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The Relationship Between Leaf Area and Light Interception by Spur and Extension Shoot Leaves and Apple Orchard Productivity

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Abstract. **The study evaluated the relationship of spur vs. extension shoot leaf area and light interception to apple (*Malus* ×*domestica* Borkh.) orchard productivity. Fifteen-year-old 'Marshall McIntosh'/M.9 trees had significantly greater leaf area and percentage of light interception at 3–5 and 10–12 weeks after full bloom (AFB) than did 4-year-old 'Jonagold'/ Mark trees. Despite significant increases in leaf area and light interception with canopy development, linear relationships between total, spur, and extension shoot canopy leaf area index (LAI) and 1) light interception and 2) fruit yield were similar at both times. Mean total and spur canopy LAI and light interception were significantly and positively correlated with fruit yield; however, extension shoot LAI and light interception were poorly correlated with yield. In another study total, spur and extension shoot canopy light interception varied widely in five apple production systems: 15-year-old central leader 'Redchief Delicious' MM.111, 15-year-old central leader 'Redchief Delicious' MM.111/M.9, 16-year-old slender spindle 'Marshall McIntosh' M.9, 14-year-old 'Jerseymac' M.9 on 4-wire trellis, and 17-year-old slender spindle 'MacSpur' M.9. Yields in these orchards were curvilinearly related to total and extension shoot canopy light interception and decreased when total light interception exceeded 60% and extension shoot interception exceeded 25%. Fruit yields were linearly and highly correlated (r^2 = 0.78) with spur light interception. The findings support the hypothesis that fruit yields of healthy apple orchards are better correlated with LAI and light interception by spurs than by extension shoots. The results emphasize the importance of open, well-illuminated, spur-rich tree canopies for high productivity.**

In young and mature apple orchards with open, well-exposed canopies, yield increases linearly with light, i.e., photosynthetic photon flux (*PPF*), interception (see compilation in Lakso, 1994). However, yields often decline in trees that develop dense canopies or in very dense planting systems (Jackson and Palmer, 1977; Lakso and Corelli Grappadelli, 1993; Lakso and Wünsche, unpublished data). Even though total light interception should be high in these situations, the lowered productivity is probably due to excessive growth of extension shoots (single, vegetative, long, first-year shoots). Such shoots are located on the exterior of the tree canopy and thus capture a disproportionate amount of the incident sunlight. The fruit-bearing spurs (short shoots that typically bear the flower cluster, fruit and bourse shoot), which usually develop on 2-year and older wood, are shaded; this leads to less carbohydrate partitioning toward the fruit, resulting in fruit abscission, smaller fruit and poor flower bud formation (Byers et al., 1991; Jackson and Palmer, 1977; Kondo and Takahashi, 1987; Lakso et al., 1989; Lakso and Corelli Grappadelli, 1993; Schneider, 1977).

Spur leaves provide the primary carbohydrate support for fruit development in the first 3–5 weeks after full bloom; this period is critical in determining potential fruit size and final fruit set. In contrast, leaves of actively growing extension shoots primarily support the growth of the shoot tip (Corelli Grappadelli et al., 1994; Hansen 1971; Lakso, 1994; Lakso et al., 1989; Lakso and Corelli Grappadelli, 1993; Tustin et al., 1992). Additionally, when clouds or shading limit incident light, shoot tip growth appears to have priority over fruit growth (Bepete and Lakso, 1998). During early fruit development, shading may limit yield by restricting carbohydrate flow to the fruit, and may also reduce flower initiation. Open canopies, in which fruit-bearing spurs are well-exposed throughout the growing season, produce many fruit that are large and highly colored (Barritt et al., 1991; Jackson, 1980; Palmer, 1989; Robinson and Lakso, 1989). By comparison, dense canopies appear to reduce both fruit yield and quality because of poor interior light distribution, especially if the canopy closes early in the growing season (Jackson and Palmer, 1977; Lakso et al., 1989; Lakso and Corelli Grappadelli, 1993; Robinson and Lakso, 1989).

Based on these findings, Wünsche et al. (1996) hypothesized that yield of an apple orchard is controlled primarily by the amount of sunlight captured by the spur rather than the extension shoot canopy; they first evaluated the hypothesis on four mature 'Empire' apple production systems. Although the results supported the hypothesis, the healthy, well-pruned mature trees with open, spurry canopies used in that study did not provide the range of differences in spur vs. extension shoot light interception needed for a rigorous test of the hypothesis and an evaluation of the effect of time of light interception on fruit yield. Thus, the current study evaluated the importance to productivity of leaf area and light interception by spur vs. extension shoot canopies in healthy orchards having a greater range of differences in spur vs. shoot balance.

