis of 'Golden Delicious' apple. *J. Amer. Soc. Hort. Sci.* 107:1182-1186.
- Gifford, R.M. and C.L.D. Jenkins. 1982. Prospects of applying knowledge of photosynthesis toward improving crop production, p. 419-457. In: *Photosynthesis*, Govindjee (ed.). Academic Press, New York.
- Goffinet, M.C., T.L. Robinson and A.N. Lakso. 1995. A comparison of 'Empire' apple fruit size and anatomy in unthinned and hand-thinned trees. *J. Amer. Soc. Hort. Sci.* 70:375-387.
- Hansen, P. 1971. 14C-studies on apple trees. VII. The early seasonal growth in leaves, flowers and shoots as dependent upon current photosynthates and existing reserves. *Physiol. Plant.* 25:469-473.
- Hansen, P. 1977. Carbohydrate allocation, p 247-259. In: *Environmental Effects on Crop Physiology*, J.J. Landsberg, C.V. Cutting (eds.). Academic Press, London.
- Jackson, J.E. 1978. Utilization of light resources by high density planting systems. *Acta Hort.* 65:61-70.
- Jackson, J.E. 1980. Light interception and utilization by orchard systems. *Hort. Rev.* 2:208-267.
- Jones, H.G. 1992. Photosynthesis and respiration, p. 163-214. In: *Plants and Microclimate*, H.G. Jones (ed.). Cambridge University Press, Cambridge.
- Lakso, A.N. 1994. Apple, p. 3-42. In: *Environmental Physiology of Fruit Crops*, B. Schaffer and P.C. Andersen (eds.). Vol. I, Temperate Fruits. CRC Press, Boca Raton, Fla.
- Lakso, A.N. and L. Corelli Grappadelli. 1993. Implications of pruning and training practices to carbon partitioning and fruit development in apple. *Acta Hort.* 332:231-240.
- Lakso, A.N., T.L. Robinson and R.M. Pool. 1989. Canopy microclimate effects on patterns of fruiting and fruit development in apples and grapes, p. 263-274. In: *Manipulation of Fruiting*, C.J. Wright (ed.). Butterworths, London.
- Lakso, A.N., L. Corelli Grappadelli, J. Barnard and M.C. Goffinet. 1995. An exponential model of the growth pattern of the apple fruit. *J. Hort. Sci.* 70:389-394.
- Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. *Phil. Trans. Roy. Soc. Lond. B.* 281:277-294.
- Palmer, J.W. 1988. Annual dry matter production and partitioning over the first five years of a bed system of Crispin/M.27 apple trees at four spacings. *J. Appl. Ecol.* 25:569-578.
- Palmer, J.W. 1989. Canopy manipulation for optimum utilization of light, p. 245-262. In: *Manipulation of Fruiting*, C.J. Wright (ed.). Butterworths, London.
- Palmer, J.W., R. Giuliani and H.M. Adams. 1997. Effect of crop load on fruiting and leaf photosynthesis of 'Braeburn'/M.26 apple trees. *Tree Physiol.* 17:741-746.
- Robinson, T.L. and A.N. Lakso. 1991. Bases of yield and production efficiency in apple orchard systems. *J. Amer. Soc. Hort. Sci.* 116:188-194.
- Robinson, T.L., E.J. Seeley, B.H. Barritt. 1983. Effect of light environment and spur age on 'Delicious' apple fruit size and quality. *J. Amer. Soc. Hort. Sci.* 108:855-861.
- Scurlock, J.M.O., S.P. Long, D.O. Hall and J. Coombs. 1985. Introduction, p. xxi-xxiv. In: *Techniques in Bioproductivity and Photosynthesis*, J. Coombs, D.O. Hall, S.P. Long, J.M.O. Scurlock (eds.). Pergamon Press, Oxford.
- Tustin, S., L. Corelli Grappadelli and G. Ravaglia. 1992. Effect of previous-season and current light environment on early season spur development and assimilate translocation in 'Golden Delicious' apple. *J. Hort. Sci.* 67:351-360.
- Verheij, E.W.M. and F.L.J.A.W. Verwer. 1973. Light studies in a spacing trial with apple on a dwarfing and semi-dwarfing rootstock. *Scientia Hort.* 1:25-42.
- Wagenmakers, P. 1989. Productivity growth and light interception in the ISHS planting systems trial in the Netherlands. *Acta Hort.* 243:249-252.
- Wagenmakers, P.S. 1991. Planting systems for fruit trees in temperate climates. *Crit. Rev. Plant Sci.* 10:369-385.
- Wagenmakers, P.S. and O. Callesen. 1995. Light distribution in apple orchard systems in relation to production and fruit quality. *J. Hort. Sci.* 70:935-948.
- Wünsche, J.N., A.N. Lakso, T.L. Robinson, F. Lenz and S.S. Denning. 1996. The bases of productivity in apple production systems: The role of light interception by different shoot types. *J. Amer. Soc. Hort. Sci.* 121:886-893.
- Wünsche, J.N. and A.N. Lakso. 2000. The relationship between leaf area and light interception by spur and extension shoot leaves to apple orchard productivity. *HortScience* in press.
- Wünsche, J.N., D.H. Greer and J.W. Palmer. 2000. Effects of crop load on fruiting and gas-exchange characteristics of 'Braeburn'/M.26 apple trees at full canopy. *J. Amer. Soc. Hort. Sci.* 125:93-99.