Summary The effect of two training systems (Central Leader with branch pruning versus Centrifugal Training with minimal pruning, i.e., removal of fruiting laterals only) on canopy structure and light interception was analyzed in three architecturally contrasting apple (Malus domestica Borkh.) cultivars: ‘Scarletspur Delicious’ (Type II); ‘Golden Delicious’ (Type III); and ‘Granny Smith’ (Type IV). Trees were 3D-digitized at the shoot scale at the 2004 and 2005 harvests. Shoots were separated according to length (short versus long) and type (fruiting versus vegetative). Leaf area density (LAD) and its relative variance (ξ), total leaf area (TLA) and crown volume (V) varied consistently with cultivar. ‘Scarletspur Delicious’ had higher LAD and ξ and lower TLA and V compared with the other cultivars with more open canopies. At the whole-tree scale, training had no effect on structure and light interception parameters (silhouette to total area ratio, STAR; projected leaf area, PLA). At the shoot scale, Centrifugal Training increased STAR values compared with Central Leader. In both training systems, vegetative shoots had higher STAR values than fruiting shoots. However, vegetative and fruiting shoots had similar TLA and PLA in Centrifugal Trained trees, whereas vegetative shoots had higher TLA and PLA than fruiting shoots in Central Leader trees. This unbalanced distribution of leaf area and light interception between shoot types in Central Leader trees partly resulted from the high proportion of long vegetative shoots that developed from latent buds. These shoots developed in the interior shaded zone of the canopy and therefore had low STAR and PLA. In conclusion, training may greatly affect the development and spatial positioning of shoots, which in turn significantly affects light interception by fruiting shoots.

Keywords: canopy structure, central leader, centrifugal training, Malus domestica, reiteration, shoot type, spatial pattern, tree ideotype.
scale (Tustin et al. 1998). However, light environment has rarely been investigated at the shoot scale. According to Elfving and Forshey (1976) and Wünsche et al. (2000), a major drawback of most training systems is that pruning keeps fruiting shoots inside the tree canopy, whereas vegetative shoots are located in the outer part. This arrangement is contrary to the main objective of tree training which is not only to maximize light interception at the tree scale but also to optimize light penetration to the fruiting shoots, especially early in the season (Lakso and Corelli-Grappadelli 1992). This is particularly true in apple trees where fruit growth is closely related to light interception by spur leaves close to the flower/fruit cluster. Spur leaves appear to be the main supporters of early fruit growth (Volz et al. 1994).

Recently, a Centrifugal Training system for apple was proposed with the aim of improving light interception by fruiting shoots. It is based on the removal of young spurs along the trunk, and at the base and on the underside of branches (Lauri et al. 1997). The resulting light well and the porous mantle significantly increased total light interception and allocation to fruiting shoots (Willauve et al. 2004) and resulted in larger fruits (Lauri et al. 2007).

Several methods have been proposed for studying light interception by orchard trees. On the one hand, empirical studies based on light measurements within and below the canopies have been attempted (Ferree et al. 1992, Robinson et al. 1991). On the other hand, modeling approaches relating canopy geometry to light interception have been developed. Most models have been based on the turbid medium analogy (Ross 1981), where trees are abstracted as simple geometric shapes with a uniform density of leaf area (Charles-Edwards and Thorpe 1976, Palmer 1977, Green et al. 2003, Oyarzun et al. 2007). These models compute total light interception at the orchard scale and light distribution within tree crowns. For the latter, isolines of light transmission are computed to define the fraction of leaf area or canopy volume where available light is above or below a given threshold (Jackson and Palmer 1981).

Another way to compute light microclimate from canopy structure is to use 3D plant mock-ups where plant geometry is explicitly described (Sinoquet et al. 1998). This entails defining tree structure by the geometric attributes of all leaves on the tree, namely size, spatial position and orientation. Plant mock-ups can be created from field measurements on real plants with a 3D digitizer (Sinoquet and Rivet 1997) or from morphogenetic rules (Prusinkiewicz and Lindenmayer 1990). Although field data acquisition is tedious, the 3D approach is powerful, because it allows the computation of light interception at any scale.