Materials and Methods

Experimental orchards. In 1992, trials were conducted within a 'Jonagold'/Mark orchard at the New York State Agricultural Experiment Station (NYSAES) and a 'Marshall McIntosh'/ M.9 commercial apple orchard, both located at Geneva, N.Y. (Table 1). Trees were trained as slender spindles and rows were oriented north-south. Within each production system, 15 representative trees were selected for uniformity in extension shoot : spur ratio. Data were collected for each sample tree within each production system.

In 1993, six representative trees within each of several commercial apple orchards with various cultivar/rootstock combinations (Table 1) were selected in the Central New York apple production region to compare trees having a range of light interception and relative canopy openness. The 'MacSpur' and 'Jerseymac' trees had extremely high vigor and dense canopies because of a strong development of extension shoots in early season. The 'Redchief Delicious' trees were

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Table 1. Characteristics of several apple production systems used for the studies in 1992 and 1993.

Cultivar	Training system	Rootstock	Spacing (m)	Trees (no./ha)	Year of planting
		1992 experiment:			
Jonagold	Slender spindle	Mark	1.7 × 4.0	1429	1988
Marshall McIntosh	Slender spindle	M.9	1.7 × 4.0	1429	1977
		1993 experiment:			
Redchief Delicious	Central leader	MM.111	6.1 × 8.0	205	1978
Redchief Delicious	Central leader	MM.111/M.9	3.0 × 5.5	606	1978
Jerseymac	4-wire trellis	M.9	2.1 × 4.0	1190	1979
MacSpur	Slender spindle	M.9	1.8 × 4.0	1389	1976
Marshall McIntosh	Slender spindle	M.9	1.7 × 4.0	1429	1977

low in vigor and had spurry, open canopies. The 'Marshall McIntosh' trees were moderate in vigor and extension shoot and spur growth were balanced. Data were collected for each sample tree within each production system.

In both years, the experimental design consisted of blocking for location, i.e., the selected cultivars were all in different orchard blocks. By including several scion/rootstock/training system/tree age combinations we intended to evaluate closely the relationship between yield and spur vs. extension shoot light interception regardless of "confounding" orchards effects.

Leaf area. Whole canopy leaf area was estimated only during the 1992 experiment using methods similar to those described by Lakso (1984), Palmer (1987), and Wünsche and Palmer (1998). The number of spurs and extension shoots were counted on each test tree at tight cluster stage. At 3–5 weeks after full bloom (AFB) and again at full canopy (10–12 weeks AFB), after the cessation of shoot growth and leaf area development, a total of 40 spurs and 25 extension shoots were randomly taken from adjacent trees of similar growth habit within each production system. The area of all unfolded leaves of each shoot was measured using an image analysis system (Decagon AG Vision Color System; Decagon Devices, Pullman, Wash.). Leaf areas on spur and extension shoots were estimated by multiplying the numbers of shoots and spurs by the average respective leaf area. Adding both leaf areas provided an estimate of total leaf area of the whole canopy. The leaf area per hectare for spurs and extension shoots and their sum were expressed as leaf area index (LAI), defined as leaf area per hectare (ha) of land area.

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 spur vs. extension shoot leaves. The laser-assisted canopy scanning device, as described by Wünsche et al. (1997), is based on directing a laser-simulated "sunbeam" in a grid pattern into the tree canopy and recording the part of the canopy [spur leaf, lateral short shoot (single vegetative shoot <5 cm in length from lateral buds on previous-season's growth) leaf, extension shoot leaf, fruit, and wood] contacted by the beam. The ratio of spur or extension shoot leaf contacts to total sampling points was used as an estimate of relative light intercepted by the spur and extension shoot canopies. Data for 54 sampling points were collected for each test tree at 3–5 and 10–12 weeks AFB.

