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The Bases of Productivity in Apple Production Systems: The Role of Light Interception by Different Shoot Types

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Abstract. **Although apple (*Malus domestica* Borkh.) system yield differences are generally related to whole-canopy light interception, this study tested the hypothesis that these orchard yields are related primarily to total light intercepted by the spur canopy. Seasonal leaf area development of different shoot types, exposed bourse shoot leaf net photosynthesis, fruit growth, whole canopy light interception (by image analysis of fisheye photographs) and relative light interception by different shoot types (by a laser assisted canopy scanning device) were estimated within four 14-year-old 'Empire' apple production systems (slender spindle/M.9, central leader/M.7, central leader/M.9/MM.111 and Y-trellis/M.26). The final LAI values were CL/M.7 = 1.8, CL/9/111 = 2.3, SS/M.9 = 2.6 and Y/M.26 = 3.6. Exposed leaf net photosynthesis showed few differences and was not dependent upon the production system. Yields of the pyramidal shaped tree forms were 40 to 42 t·ha^{-1} while Y-trellis produced 59 t·ha^{-1}, with similar fruit sizes. Again, yields were primarily related to the percentage of light intercepted by the whole canopy, 48% to 53% for conic forms versus 62% for the Y-trellis system. Laser analyses showed that the Y-trellis system intercepted about 20% to 30% more light with the spur canopy than the conic tree forms, supporting the hypothesis. Yields were better correlated with spur canopy LAI and spur canopy light interception than with extension shoot canopy LAI and light interception.**

The net total dry matter productivity of apple orchard systems is a function of light availability, light interception, photosynthesis, and respiration. Incident solar radiation is determined primarily by the climate and thus is independent of the production system. The amount of photosynthetic photon flux (PPF, 400 to 700 nm) intercepted by an apple planting, however, depends primarily on orchard design, leaf area index and the length of the growing season, various factors that have been well researched over the past 20 to 25 years (Jackson, 1980; Jackson and Palmer, 1972; Lakso, 1994; Palmer, 1981, 1989; Robinson et al., 1991; Wagenmakers, 1991; Wertheim, et al. 1986). The proportion of intercepted photosynthetic energy that is converted into biomass relates to photosynthesis rates and leaf area. Because the maximum photosynthesis rates per unit leaf area are similar for healthy, well-maintained apple orchards with different yields (unpublished data), photosynthesis rates do not seem to be a primary factor governing variations in productivity. However, variations in leaf area and thus whole-canopy photosynthesis appear to be more important. Respiratory losses as required for growth and maintenance of apple tissues constitute a potentially substantial, but poorly documented, limitation on orchard productivity (Lakso, 1994). Of these four key components, light interception (light is used in a more general sense, but it always refers to the interception of PPF as used in legends of tables and figures) as related to whole canopy photosynthesis appears to be 1) a major factor limiting total orchard productivity and 2) via orchard/tree design and canopy display, the only manageable process in influencing potential productivity.

Then, why are certain apple orchard systems more productive than others in a given environment with similar fertility and water? Considerable research has gone into the identification of the bases of productivity in different apple orchards. Early observations suggested that perhaps tree density, percent ground cover, canopy volume or tree surface area may be related to orchard productivity. These factors correlate to tree size, tree mass or leaf area in many orchards; however, these correlations do not hold for all tree shapes or all types of canopy management (Robinson et al., 1991). Furthermore, several studies on orchard productivity have shown close relationships between fruit yield and seasonal total leaf area (Barritt, 1989; Palmer, 1988). However, a much more biologically sound principle found in the last 20 years is that total dry matter

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production as well as fruit yield of an orchard are related to the total amount of sunlight intercepted by the orchard (Jackson 1978; Monteith, 1977; Palmer, 1989; Robinson and Lakso, 1991; Wagenmakers, 1991).

However, increasing the potential orchard productivity by increasing light interception by higher and higher planting densities of very dense canopies does not necessarily lead to the highest yield and quality fruit. This is apparently because the partitioning of total dry matter into fruit requires specific light distribution within the canopy to the fruiting sites to assure good partitioning into the fruit. The amount of light available to the fruit-bearing spurs (the short shoot complex that typically bears the flower cluster, fruit and lateral bourse shoot; extension shoots refer to single vegetative long first year shoots; lateral short shoots refer to single vegetative shoots from lateral buds on previous season's growth that reach <5 cm in length) declines in dense canopies. Fruit yield potential is a function of flower numbers initiated the previous year. Flower bud initiation and development is dependent on light exposure of generally >30% of available light during the 2 months after bloom (Jackson, 1980; Palmer, 1989). Fruit number and fruit size appear to be also dependent on early season canopy light microclimate and assimilate partitioning patterns (Lakso, 1994; Lakso et al., 1989). Previous research has shown that during the first month after bloom, during the critical early growth period of fruit cell division, when final set and potential size are determined, the fruit growth is supported primarily by the spur canopy (Hansen 1971, 1977; Lakso et al., 1989; Lakso and Corelli Grappadelli, 1992; Corelli Grappadelli et al., 1994). Short-term shade at that time period causes an enhanced retention of assimilates in vegetative sinks, a reduction in carbohydrate availability to the fruitlets, limited fruit growth rates and eventually fruit shedding (Byers et al., 1991; Kondo and Takahashi, 1987; Lakso et al., 1989; Lakso and Corelli Grappadelli, 1992; Schneider, 1977). By comparison, growing extension shoots utilize their own photosynthates for their own growth for about 3 to 5 weeks after bloom and do not export carbohydrates into the fruits (Hansen 1971, 1977; Johnson and Lakso, 1986; Lakso et al., 1989; Lakso and Corelli Grappadelli, 1992; Corelli Grappadelli et al., 1994).