Previously, we analyzed the influence of canopy manipulation on architecture (Stephan et al. 2007). Here, we have used 3D apple tree mock-ups to study relationships between canopy structure and light interception at the whole-tree, shoot-type and individual-shoot scales. We aimed to compare the responses of three apple cultivars of contrasting architectural types, and to assess effects of changing from a classical central leader training system to a centrifugal system. For this purpose, field-grown apple trees were 3D-digitized over 2 years.

We studied trees in a low-density orchard (714 trees ha⁻¹) to ensure optimal architectural development of each tree according to training system. However, as previously shown by Hampson et al. (2004), there are complex interactions between tree density and training system in determining yield and individual fruit quality (especially fruit mass and color). Because there is a predominant effect of tree density on yield in the early years, whereas there is no significant effect of training system before the sixth year in the orchard, we did not conduct a yield analysis.

Materials and methods

Plant material and training systems

The experiment was located in the Bekaa valley, at 900 m a.s.l. at the American University of Beirut research field (Haouch Sneid; 33°95'N, 36°02' E) in Lebanon. Trees of three cultivars were planted in 1999 in a randomized block design. The cultivars belonged to contrasting ideotypes according to Lespinasse’s (1992) typology: ‘Scarletspur Delicious’ (Type II), ‘Golden Delicious’ (Type III) and ‘Granny Smith’ (Type IV), hereafter referred to as ‘Scarletspur’, ‘Golden’ and ‘Granny’, respectively. Trees were grafted on M7 rootstock. The orchard layout was 4 x 3.5 m, with North–South orientation, and included three blocks of trees. Agricultural practices included irrigation with micro-sprinklers, standard fertilization and spraying.

From planting, trees of all cultivars were trained to obtain a Central Leader (Heinicke 1975). The leader was pruned from the first year to obtain a stronger trunk made of consecutive reiterated complexes. One-third of each 1-year-old lateral shoot was pruned to reduce competition between branches and trunk. Only shoots competitive with the trunk were pruned. In winter 2004, six healthy trees of each cultivar (two trees per block) were chosen at random excluding border trees. In each pair, one tree was trained as a Central Leader (L) and the other according to the Centrifugal Training system (C) as described by Willauve et al. (2004). In winter 2004, C-training consisted of making a light well by removing all shoots and buds (extinction pruning) along the trunk and on the underside of each branch. All branches along the trunk were kept. In 2005, almost no regrowth was found at sites subjected to extinction pruning in 2004. Complementary extinction pruning was carried out to maintain the same crop load as in 2004. Extinction pruning on C trees and shortening cuts on L trees were made before full bloom and bud burst, respectively. In both treatments, fruit was thinned to one per flower cluster.

3D digitizing of trees and foliage reconstruction

Trees were 3D digitized at the current-year shoot level one month before harvest in 2004 and 2005, in August or September of each year depending on the cultivar. Digitizing involves measuring the spatial coordinates of the proximal and distal tips of all shoots with a digitizer Polhemus Fastrak (Polhemus, Cochester, VT) (Sinoquet and Rivet 1997). The method requires an operator to locate the digitizer pointer at each point.
to be measured. The spatial coordinates of each point are recorded (Polhemus 1993). Data acquisition is driven by Pol95 Version 1.0 software (1999; B. Adam, UMR PIAF INRA-UBP, Clermont-Ferrand) available at http://www2.clermont.inra.fr/piaf/eng/download/download.php.

While digitizing, the operator recorded shoot type. Current-year shoots were classified as fruiting shoots (FS) or vegetative shoots (VS) according to Lauri and Kelner (2001) and Willaume et al. (2004): the FS included the fruited or aborted bourse and its associated bourse shoot(s). Vegetative shoots were classified as short (SVS, < 4 cm) or long (LVS, > 4 cm) shoots. Reiterated LVS originating from latent buds were distinguished and termed R-LVS, and LVS resulting from terminal growth of existing shoots were termed T-LVS.