Total light interception. Average daily percentage of light interception by the whole canopy was estimated at 3–5 weeks and 10–12 weeks AFB by instantaneous ceptometer (Decagon Devices) light measurements taken in a below-tree canopy grid pattern over the entire area allotted per test tree. The method used was similar to that described by Wünsche et al. (1995). For each tree, a set of 20 below-canopy readings, 10 on each side, and three open-sky readings were taken under cloudy, diffuse sky conditions. Average daily percentage of light interception by the spur vs. extension shoot canopy was estimated by multiplying the percentage of light interception by the whole canopy, as obtained via ceptometer, by the percentages of light interception by the spur vs. extension shoot canopy, as obtained via laser scanning. Average daily light interception ($J \cdot ha^{-1}$) by the whole canopy and by the spur and extension shoot canopy was estimated over a 2-week period at each of the two sampling times by multiplying the incident radiation ($J \cdot ha^{-1}$) by the appropriate percentage of light interception at each sampling time. The available photosynthetic photon flux (*PPF*) during each 2-week period was obtained from the weather station near the experimental sites, assuming that 50% of total incident radiation was *PPF* (Robinson and Lakso, 1991).

Fruit yield. Fruit number and yield per tree were recorded in all systems at the commercial harvest periods for each cultivar (mid-August for 'Jerseymac', mid-September for 'Marshall McIntosh' and 'MacSpur', early October for 'Delicious', and mid-October for 'Jonagold').

Statistical analysis. Analysis of variance (ANOVA) using Genstat (Rothamsted Experimental Station, U.K.) was performed to analyze the effect of production system on yield and on total, spur, and extension shoot LAI, and light interception at 3–5 and 10–12 weeks AFB, respectively. Regression analysis was utilized to evaluate relationships between yield and leaf area and yield and light interception. The commercial orchards were selected to provide a wide range of variability in yield and spur-to-shoot light interception needed to test the hypothesis that yields were primarily related to spur canopy light interception.

Results and Discussion

1992 experiment. Total and spur canopy LAI were significantly higher in the 'Marshall McIntosh'/M.9 than in the 'Jonagold'/Mark production system at 3–5 and 10–12 weeks AFB (Table 2). Extension shoot canopy LAI, however, did not differ significantly between the two production systems at either sampling time. At both sampling times the whole canopy and spur leaves of the 'Marshall McIntosh'/M.9 trees intercepted significantly more light than did those of the 'Jonagold'/Mark trees, whereas light interception by extension shoot leaves was similar in both systems (Table 2).

Total, spur, and extension shoot canopy LAI in both systems increased significantly between 3–5 and 10–12 weeks AFB, leading to significant increases in light interception by the whole canopy and extension shoot canopy, but not by spur leaves, even though spur LAI increased 40%. This indicates that the extension shoots developing on the exterior of the canopy prevented any additional light penetration to the spur leaves within the canopy.

Yield per tree and per hectare of the mature 'Marshall McIntosh'/M.9 trees was about twice that of the young 'Jonagold'/Mark trees (Table 3).

1993 experiment. Light interception in all production systems did not change significantly between 3–5 and 10–12 weeks AFB (data not shown) because of a rapid increase in leaf area, followed by an early cessation of shoot growth as a result of a dry and warm growing season. There were, however, significant differences among the five production systems in percentage of light interception by total, spur, and extension shoot canopies (Table 4). Average daily percentage of total light interception varied from 27% in the widely spaced 'Redchief Delicious'/MM.111 system to 75% in the 'MacSpur'/M.9 system. In the spurry 'Redchief Delicious' canopies, more of the available light was intercepted by spur than by extension shoot leaves, whereas the reverse was true in the 'MacSpur'/M.9 canopies. Yield of the various production systems provided a desired range for evaluating the interactions between yield and light interception (Table 3).

The relationship between leaf area and fruit yield. The relationship between leaf area and fruit yield was expected to be curvilinear (Wünsche et al., 1996), paralleling the relationship between leaf area and light interception (Palmer, 1989; Wünsche et al., 1996). As leaf area increases, therefore, the increase in light interception or potential yield declines because of increases in mutual shading among the leaves. Despite the fact that continued increases in yields are not expected at very high LAI, the relationship between whole canopy leaf area and yield in the 1992 study

Table 2. Estimated total, spur, and extension shoot canopy LAI, and average daily percentage of *PPF* interception at 3–5 and 10–12 weeks AFB in the 1992 growing season in a 'Jonagold'/Mark and a 'Marshall McIntosh'/M.9 slender spindle apple production system.

Cultivar/	LAI			*PPF* interception (%)		
rootstock	Total	Spur	Shoot	Total	Spur	Shoot
	3–5 weeks AFB					
Jonagold/Mark	1.30	0.75	0.49	35.8	19.2	11.0
Marshall McIntosh/M.9	1.97***	1.33***	0.56NS	43.3***	28.1***	7.1*
$LSD_{0.05}$	0.094	0.074	0.068	1.93	1.32	1.46
	10–12 weeks AFB					
Jonagold/Mark	2.21	1.06	1.07	50.3	19.6	20.6
Marshall McIntosh/M.9	3.06***	1.84***	1.11NS	59.1***	31.3***	20.6NS
$LSD_{0.05}$	0.147	0.103	0.125	1.49	2.81	3.45

NS,*,***Nonsignificant or significantly different from 'Jonagold' at $P \leq 0.05$ or 0.001, respectively.