Based on the importance of the early spur leaf exposure, the following hypothesis was developed and tested: Although the potential productivity of a healthy well-maintained apple orchard is related to the total amount of sunlight intercepted by the orchard, the actual apple orchard productivity is limited primarily by the total light interception by the spur canopy versus the extension shoot canopy. With this hypothesis it was assumed there were no losses due to frost, pests, drought, etc. that would reduce bloom or leaf function. The hypothesis integrates the factors of spur number, spur leaf area and spur exposure.

Materials and Methods

Plant material and experimental design. The study was conducted in 1991 at the New York State Agricultural Experiment Station, Geneva, N.Y., in a 14-year-old apple production system comparison trial with a documented history of differing yields per hectare (Robinson and Lakso, 1991). The north–south oriented production systems (the combination of rootstock, tree spacing and training/pruning regime) with 'Empire' as the test cultivar were three conic forms and one Y-shaped form (system details in Table 1). Four representative trees within each of the four production systems were selected for sampling and data collection by using prior field data to determine trees that represented the long-term growth and yield behavior of the block and were healthy.

By including the four production systems it was intended to establish a wide range of varying leaf areas and light interception, not to emphasize a comparison of treatment means but to evaluate closely the relationship of yield to spur versus extension shoot light interception regardless of production system.

Leaf area. The numbers of flowering spurs, nonflowering spurs and terminal extension shoots were counted on the test trees at the tight cluster stage. After bloom when new shoots from lateral buds on the previous year's extension shoots had clearly differentiated into lateral extension shoots (>5 cm) versus lateral short shoots (<5 cm), separate counts were taken. Beginning on 7 May (full bloom), in each production system 12 representative samples of each shoot type were taken from adjacent trees of similar growth at 7- to 14-d intervals until the leaf area development had stopped in midsummer (Lakso, 1984; Palmer, 1987). The leaf area of unfolded leaves of each sample was measured with an image analysis system (Decagon AG Vision Color System, Decagon Devices, Pullman, Wash.). To estimate the leaf areas of the different types of growth per tree, the mean leaf area of each shoot type was multiplied by the tree counts of that shoot type and summed to estimate the total leaf area per tree. When multiplied by the number of trees per hectare, an estimate of the leaf areas for each shoot type and total leaf area per hectare was calculated. Total leaf area per hectare is expressed as leaf area index (LAI), defined as the area of leaves in square hectares per hectare land area of the orchard.

Leaf net photosynthesis. At 2-week intervals throughout the growing season leaf net photosynthesis was measured on each test tree using the ADC portable gas exchange system (model LCA-2 with broad leaf chamber; Analytical Development Co. Ltd., Hoddesdon, Herts., U.K.). Typically, healthy well-exposed bourse shoot leaves were measured with four readings per replicate tree (i.e., 16 per tree form) to determine if exposed leaf gas-exchange rates differed among the various production systems. The order of trees sampled were blocked over time and randomized within each production system. Readings were taken middays on sunny days to obtain light-saturated photosynthesis rates (Lakso and Seeley, 1978).

Relative light interception by different shoot types. A modification of the classic point quadrat method (Warren Wilson, 1965, 1967) and the laser technique (Vanderbilt et al., 1979) was utilized to estimate the relative light interception by various shoot types within apple tree canopies (Wünsche et al., 1996). The laser assisted canopy scanning device is based on aiming a laser beam as a simulated sunbeam in a set grid pattern into the tree canopy and recording the part of the canopy contacted by the beam. The ratio of contacts by a tree canopy component (i.e., spur leaf, extension shoot leaf, fruit or limb) to total tree contacts was used as an estimate of relative light intercepted by this canopy component. For laser positioning a stationary laser positioner was used as described in detail by Wünsche et al. (1996). The laser was attached to a positioner with two micrometer adjusting screws for vertical and horizontal laser rotation. The laser positioner was

Table 1. Characteristics of four 14-year-old 'Empire' apple production systems used in this study (modified from Robinson et al., 1991).

Production system	Rootstock/ Interstock	Spacing (m)	Trees/ ha	Mature tree ht (m)
Y–trellis	M.26	2.1 × 3.7	1283	2.5
Slender spindle	M.9	1.5 × 3.4	1957	2.2
Central leader/ interstem	MM.111/M.9	2.4 × 4.3	961	3.0
Central leader	M.7	3.7 × 6.1	450	4.5

mounted on the basket of a mechanical lift to elevate it and the operator above the orchard and was positioned on the south side of the test trees. The laser beams were shot into a representative portion of the whole tree canopy by using an 8×8-point square grid and canopies were analyzed at solar noon position. Sampling points were collected for each test tree at 3, 8, and 16 weeks after bloom at the same time when whole canopy light interception was estimated.