In addition to shoot-level digitizing, 20 annual shoots of each category of each cultivar were randomly chosen and digitized at the leaf level according to Sinoquet et al. (1998). For each leaf, the pointer was set at the junction between the petiole and lamina, with the pointer oriented parallel to both the midrib axis and the lamina plane. This setup allowed us to derive leaf orientation angles (i.e., midrib azimuth and inclination) and lamina rolling around the midrib. Leaf length and width were also measured. Leaf samples were harvested for individual leaf area measurement. Leaves were scanned and the images processed with Scion software (Frederick, MD). Allometric relationships and leaf angle distributions were computed.

Foliage associated with each shoot in the crown was reconstructed according to the method of Sonohat et al. (2006): (1) shoot length was computed from spatial coordinates of shoot tips; (2) allometric relationships between shoot length, leaf area and number of leaves were computed for each year, cultivar and shoot type, according to the method proposed by Palmer (1987); (3) all leaves in a shoot were assumed to have the same area and to be regularly positioned along the shoot axis; (4) leaf length and width were computed from an allometric relationship for leaf area and length, respectively; and (5) leaf angles were randomly sampled in the distribution set from digitized data at the leaf scale. This sequence of computations was implemented in software written in FORTRAN, where inputs were the digitized tip coordinates of shoots and the parameters of the reconstruction rules. The reconstruction output was a collection of leaves with spatial coordinates, orientation angles and dimensions (Figure 1). The method was previously shown suitable for computing light properties at the tree and shoot scales for peach trees (Sonohat et al. 2006). The method has also been used with apple trees (Willaume et al. 2004).

**Derivation of tree canopy structure parameters**

Canopy structure parameters were computed from the reconstructed foliage data. Total leaf area (TLA) was computed as the sum of areas of all leaves at the scales of the whole tree and the shoot types (FS and VS). Crown volume (V) was computed as follows. A bounding box was defined around the tree according to the minimum and maximum values of leaf coordinates along axes x, y and z. The bounding box was then divided into cubic volume elements of 0.2 m called voxels. Crown volume was finally approximated as the cumulated volume of vegetated voxels, i.e., voxels containing at least one leaf (Figure 1). Mean leaf area density (LAD) was computed as the ratio of TLA to V. The relative variance of LAD (ξ) —which has previously been reported as a main contributor to foliage clumping (Sinoquet et al. 2005) —was computed from values of LAD in voxels:

\[
\xi = \frac{1}{n_v} \sum_{i=1}^{n_v} \left( \frac{LAD_i - \bar{LAD}}{LAD} \right)^2
\]

where \(n_v\) is the number of vegetated voxels, \(LAD_i\) is LAD in voxel \(v\) and \(\bar{LAD}\) is mean LAD in the tree crown (LAD = TLA/V).

The spatial distribution of leaf area was also visually assessed by dividing the canopy space into toric voxels of squared section (0.2 × 0.2 m) that are vertically symmetric about the tree trunk. Leaves were assigned to toric voxels according to their spatial coordinates. Such spatial division allowed us to derive 2D maps of changes in LAD as a function of altitude and distance from the tree trunk. This was computed at the tree scale and per shoot type (FS and VS).

**Computation of light interception attributes**

Light interception at both the tree and shoot scales was computed from the 3D plant mock-ups. Projected leaf area (PLA, m²)—also called silhouette area—and silhouette to total area ratio (STAR, Carter and Smith 1985, Oker-Blom and Smolander 1988, Hemmerlein and Smith 1994) were computed with VegeSTAR Version 3.0 software (2002; B. Adam, N. Donèse and H. Sinoquet, UMR PIAF INRA-UBP, Clermont-Ferrand). Projected leaf area characterizes light intercepting leaf area, whereas STAR corresponds to mean leaf irradiance relative to incident radiation. The two variables are related as

\[
\text{STAR} = \frac{\text{PLA}}{\text{TLA}}.
\]

Unlike STAR computations for conifers (Carter and Smith 1985, Oker-Blom and Smolander 1988), TLA of the apple trees was defined as one-sided leaf area. VegeSTAR software computes PLA by processing 3D tree mock-ups (Sinoquet et al. 1998). Leaf area lit by a light source of a given direction (e.g., the sun direction) is the same as leaf area seen on a tree photograph taken in the same direction with an orthographic camera. Therefore, PLA can be computed by counting vegetation pixels in the image. Moreover, assigning a different false color to each shoot in the tree makes it possible to compute PLA at the intra-tree level, namely the shoot scale.