Table 3. Yield performance in several apple production systems in 1992 and 1993.

Cultivar/rootstock	Training system	Fruit (no./tree)	Yield (kg/tree)	Yield ($t \cdot ha^{-1}$)
	1992			
Jonagold/Mark	Slender spindle	76	22.0	31.5
Marshall McIntosh/M.9	Slender spindle	275z	42.0z	60.0z
$LSD_{0.05}$		11.3	1.56	2.23
	1993			
Redchief Delicious/MM.111	Central leader	411 ey	75.0 e	15.4 a
Redchief Delicious/MM.111/ M.9	Central leader	267 c	53.0 d	32.1 c
Jerseymac/M.9	4-wire trellis	362 d	40.5 c	48.2 d
MacSpur/M.9	Slender spindle	137 a	19.2 a	26.6 b
Marshall McIntosh/M.9	Slender spindle	192 b	33.2 b	47.5 d
$LSD_{0.05}$		27.9	4.51	3.26

zSignificantly different from 'Jonagold' at $P \leq 0.001$.
yMean separation within columns by LSD, $P \leq 0.05$.

Table 4. Estimated mean daily percentage *PPF* interception at 3–5 and 10–12 weeks AFB of total, spur, and extension shoot canopies in five apple production systems in 1993.

Cultivar/rootstock	Training system	*PPF* interception (%)		
		Total	Spur	Shoot
Redchief Delicious/MM.111	Central leader	27.1 az	19.1 a	2.8 a
Redchief Delicious/ MM.111/ M.9	Central leader	34.1 b	26.5 c	3.9 a
Jerseymac/ M.9	4-wire trellis	72.7 d	41.7 e	24.5 c
MacSpur/ M.9	Slender spindle	74.8 e	22.3 b	32.8 d
Marshall McIntosh/ M.9	Slender spindle	47.9 c	32.4 d	14.7 b
$LSD_{0.05}$		2.02	1.68	1.61

zMean separation within columns by LSD, $P \leq 0.05$.

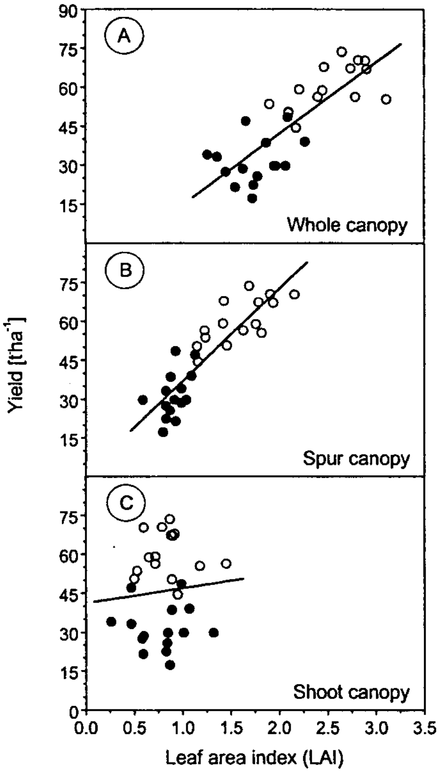

Fig. 1. The relationship between fruit yield ($t \cdot ha^{-1}$) and mean whole canopy, spur canopy, and extension shoot canopy LAI (average for 3–5 and 10–12 weeks AFB) in a 4-year-old 'Jonagold'/ Mark (●) and a 15-year-old 'Marshall McIntosh'/M.9 (○) slender spindle apple production system in 1992. Linear regression equations (n = 30) are: (A) Yield = −12.74 + 27.37 (total LAI), $r^2 = 0.656$; $P \leq 0.0001$; (B) Yield = 1.29 + 35.63 (spur LAI), $r^2 = 0.774$; $P \leq 0.0001$; (C) Yield = 41.12 + 5.75 (shoot LAI), $r^2 = 0.008$; $P \leq 0.643$.

appeared to be linear up to the LAI of 3 (Fig. 1A).