Total light interception. Whole canopy average daily percent light interception was estimated for each production system by hemispherical photography at 3 weeks after bloom during the critical, early fruit growth period of cell division, 8 weeks after bloom at the termination of leaf area development and shoot growth and 18 weeks after bloom after summer pruning was completed (Wünsche et al., 1995). Fisheye photographs were taken in uniform grid patterns underneath the tree canopies over the entire area allocated to each test tree with the number of photos per tree as follows for the various production systems: 15 for SS/M.9; 20 for Y/M.26; 25 for CL/9/111 and 35 for CL/M.7. Photographs were analyzed by digitizing the negative image and estimating both full sky diffuse and solar track direct radiation with an image analysis system (Gould DeAnza Image Analysis System) as described by Robinson and Lakso (1991).

Average daily percent light interception by the spur versus extension shoot canopy was estimated for each production system by whole canopy percent light interception, obtained via fisheye photography, and multiplied by the fraction of percent relative light interception by the spur versus extension shoot canopy, obtained via laser scanning. Joules of light interception by the whole canopy per hectare and by spur versus extension shoot canopy per hectare were estimated for each production system over 2 weeks at each of the three sampling times by multiplying the Joules of available light per hectare by the appropriate percent light interception at the particular sampling time, respectively. The available PPF flux at each 2-week period was obtained from the Experiment Station weather station near the experimental site, assuming 50% of total incident radiation was PPF (Robinson and Lakso, 1991). Mean seasonal percent and Joules of light interception by the whole canopy per hectare and by spur versus extension shoot canopy per hectare of each production system were calculated as averages of the three times when fisheye photographs were taken.

Yield and fruit weight. Fruit number and yield per tree were recorded at harvest on 23 Sept. 1991. Individual fruit weights and maximum diameter were measured on 15-fruit random samples from each test tree.

Statistical analysis. Regression analysis was utilized to evaluate relationships between yield, whole-canopy leaf area and light interception leaf area of different shoot types, and light interception by different shoot types. Analysis of variance (ANOVA) was performed using Tukey HSD multiple mean separation at the 5% significance level to compare the four production systems.

Results

Leaf area development. The development pattern of the spur canopy leaf area, extension shoot canopy leaf area and whole canopy leaf area was similar in all four production systems: a slight increase until about bloom, then a rapid rise up to 2 months after bud break and then termination of growth in the midseason (Fig. 1). At bloom all four production systems had about 20% of their final leaf area. Spur and extension shoot canopy development were relatively complete at about 2 months after bloom (Fig. 1 A and B). The abnormally early shoot termination was likely due to the dry spring in 1991. Leaf area differences among these mature production systems were surprisingly large. The Y-trellis had more than twice the leaf area of Central Leaders, about 40% more leaf area than Interstems and 30% more leaf area than Slender Spindle trees (Table 2, Fig. 1C). The final total LAIs were 3.6, 2.6, 2.2 and 1.7 for Y/M.26, SS/M.9, CL/9/111 and CL/M.7, respectively. The differences in leaf area between the Y-trellis system and the conic tree forms were due to a 1) higher number of each shoot type per hectare, except lateral extension shoot, and 2) larger leaf area per individual growth type. The final spur canopy LAI was 2.06 for Y/M.26 and 1.08