Values of PLA and STAR depend on the direction of incident light. For directional integration over the sky hemisphere, the sky was discretized into 46 solid angle sectors of equal area according to the Turtle sky proposed by den Dulk (1989). Directional PLA and STAR values were computed for the central direction of each solid angle sector. Directional values were summed over the sky hemisphere using weighting coefficients derived from the Standard OverCast distribution of sky radiation (Moon and Spencer 1942).
We computed PLA and STAR for the actual trees, their crown envelopes and the corresponding homogeneous canopies. On the one hand, PLA of the crown envelope, i.e., the projected envelope area (PEA, m²), was computed with VegeSTAR by replacing the leaves by the set of voxels making the crown volume. On the other hand, the homogeneous canopy was built by randomly locating leaves in the crown volume defined by the set of vegetated voxels. The PEA of the actual tree crown and PLA of both actual and homogeneous (subscript H) tree canopies were used to compute crown porosity $P_0$ and $P_{0,H}$, respectively:

$$P_0 = 1 - \frac{\text{PLA}}{\text{PEA}} \quad \text{and} \quad P_{0,H} = 1 - \frac{\text{PLA}_H}{\text{PEA}}$$  \hspace{1cm} (2)

Foliage clumping ($\mu$) was derived from porosity terms according to Nilson (1971):

$$P_0 = P_{0,H}^{\mu} \quad \text{hence} \quad \mu = \frac{\ln P_0}{\ln P_{0,H}}$$  \hspace{1cm} (3)

Parameter $\mu$ is unity in the case of random leaf dispersion in the crown and less than 1 if foliage shows clumping.

Finally the leaf area index of the tree was defined as $\text{LAI} = \text{TLA} / \text{PEA}$ (Sinoquet et al. 2007).

**Statistical analyses**

The following variables were subjected to analysis of variance (ANOVA): (1) canopy structure parameters: LAD, TLA at entire tree and shoot (FS, VS) scales; and (2) light interception parameters: PLA, STAR at the shoot scale and PEA, LAI and $\mu$ at the tree scale. A Duncan multiple mean comparison test was performed when the cultivar effect was significant. The comparisons between training systems (C versus L) and between shoot types (VS versus FS) were performed with the independent $t$-test. A 95% degree of confidence ($P < 0.05$) was applied to all tests. The STAR distributions of FS shoots between training systems or cultivars, or both, were compared by the non parametric $\chi^2$ test.

**Results**

**Tree-scale canopy structure**

A qualitative analysis of the spatial distribution of LAD of total tree foliage showed that canopy volume depended on cul-
tivar (Figure 2), with the smallest and largest volumes for ‘Scarletspur’ and ‘Granny’, respectively. The three cultivars showed similar gradients in LAD, with higher LAD in the central part of the tree and lower values at the crown periphery. The C-training reduced LAD only in ‘Granny,’ but had no clear effect in the other cultivars. Crown volume of ‘Granny’ trees was larger in C-trained trees than in L-trained trees. For all cultivars, C-training, which resulted in a light well in the tree canopy, reduced LAD around the trunk, and this effect was striking for ‘Granny’.

One-way ANOVAs showed that structural parameters differed significantly between ‘Scarletspur’ and the other cultivars (Table 1). ‘Scarletspur’ TLA was about half that of ‘Golden’ and ‘Granny’ (6.8 versus 13.5 m²). ‘Scarletspur’ crown volume was about 1/3 that of the other cultivars (1.5 versus 4.6 m³). Consequently LAD was higher in ‘Scarletspur’ compared with the other cultivars. ‘Scarletspur’ also had a higher \( \xi \).