The relationships between total, spur, and extension shoot canopy LAI and fruit yield were similar at both sampling times, despite the increase in leaf area with canopy development (data not shown). Averaged over the two 2-week sampling periods, mean total and spur canopy LAI were significantly and positively correlated with yield, whereas the extension shoot LAI was not (Fig. 1 B and C). These results are similar to those in previous reports on apple, which indicated positive linear relationships between yield and leaf areas of the whole canopy and spurs (Barritt et al., 1991; Palmer, 1988, 1989; Wünsche et al., 1996); they also parallel data that indicate a better correlation of yield with spur leaf area than with extension shoot leaf area in apple trees on various rootstocks (Sansavini and Corelli Grappadelli, personal communication; Strong and Miller-Azarenko, 1991). Although the results reported here show a good correlation between spur LAI and fruit yield, observations from the field suggest that, with the same spur leaf area, a tree with heavy shading from exterior extension shoots will not yield as well as one with few extension shoots. Consequently, spur LAI may be a controlling factor in very open canopies, as found in young orchards, but not necessarily in denser canopies with many exterior extension shoots.

The relationship between light interception and fruit yield. Several studies on apple orchard productivity have revealed good relationships between yield and total light interception (Barritt, 1989; Jackson, 1978; Lakso, 1994; Palmer 1988, Robinson and Lakso, 1991; Wagenmakers and Callesen, 1989; Wertheim et al., 1986) or spur light interception (Wünsche et al., 1996). Our data support these findings. In 1992, the relationships between total, spur, and extension shoot canopy light interception and fruit yield were similar at both sampling times despite a significant increase in light interception with canopy development; thus the means for both times were plotted. Across both production systems, the mean total and spur canopy light interception were significantly and positively linearly correlated with yield, with r^2 values around 75%; however, the amount of available light captured by the extension shoot canopy was not correlated with yield (Fig. 2 A–C).

In the 1993, study the relationship between fruit yield and mean total light interception was curvilinear (Fig. 2D). The total light interception of the 'MacSpur'/M.9 system with dense canopies averaged ≈75%, but yield was only ≈20 $t \cdot ha^{-1}$. This low yield was probably a multiple-year effect of overly dense tree canopies and possible carry-over effects on: 1) flowering; 2) fruit development; or 3) both. Jackson and Palmer (1972) reported low productivity associated with very high light interception levels, and cited two cases where maximum total light interception of ≈80% was not associated with maximum yield. These findings agree with those of Wagenmakers (personal communication). Moreover, Verheij (1968) found that thinning-out of very dense orchards increased yield and fruit quality, although total light interception was presumably reduced. This probably resulted from improved light distribution patterns and better exposure of the spur canopy. A summary of reports on the