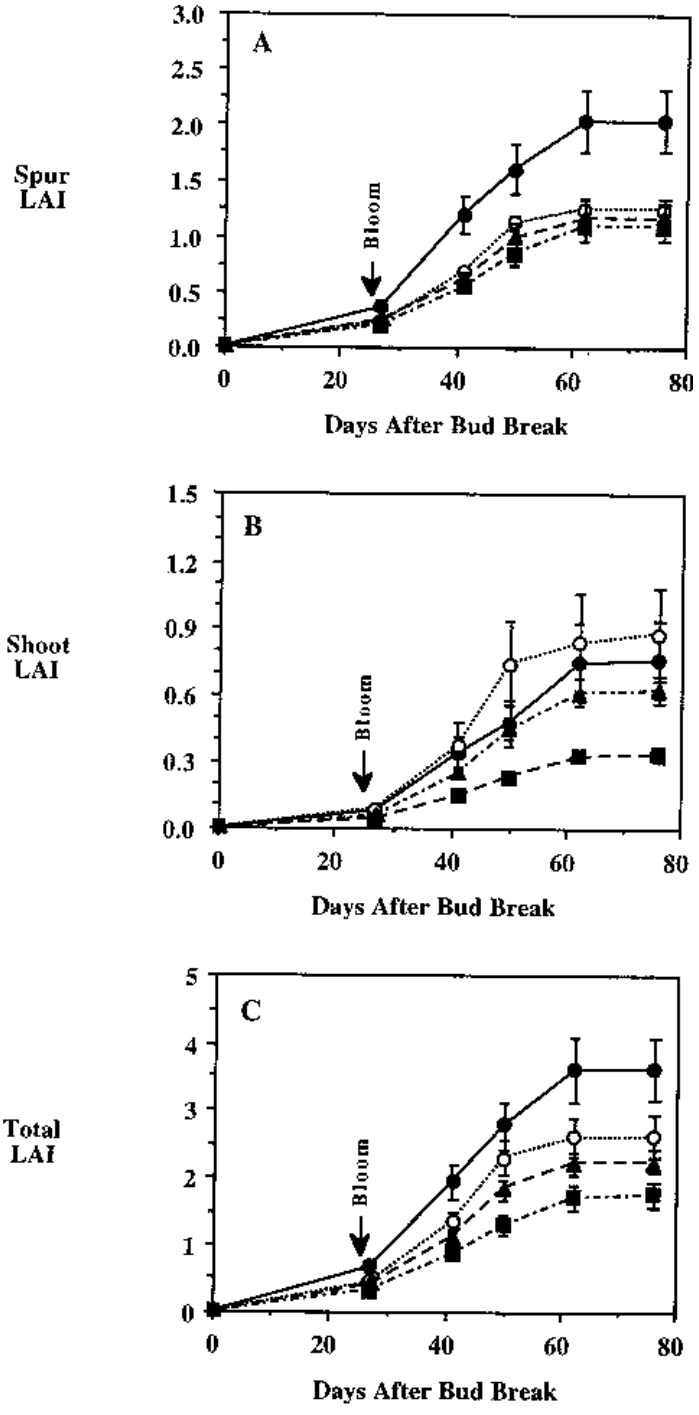

Fig. 1. Development patterns of spur leaf area index (LAI) (**A**), extension shoot LAI (**B**), and whole canopy LAI (**C**) in four 'Empire' apple production systems: ● Y/M.26, ❍ SS/M.9, ▲ CL/9/111, ■ CL/M.7. Data points at each date represent means SE, n = 4.

Table 2. Maximum leaf area indices (LAIs) of different shoot types in the fourteenth year of four 'Empire' apple production systems.

Production system	LAI				
	Spurs		Short shoot	Extension shoot	
	Fruiting	Nonfruiting	lateral	Lateral	Terminal
Y/M.26	1.58 a[z]	0.48 a	0.82 a	0.32 a	0.43 a
SS/M.9	1.01 ab	0.24 b	0.49 ab	0.51 a	0.36 ab
CL/9/111	0.97 b	0.20 b	0.43 ab	0.33 a	0.30 ab
CL/M.7	0.88 b	0.20 b	0.32 b	0.14 a	0.20 b

[z]Mean separation within each column by Tukey HSD test ($P \leq 0.05$) n = 4.

Table 3. Estimated mean seasonal relative light interception (%) by different tree canopy components in the fourteenth year of four 'Empire' apple production systems.

Production system	Relative light interception (%)			
	Spur	Lateral Short shoot	Extension shoot	Fruit or wood
Y/M.26	67 a[z]	10 b	9 a	14 a
SS/M.9	61 ab	14 ab	12 a	13 a
CL/9/111	62 ab	16 ab	9 a	13 a
CL/M.7	57 b	18 a	14 a	11 a

[z]Mean separation within each column by Tukey HSD test ($P \leq 0.05$) n = 5 (four trees measured at solar noon position at 3, 8, and 18 weeks after bloom by using a stationary laser positioner).

Table 4. Estimated mean seasonal light interception (%) by the whole canopy and by different shoot types per hectare in the fourteenth year of four 'Empire' apple production systems.

Production system	Photosynthetic photon flux interception (%)[z]			
	Total	Spur	Lateral short shoot	Extension shoot
Y/M.26	62.4 a[y]	42.9 a	7.1 a	7.1 a
SS/M.9	53.7 ab	35.0 b	6.2 a	7.0 a
CL/9/111	48.4 b	29.5 b	7.2 a	4.1 a
CL/M.7	46.7 b	29.3 b	5.6 a	6.2 a

[z]Total light interception per hectare, estimated by using fisheye photography/image analysis at 3, 8, and 18 weeks after bloom. Light interception by different shoot types per hectare, estimated by multiplying whole canopy value by shoot fractional light interception (laser scanning method at solar noon position) at 3, 8, and 18 weeks after bloom.
[y]Mean separation within each column by Tukey HSD test ($P \leq 0.05$) n = 4.

to 1.25 for the three conic shaped tree form systems (Table 2). Although not always considered very important in mature canopies, the lateral short shoot LAIs accounted for about 20% of the whole canopy leaf area in all production systems (Table 2).

Leaf net photosynthesis. Net photosynthesis rate of exposed bourse shoot leaves showed few differences among the production systems, varying from about 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in early summer to about 8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at harvest time. These values are similar to those reported earlier for apple (see compilation in Flore and Lakso, 1989). Thus, photosynthesis rate per unit leaf area did not appear to be the basis of observed variation in orchard productivity.

Relative light interception by different shoot types. Mean seasonal percent relative light interception was greatest by the spur canopy in all four production systems; however, there were some differences in the amount of relative spur leaf light interception among the systems varying from 67% with the Y/M.26 system to 57% with the CL/M.7 system (Table 3). The mean seasonal percent relative light interception by lateral short shoot and extension shoot leaves was only about 9% to 18% in the four production systems, as may be expected for mature trees with limited extension growth in a dry year.

Total light interception. Total light interception of each production system did not differ significantly at 3, 8, and 18 weeks after bloom, due to the early cessation of leaf area development and the minimal effect of summer pruning on light interception. There were, however, clear differences in mean seasonal whole canopy light interception among the four production systems. Similar to the report of Robinson and Lakso (1991), the Y/M.26 system had the highest average daily whole canopy light interception at 62%, about 15% to 25% higher than the three conic shaped tree forms (Table 4). Spur canopy light interception was the only component that varied significantly among the shoot type light interception. The Y/M.26 system spur canopy intercepted the most available light per hectare at 43% and was significantly higher than the conic tree forms (Table 4). Mean seasonal light interception by lateral short shoot and extension shoot leaves did not differ among the four production systems and amounted to only 5 to 7% (Table 4).