Significant changes in structural parameters occurred between 2004 and 2005, especially in TLA, LAD and \( \xi \), where values were higher in 2005. One-way ANOVA showed no effect of training system on canopy structure at the tree scale (Table 1).

**Tree-scale light interception**

There were no significant differences in STAR between cultivars, with values around 0.30 (Table 1). In contrast, STAR decreased significantly from 0.32 to 0.28 between 2004 and 2005. Training had no significant effect on STAR. Values of PLA differed among cultivars, with lower PLA in ‘Scarletspur’ and similar values in ‘Golden’ and ‘Granny’. Although PLA was slightly higher in 2005 and for C-trained trees, tree age and training system had no significant effect on PLA (Table 1).

Determinants of light interception differed significantly among cultivars. The only exception was LAI, where cultivar differences were small and nonsignificant (Table 1). ‘Scarletspur’ PEA was less than half that of ‘Golden’ and ‘Granny’. Similarly, \( \mu \) was significantly lower in ‘Scarletspur’ than in the other cultivars, indicating clumpier foliage. Temporal changes between 2004 and 2005 were significant only for LAI and \( \mu \), with slightly more LAI and clumpiness in 2005. There was a trend for larger PEA in C-trained trees than in L-trained trees (Table 1).

**Intra-tree-scale canopy structure**

The spatial distribution of LAD on both FS and VS is shown in Figures 3 and 4, respectively. In ‘Scarletspur’, FS leaf area was distributed in a smaller and lower canopy space than VS leaf area, whereas FS and VS of ‘Golden’ and ‘Granny’ trees occupied about the same space. For all cultivars, C-training markedly reduced the number of zones with a high density of FS foliage, especially for ‘Scarletspur’ (Figure 3). In C-trained trees, zones of higher LAD of FS were further from the tree trunk than in L-trained trees (Figure 3). In ‘Scarletspur’, LAD of VS showed high density in both training systems (Figure 4). The C-trained trees of ‘Golden’ showed zones with high LAD, but they were further from the trunk. C-Training did not induce clear changes in LAD distribution in ‘Granny’ trees.

We found significant differences in TLA between VS and FS in ‘Scarletspur’ and ‘Golden’, with about double the leaf area for VS compared with FS (Table 2). In contrast, ‘Granny’ FS and VS had roughly equal leaf areas. The TLA of FS was also significantly lower than that of VS in 2004 and in L-trained trees, whereas differences were not significant in 2005 or in C-trained trees (Table 2).

**Intra-tree-scale light interception**

Values of STAR for FS and VS foliage showed no significant differences among cultivars or between training systems (Table 2). Only STAR of VS showed a value significantly higher in 2005 than in 2004. In contrast, STAR values were always significantly higher for VS than for FS, with the difference ranging from 0.04 in ‘Granny’ to 0.12 in ‘Golden’. Changes in PLA at the shoot-type level were similar to changes in TLA.
Table 2: PLA values of both FS in ‘Granny’ and VS in ‘Golden’ were significantly higher than in the other cultivars. The VS foliage generally had higher PLA than the FS foliage, especially in the ‘Scarletspur’ and ‘Golden’ cultivars, and also in L-trained trees. In contrast, ‘Granny’ and C-trained trees showed no significant difference in PLA between FS and VS foliage (Table 2).

Table 3 shows light interception by LVS at the shoot scale, where terminal (T-LVS) and reiterated (R-LVS) shoots were distinguished. As ‘Scarletspur’ trees mainly displayed SVS with few LVS, they were excluded from the analysis. The R-LVS were much less frequent on C-trained trees than on L-trained trees (Table 3). This was directly related to training system. However, the growth patterns of T-LVS and R-LVS within L-trained trees differed depending on cultivar (Table 3). For ‘Golden’, R-LVS behaved similarly to T-LVS, with higher LA, STAR and PLA values on L-trained trees than on C-trained trees. For ‘Granny’, the only significant difference observed was for STAR, with higher values in L-trained trees than in C-trained trees.