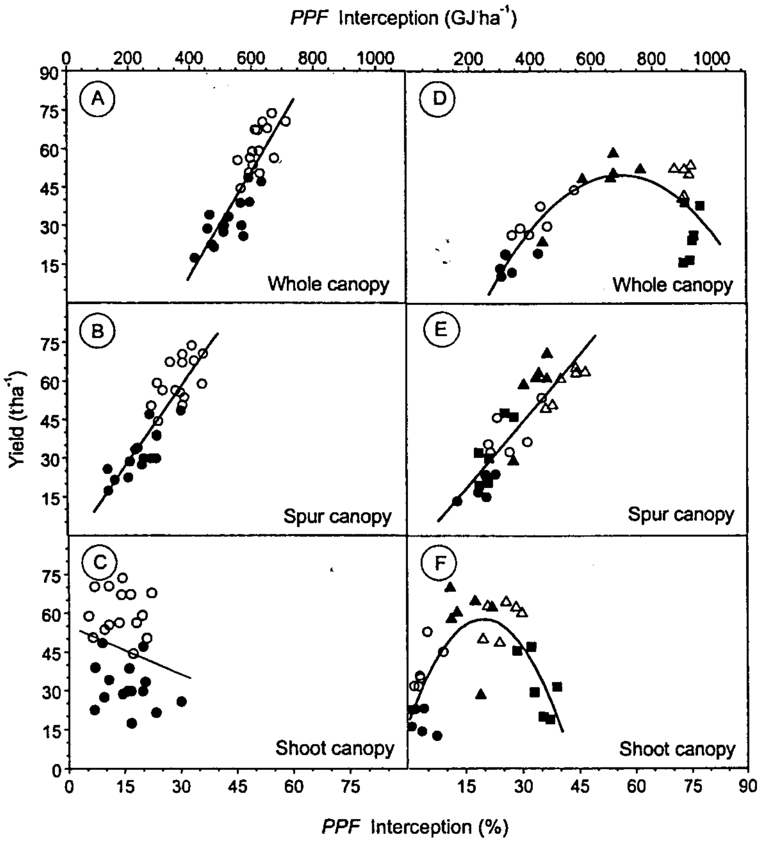

Fig. 2. The relationship between fruit yield (t·ha^{-1}) and mean whole canopy, spur canopy, and extension shoot canopy *PPF* interception (average energy intercepted over 2 weeks and average percentage of available light intercepted daily at 3–5 and 10–12 weeks AFB) in several apple production systems. *1992 growing season* (**A, B, C**): 4-year-old 'Jonagold' slender spindle/Mark (●) and 15-year-old 'Marshall McIntosh' slender spindle/M.9 (○). Linear regression equations (n = 30) are: (**A**) Yield = –70.97 + 2.48 [0.203] (% [GJ] PPF by canopy), r^2 = 0.744; $P \leq 0.0001$; (**B**) Yield = –5.47 + 2.09 [0.171] (% [GJ] *PPF* by spurs), r^2 = 0.769; $P \leq 0.0001$; (C) Yield = 55.01 – 0.62 [0.051] (% [GJ] *PPF* by shoots), r^2 = 0.048; $P \leq 0.243$. *1993 growing season* (**D, E, F**): 15-year-old 'Redchief Delicious' central leader/ MM.111 (●), 15-year-old 'Redchief Delicious' central leader/ MM.111/M.9 (○), 16-year-old 'Marshall McIntosh' slender spindle/ M.9 (▲), 14-year-old 'Jerseymac' 4-wire trellis/ M.9 (Δ), and 17-year-old 'MacSpur' slender spindle/M.9 (■). Regression equations (n = 30) are: (**A**) Yield = –69.83 + 4.26 [0.344] (% [GJ] PPF by canopy) –0.038 [–0.00025] (% [GJ] *PPF* by canopy)^2, r^2 = 0.600; $P \leq 0.0001$; (**B**) Yield = –7.09 + 1.44 [0.116] (% [GJ] *PPF* by spurs), r^2 = 0.779; $P \leq 0.0001$; (**C**) Yield = 15.64 + 3.32 [0.268] (% [GJ] *PPF* by shoots) –0.085 [–0.00055] (% [GJ] *PPF* by shoots)^2, r^2 = 0.547; $P \leq 0.0001$.

relationship between yields and total light interception by Lakso (1994) included several documented cases of low yields in planting systems in which light interception was ≥60% of incident light.

In agreement with our previous findings (Wünsche et al., 1996), a high proportion (78%) of the variation in fruit yield across the various production systems was explained by mean spur light interception (Fig. 2E). Note that the 'Jerseymac' SS/M.9 system was an exception, in that most (≈80%) of the fruit was born on lateral buds of last year's extension shoots. The fruit-bearing, lateral, short shoots, located on the outside of the canopy, intercepted ≈50% of the incident solar radiation, whereas the spur canopy intercepted only 15%. Therefore, to adjust for this difference, the light intercepted by leaves of short lateral shoots was added to that intercepted by the older spur leaves to give the "spur" light interception for this system. Despite reduced productivity at the high total light interception in the 'MacSpur'/M.9 system, the low light interception by the spur canopy corresponded well with low fruit yield and was comparable with the other systems (Fig. 2 D and E).

Yields were curvilinearly related to mean light interception by extension shoots (Fig. 2F), similar to the relationship between yield and total light interception. This indicates that increasing the amount of light intercepted by the extension shoots eventually reduces yields because of shading of fruiting sites within the canopy.

Conclusions

Clearly, apple fruit yields may be limited by many cultural practices (thinning, heavy pruning) and by environmental (frost, nutrient deficiency, water stress) and biotic stresses (arthropods, diseases, weeds). However, yields of healthy, well-maintained orchard systems still vary dramatically. The results of this study indicate that fruit yields among various scion/rootstock/system combinations were better correlated with LAI and light interception by the spur canopy than by the extension shoots. The fact that the results were consistent across a range of orchards strengthens the generality of the hypothesis we examined. The results emphasize the importance to cropping of having both high total and spur canopy light interception. The importance of extension shoots for canopy development in young orchards and for late-season support of fruit growth, especially in heavily cropped trees, however, should not be ignored. For long-term cropping, canopy management of apple cultivars with normal growth habit should emphasize the early-season development and midseason maintenance of open, well-illuminated, spur-rich canopies.

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