Yield and fruit weight. Yield per tree and number of fruit per tree were related to tree size. The CL/M.7 system had the highest yield per tree, followed by the Y-trellis, the Central Leader/Interstem and the Slender Spindle systems, respectively (Table 5). However, in yield per hectare the conic tree forms were similar at 40 to 42 $t \cdot ha^{-1}$, while Y-trellis produced 59 $t \cdot ha^{-1}$ but differences were not statistically significant (Table 5). Also there were no significant differences in final fruit size among the four production systems. Average final fruit size was only 62.3 mm which is not unusual for 'Empire', but was smaller than typically produced by these apple plantings (Robinson et al., 1991). This was due to an abnormally dry season and late season mite damage that limited final fruit sizing.

Discussion

The relation of leaf area to light interception. Differences in whole canopy percent light interception among the four production systems were related to orchard and tree design and to leaf area index. The specific geometric shape of the Y-hedgerow combined with the highest maximum leaf area index of 3.6 gave the greatest

Table 5. Number of fruit per tree, fruit weight and yield per tree and per hectare in the fourteenth year of four 'Empire' apple production systems.

Poduction system	Fruit/tree (no.)	Mean fruit wt (g)	Yield (kg/tree)	Yield ($t \cdot ha^{-1}$)
Y/M.26	503 b[z]	91.0 a	45.8 b	58.7 a
SS/M.9	218 c	95.4 a	20.8 c	40.7 a
CL/9/111	477 bc	92.5 a	44.1 b	42.4 a
CL/M.7a	951 a	97.6 a	92.9 a	41.8 a

[z]Mean separation within each column by Tukey HSD test ($P \leq 0.05$) n = 4.

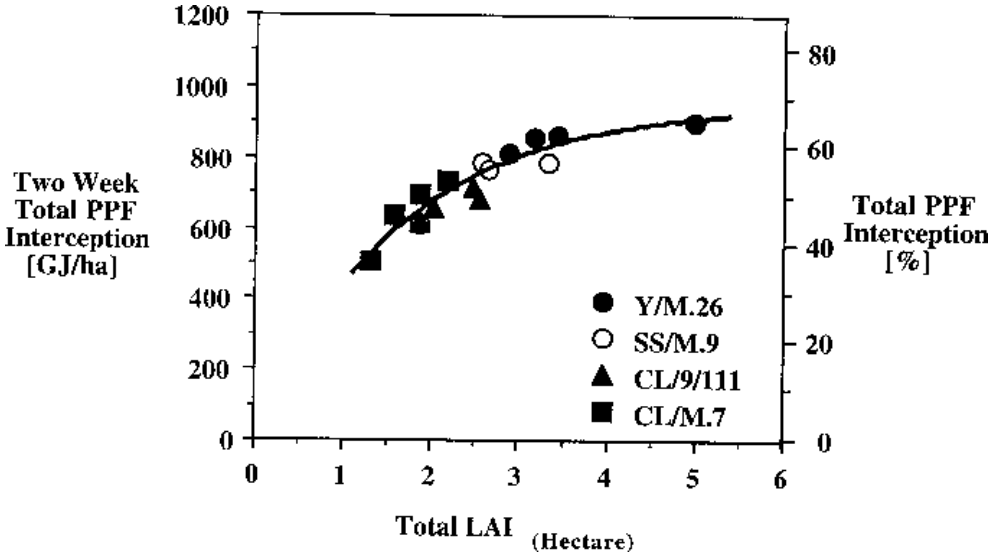

Fig. 2. The relationship of maximum seasonal whole canopy leaf area index (LAI) to mean seasonal whole canopy photosynthetic photon flux (PPF) interception (expressed as average energy intercepted over 2 weeks and average daily percentage available light intercepted at 3, 8, and 18 weeks after bloom) in four 'Empire' apple production systems. Exponential regression equations $r^2 = 0.88$, (n = 16) are total (GJ PPF) interception = 953.4 (1–exp{–581.7 × LAI/953.4}); total (% PPF) interception = 69.3 (1–exp{–42.3 × LAI/69.3}).

light interception. Due to the arms of the Y/M.26 system growing over the tractor alleyway and leaving just a 1-m gap between the tree rows, less incident light penetrated to the alleys (Robinson and Lakso, 1991). In the other three production systems with conic trees considerable light was lost due to the extensive, unproductive alleys between the rows. Even in the SS/M.9 system with a 30% higher tree density compared to the Y/M.26 system, only about 50% of the available light was intercepted, demonstrating the importance of canopy display rather than planting density.

When correlated to mean seasonal whole canopy light interception, the maximum seasonal whole canopy LAIs of the four 14-year-old 'Empire' production systems accounted for almost 90% of the variance (Fig. 2), confirming field observations (Barritt et al., 1991; Lakso, 1980; Palmer and Jackson, 1977) and computer model expectations (Palmer, 1981). All four systems showed the same relationship, but differed only in the total leaf area attained. The fitted exponential function showed little gain in light interception at higher LAIs due to the increasing self-shading at higher LAIs. Therefore, at low LAIs such as in young developing orchards where the trees have not yet filled the allotted land area or in mature orchards of trees with open canopies, increasing leaf area will increase light interception. But at high LAIs, as in older, dense orchard systems, further increases in leaf area will not lead to any increase in light interception, and only result in additional internal shading.