Leaf irradiance distribution between individual FS is shown in Figure 5 for years 2004 and 2005. For all cultivars except ‘Golden’ in 2004, C-training significantly improved STAR distribution ($\chi^2$ test, $P < 0.01$), with fewer shaded and more sunny shoots. For both C- and L-trained trees, shoot irradiance distribution differed significantly among cultivars, with improved distribution increasing from ‘Scarletspur’ to ‘Golden’ and then ‘Granny’ ($P < 0.01$, data not shown).

Discussion

Advantages and limitations of virtual experiments

The combination of making 3D tree mock-ups with light computations based on projection methods allowed detailed study of canopy structure and light interception attributes. First, structural parameters at the tree scale were computed from the databases where canopy geometry is described at the leaf scale. These computations can be considered actual measurements of the parameters: TLA estimation was similar to the detailed shoot sampling method proposed by Wünsche and Palmer (1997); and crown volume was derived from accurate localization of shoots in space. Additionally, we were able to describe the spatial distribution of LAD in the tree crowns (Figure 2). Only a few measurements based on 2D or 3D leaf clipping have been reported in fruit trees (Cohen and Fuchs 1987, Palmer et al. 1992) and vineyards (Mabrouk et al. 1997). They are usually destructive and time-consuming. With the 3D
digitizing method, we established the spatial distribution of leaf area for FS and VS, separately (Figures 3 and 4). Second, virtual experiments allowed us to compute light interception properties and their determinants at several scales: STAR and PLA of the whole tree (Table 1), per shoot type (FS and VS) (Table 2) and at the individual shoot scale (Figure 5). Several methods have been proposed to measure total light interception at the tree scale, e.g., arrays of sensors (Oker-Blom et al. 1991, Giuliani et al. 2000), fisheye photographs below the canopy (Wünsche et al. 1995) and photographs of the shadow cast by the crown (Hemmerlein and Smith 1994). At the shoot scale, video projection and photography methods have been proposed for detached shoots (Oker-Blom et al. 1991, Niihemedets et al. 2004). Field methods for estimating light interception at the shoot scale within crowns are time consuming. Light micro-sensors can be attached to the leaf surface (Gutschick et al. 1985), but this method needs many sensors to get unbiased values of mean irradiance (Sinoquet et al. 2001).

Wünsche et al. (1996) proposed a scanner laser method to measure light partitioning between spurs and extension shoots, which are closely analogous to FS and VS, respectively. Laser beams were sent to the canopy, and the target organ was visually recorded as a spur or extension shoot leaf. The plant image processing method we used can be regarded as an extension of Wünsche’s work, where each pixel in the image corresponds to a laser beam and target classification is automated by assigning false colors to each shoot type (Figure 1) or individual shoot. The virtual computation allowed a large number of sampled beams (the image size used in VegeSTAR is 356 × 356 pixels, and one image is used for each of the 46 light directions used to abstract the sky radiation) and fine light partitioning among plant components. Virtual experiments also allowed us to compute parameters that are difficult to measure in the field. This is especially the case for μ, which expresses departure from random distribution of leaves in the canopy space (Nilson 1971). Cohen et al. (1995) inferred clumping proper-

Figure 3. Leaf area density (m² m⁻³) distribution as a function of height above the soil surface and distance from tree trunk for three apple (Malus domestica) cultivars subjected to two training systems, for fruiting shoots.

Figure 4. Leaf area density (m² m⁻³) distribution as a function of height above the soil surface and distance from tree trunk for three apple (Malus domestica) cultivars subjected to two training systems, for vegetative shoots.
Table 2. Effects of cultivar, year and training system (TS; C = Centrifugal Training, L = Central Leader) on total leaf area (TLA, m²), light interception (STAR) and projected leaf area (PLA, m²) for fruiting (FS) and vegetative shoots (VS) (*n* = number of trees) in apple (*Malus domestica*) trees. For each variable and each FS–VS pair, values in bold within rows indicate significant differences based on the Dependent *t*-test (*P* < 0.05). Within a column, values followed by different letters differ significantly based on the Duncan multiple mean comparison test for cultivars and the Student *t*-test for years and training systems (*P* < 0.05).