The relation of leaf area to fruit yield. As shown with leaf area and whole-canopy light interception, the relationship between total leaf area index and yield was also found to be exponential (Fig. 3A), although the relationship was not as good as with light interception. Previous reports by Barritt (1989) and Palmer (1988, 1989) reported close relationships between fruit yield and maximum seasonal whole canopy leaf area index in young apple plantings. Our findings in these mature planting systems were similar but with a r^2 of only about 50% (Fig. 3A). Increasing leaf area would not be expected to increase fruit yields if internal shading occurred and light interception stabilized. General observations and experiences indicate that increasing leaf area excessively not only does not increase yields, but many times decreases yields due to internal shading of fruiting sites that require good exposure for high productivity (Jackson, 1980).

The relationship of spur leaf area versus extension shoot leaf area on fruit yield has not been well researched, and so were examined in this study. The fruit yields produced in the four 'Empire' production systems were clearly better correlated to the corresponding maximum seasonal spur leaf area per hectare (r^2 = 56%) than to extension shoot leaf area per hectare (r^2 = 13%) (Fig. 3 B and C). Similar results have been found in rootstock trials (Strong and Miller-Azarenko, 1991) and in orchard systems trials (Sansavini and Corelli Grappadelli, personal communication). These results suggest the importance of spur leaf area presumably due to spur leaf light interception in support of fruit development. In these open canopies yields related well to spur leaf areas but that is not expected to always be true in denser canopies where spurs are shaded.

The relation of light interception to fruit yield. Several studies on apple orchard productivity have shown close relationships between fruit yield and seasonal total light interception (Barritt, 1989; Barritt et al., 1991; Jackson, 1978; Lakso, 1994; Palmer, 1988, 1989; Robinson and Lakso, 1989, 1991; Wagenmakers and Callesen, 1989; Wertheim et al., 1986). These previous findings are in good agreement with the present study where mean seasonal whole canopy light interception accounted for 62% of the variation in fruit yield with a linear relationship over the range of light interception encountered (Fig. 4). It is likely that there was no decline in yields at the higher light interception values due to the well-pruned nature of all trees with open, spurry canopies with minimal internal shading. A summary of reports on the relationship of yields to total light interception by Lakso (1994) showed several documented cases of lower yields in planting systems attaining light interception greater than about 60% of incident light. This suggests the importance of canopy light distribution and emphasizes the necessity to distinguish spur versus extension shoot leaf light interception and to examine their individual effects on fruit yield performance.

In these open, well-pruned tree canopies most of the light was intercepted by spur leaves (Table 4). Mean seasonal light interception by the spur canopy accounted for 64% and by the extension shoot canopy for only 4% of the variation in fruit yield across the four 'Empire' production systems (Fig. 5). These findings indicate that fruit yields were much better correlated to spur leaf light interception than to extension shoot leaf light interception.

Furthermore, the long term relationship of light interception and fruit yield was evaluated from 1988 to 1991 within the four 'Empire' apple production systems. Total spur and extension shoot canopy light interception was estimated by multiplying annual estimates of midseason whole canopy percent light interception within each production system (data from T.L. Robinson) by the fraction of the seasonal percent relative light interception by spur leaves and extension shoots leaves from the 1991 study. The calculations assumed that the patterns of relative light interception did not change over the 4-year period due to the uniformly pruned,

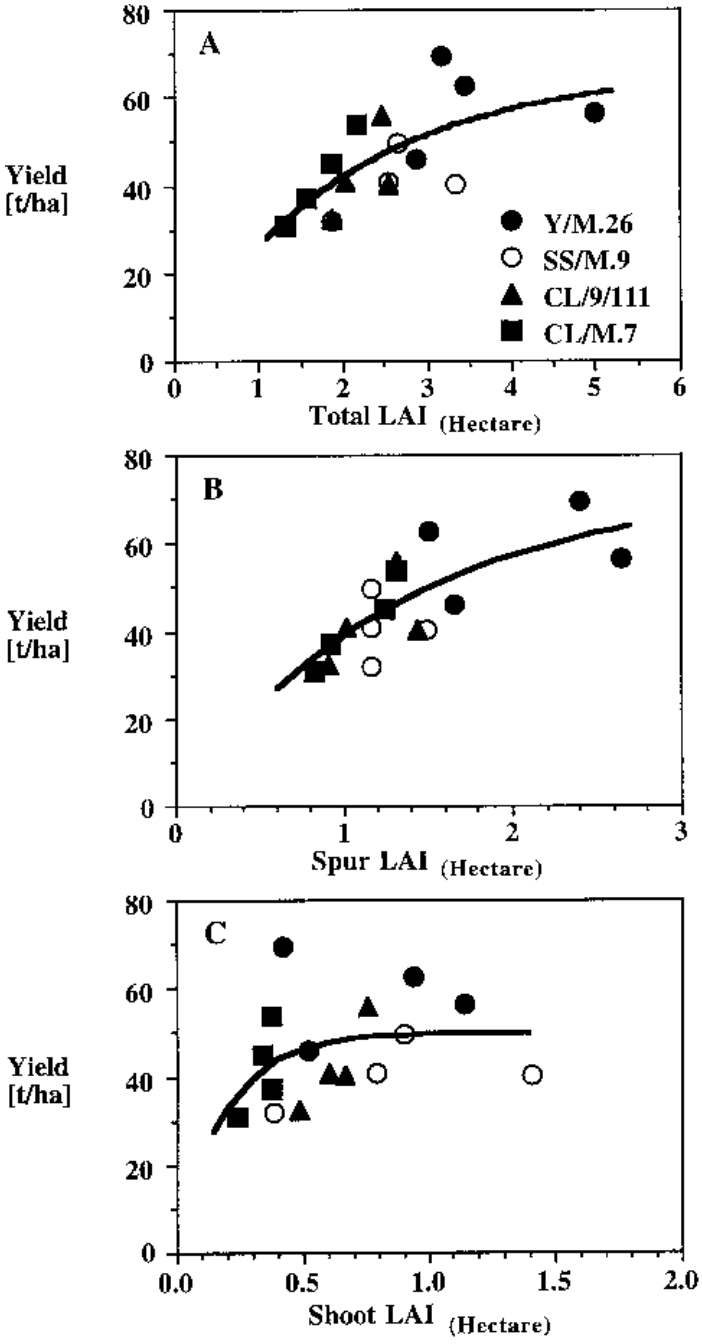

Fig. 3. The relationship of maximum seasonal whole canopy, spur and extension shoot leaf area index (LAI) to fruit yield in four 'Empire' apple production systems. Exponential regression equations (n = 16) are (**A**) total LAI: yield = 66.2 (1–exp{–32.9×LAI/66.2}), r^2 = 0.48; (**B**) spur LAI: yield = 73.4 (1–exp{–55.1×LAI/73.4}), r^2 = 0.56; (**C**) shoot LAI: yield = 49.9 (1–exp{–261.6 × LAI/49.9}), r^2 = 0.13.

open nature of the mature tree canopies. As with the single year data, the long-term fruit yields correlated much better to spur canopy light interception than to extension shoot canopy light interception although the r^2 values were slightly lower (Fig. 6). This suggests that the results of 1991 represent a consistent behavior over several years.

Our hypothesis assumes that the relationship between fruit yield and spur leaf light interception is linear; that is, yields would not be expected to decline in overly dense spur canopies with little extension shoot growth. This is assumed because in dense spurry canopies, despite the occurrence of mutual leaf shading, the available light will still be captured by leaves supportive of fruit growth. The intercepts of the regression lines of spur leaf light interception to fruit yield are near the origin suggesting a physiologically realistic relationship (Figs. 5 and 6). However, the relationship between extension shoot light interception and fruit yield suggests, perhaps not unreasonably, that significant yields could be obtained without any light interception by extension shoot leaves. Although this suggests that for quantitative yield alone, extension shoots may not be necessary, the importance of extension shoots for canopy development in young orchards and for late season support of fruit growth, especially in heavily cropped trees, cannot be ignored.

The results found here were on mature trees with most of the leaf area and fruit production on spurs. The results may be expected to differ somewhat if the fruiting habit and potential partitioning patterns were different, e.g., tip-bearing or bearing on lateral bloom on previous season's shoots. In general, higher levels of vigor would be expected to shift the balance of light interception from spurs toward extension shoots and reduce yields as seen in dense canopies with many extension shoots on the exterior.

Conclusions

The main conclusions from this study were as follows.

1) Exposed leaf net photosynthesis rate was not related to the observed yield variations of these apple production systems.
2) The Y/M.26 system differed from the conic systems by having significantly greater total and spur LAIs as well as greater total and spur canopy light interception per hectare. These gave a higher potential for greater fruit yields.
3) Actual fruit yields in 1991 and over a 4-year period were clearly better correlated to maximum seasonal spur LAI and spur canopy light interception than to maximum seasonal extension shoot LAI and extension shoot canopy light interception.
4) The findings support the stated hypothesis that in healthy apple orchards fruit yields are strongly related to spur leaf light interception and emphasize the importance of exposure of 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.
5) The nature of the uniformly well-pruned trees with open spurry canopies in all four production systems and the dry growing season did not provide the range of canopy exposure needed for a rigorous test of the hypothesis. Consequently it seems necessary to compare apple tree canopies that are being subjected to differential pruning and training methods to further evaluate the effect of spur versus extension shoot light interception on fruit yield.

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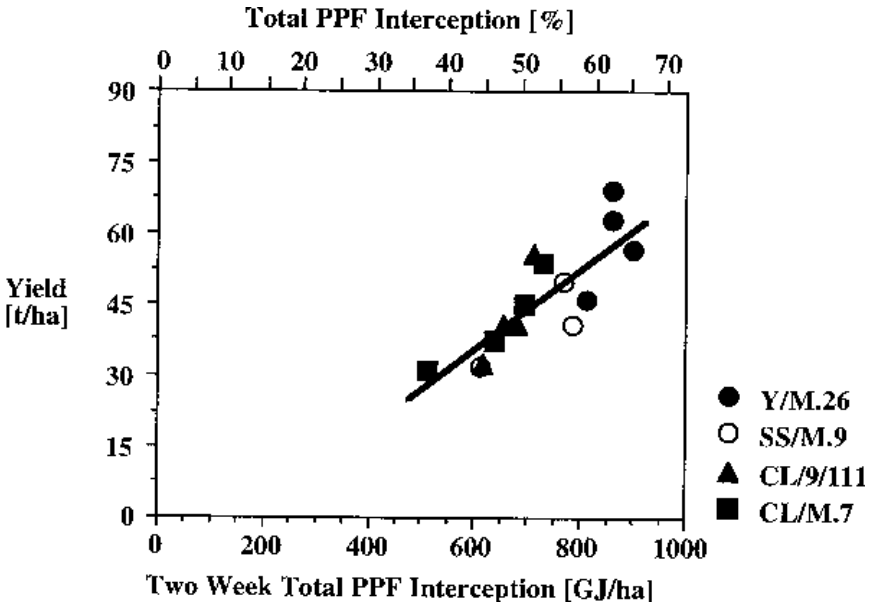

Fig. 4. The relationship of mean seasonal whole canopy photosynthetic photon flux (PPF) interception (expressed as average energy intercepted over 2 weeks and average daily percentage available light intercepted at 3, 8, and 18 weeks after bloom) to fruit yield in four 'Empire' apple production systems. Linear regression equations $r^2 = 0.62$, (n = 16) are yield = –16.4 + 0.086 (GJ PPF); yield = –16.4 + 1.185 (% PPF).