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>TS</th>
<th><em>n</em></th>
<th>FS TLA</th>
<th>STAR</th>
<th>PLA</th>
<th>VS TLA</th>
<th>STAR</th>
<th>PLA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>August 2004</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Scarletspur'</td>
<td>C</td>
<td>3</td>
<td>2.34</td>
<td>0.27</td>
<td>0.69</td>
<td>3.50</td>
<td>0.36</td>
<td>1.24</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>3</td>
<td>1.06</td>
<td>0.27</td>
<td>0.28</td>
<td>4.46</td>
<td>0.33</td>
<td>1.40</td>
</tr>
<tr>
<td>'Golden'</td>
<td>C</td>
<td>3</td>
<td>2.80</td>
<td>0.26</td>
<td>0.75</td>
<td>11.22</td>
<td>0.31</td>
<td>3.21</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>3</td>
<td>3.32</td>
<td>0.24</td>
<td>0.79</td>
<td>8.21</td>
<td>0.31</td>
<td>2.44</td>
</tr>
<tr>
<td>'Granny'</td>
<td>C</td>
<td>3</td>
<td>6.33</td>
<td>0.30</td>
<td>1.91</td>
<td>7.09</td>
<td>0.31</td>
<td>2.22</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>3</td>
<td>2.72</td>
<td>0.29</td>
<td>0.77</td>
<td>6.22</td>
<td>0.30</td>
<td>1.89</td>
</tr>
<tr>
<td><strong>August 2005</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Scarletspur'</td>
<td>C</td>
<td>3</td>
<td>2.08</td>
<td>0.33</td>
<td>0.67</td>
<td>4.25</td>
<td>0.38</td>
<td>1.54</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>3</td>
<td>2.70</td>
<td>0.22</td>
<td>0.58</td>
<td>5.40</td>
<td>0.36</td>
<td>1.78</td>
</tr>
<tr>
<td>'Golden'</td>
<td>C</td>
<td>2</td>
<td>5.28</td>
<td>0.25</td>
<td>1.30</td>
<td>10.83</td>
<td>0.51</td>
<td>5.09</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>2</td>
<td>5.06</td>
<td>0.22</td>
<td>1.09</td>
<td>7.20</td>
<td>0.35</td>
<td>2.41</td>
</tr>
<tr>
<td>'Granny'</td>
<td>C</td>
<td>3</td>
<td>12.86</td>
<td>0.30</td>
<td>3.81</td>
<td>5.95</td>
<td>0.34</td>
<td>2.01</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>3</td>
<td>5.28</td>
<td>0.28</td>
<td>1.40</td>
<td>4.96</td>
<td>0.37</td>
<td>1.65</td>
</tr>
<tr>
<td><strong>Mean per cultivar</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Scarletspur'</td>
<td>12</td>
<td></td>
<td><strong>2.05</strong> b</td>
<td>0.27 a</td>
<td>0.55 b</td>
<td>4.41 b</td>
<td>0.36 a</td>
<td>1.49 b</td>
</tr>
<tr>
<td>'Golden'</td>
<td>10</td>
<td></td>
<td><strong>3.91</strong> ab</td>
<td>0.24 a</td>
<td><strong>0.94</strong> b</td>
<td><strong>9.44</strong> a</td>
<td><strong>0.36</strong> a</td>
<td><strong>3.19</strong> a</td>
</tr>
<tr>
<td>'Granny'</td>
<td>12</td>
<td></td>
<td>6.80 a</td>
<td><strong>0.29</strong> a</td>
<td>1.97 a</td>
<td>6.06 b</td>
<td><strong>0.33</strong> a</td>
<td>1.94 b</td>
</tr>
<tr>
<td><strong>Mean per year</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>18</td>
<td></td>
<td><strong>3.10</strong> a</td>
<td><strong>0.27</strong> a</td>
<td><strong>0.86</strong> a</td>
<td><strong>6.79</strong> a</td>
<td><strong>0.32</strong> a</td>
<td><strong>2.07</strong> a</td>
</tr>
<tr>
<td>2005</td>
<td>16</td>
<td></td>
<td>5.60 a</td>
<td><strong>0.27</strong> a</td>
<td>1.51 a</td>
<td>6.11 a</td>
<td><strong>0.38</strong> b</td>
<td>2.25 a</td>
</tr>
<tr>
<td><strong>Mean per TS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C-trained trees</td>
<td>17</td>
<td></td>
<td>5.28 a</td>
<td><strong>0.29</strong> a</td>
<td>1.53 a</td>
<td>6.93 a</td>
<td><strong>0.36</strong> a</td>
<td><strong>2.40</strong> a</td>
</tr>
<tr>
<td>L-trained trees</td>
<td>17</td>
<td></td>
<td><strong>3.26</strong> a</td>
<td><strong>0.25</strong> a</td>
<td><strong>0.80</strong> a</td>
<td><strong>6.01</strong> a</td>
<td><strong>0.34</strong> a</td>
<td><strong>1.90</strong> a</td>
</tr>
</tbody>
</table>