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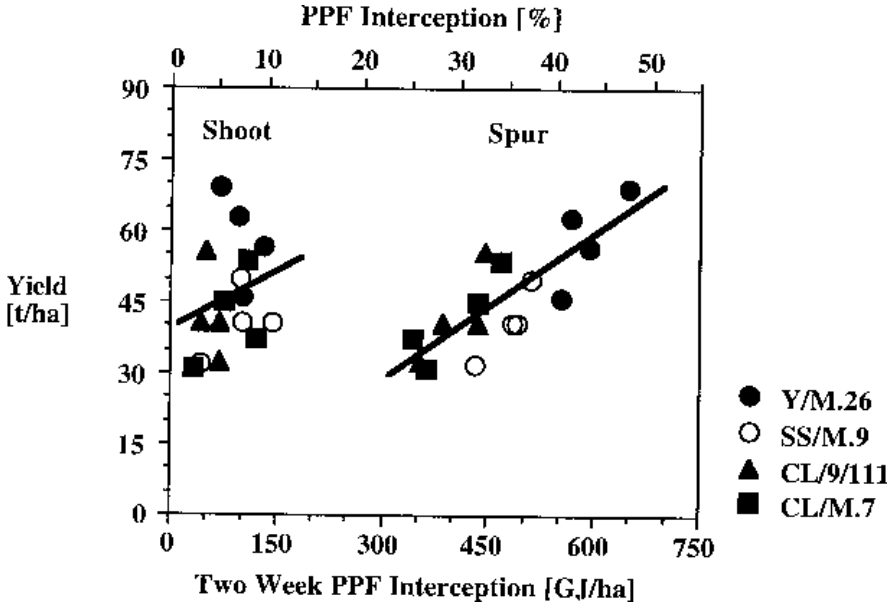
Fig. 5. The relationship of mean seasonal spur and extension shoot photosynthetic photon flux (PPF) interception (expressed as average energy intercepted over 2 weeks and average daily percentage available light intercepted at 3, 8, and 18 weeks after bloom) to fruit yield in four 'Empire' apple production systems. Linear regression equations (n = 16) are yield = –1.9 + 0.052 (GJ PPF by spurs), $r^2 = 0.64$; yield = –1.9 + 1.416 (% PPF by spurs), $r^2 = 0.64$; yield = 39.6 + 0.072 (GJ PPF by shoots), $r^2 = 0.04$; yield = 39.6 + 0.987 (% PPF by shoots), $r^2 = 0.04$.



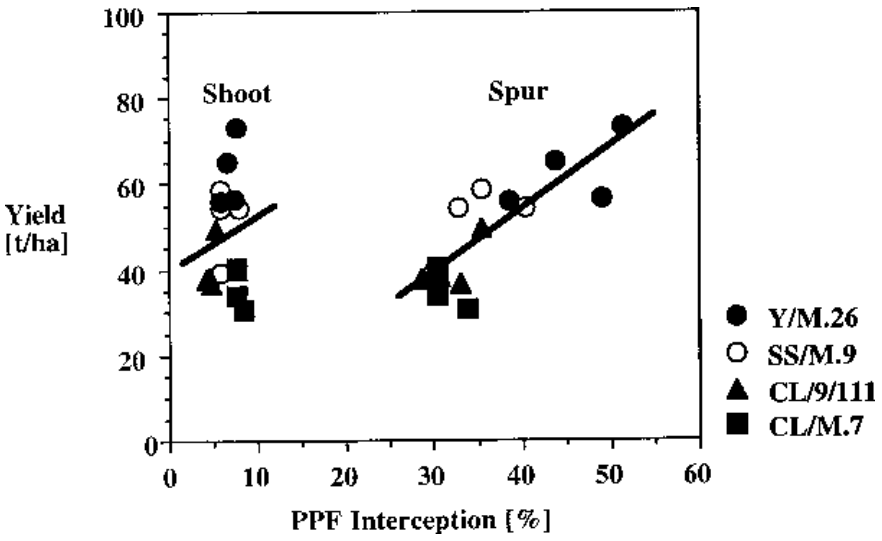


Fig. 6. The relationship of maximum seasonal spur canopy and extension shoot canopy percent photosynthetic photon flux (PPF) interception to fruit yield in four 'Empire' apple production systems from 1988–91. Total light interception values obtained for for each year were mulitplied by the fractional relative shoot interception values obtained in 1991. Linear regression equations (n = 16) are yield = 4.1 + 1.237 (% PPF by Spurs), $r^2 = 0.53$; yield = 39.8 + 1.252 (% PPF by Shoots), $r^2 = 0.02$.

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