Table 3. Leaf area (LA, dm²), light interception (STAR) and projected leaf area (PLA, dm²) of long vegetative shoots (LVS) issued from terminal (T-LVS) and reiterated (R-LVS) growth in 2005 as influenced by training system (TS; C = Centrifugal Training, L = Central Leader) and pruning (T-LVS, R-LVS) for L-trees only, for ‘Golden’ and ‘Granny’ (*n* = number of shoots). Within a column, values followed by different lowercase letters differ significantly between training systems (Independent *t*-test, *P* < 0.05). Within a row and for each variable, values followed by different uppercase letters differ significantly between T-LVS and R-LVS for L-trained trees (Independent *t*-test, *P* < 0.05).

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>TS</th>
<th>T-LVS</th>
<th>R-LVS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>n</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Golden'</td>
<td>C</td>
<td>500</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>239</td>
<td></td>
</tr>
<tr>
<td>'Granny'</td>
<td>C</td>
<td>349</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>34</td>
<td></td>
</tr>
</tbody>
</table>

| Training effect (C-trained versus L-trained) |     |       |       |
| 'Golden' | *F* | 1.82  | 1.67  | 56.72 |
|          | *P* | < 0.01| < 0.01| < 0.01|
| 'Granny' | *F* | 3.31  | 7.4   | 21.67 |
|          | *P* | < 0.01| < 0.01| < 0.01|

| Pruning effect (T-LVS versus R-LVS) in L-trained trees |     |       |       |
| 'Golden' | *F* | 0.67  | 2.72  | 1.98  |
|          | *P* | < 0.01| < 0.01| 0.02  |
| 'Granny' | *F* | 0.04  | 6.18  | 0.04  |
|          | *P* | < 0.01| < 0.01| 0.06  |
ties of apple trees by simultaneously measuring leaf area and light distribution within the tree canopy. Here we constructed a virtual homogeneous tree canopy where leaves were randomly distributed in the crown volume, and we derived μ by comparing the crown porosity of both actual and homogeneous tree crowns (Equation 4). Such computations could not be made in the field, mainly because homogeneous trees do not exist in nature.

Unfortunately, virtual experiments also have limitations. The main one is related to the construction of 3D plants. We used a 3D digitizing technique (Sinoquet and Rivet 1997) that allowed us to describe the 3D structure of the trees. However, tree digitizing in the field is time consuming. The rate of 3D data acquisition is about 1000–2000 points per day, if the tree is not too big. For tall trees, tree digitizing is impossible. We used digitizing at the leafy shoot scale associated with a reconstruction method of leaves attached to the shoot (Sonohat et al. 2006). This reduced data acquisition time, and the method has been shown to be accurate for building 3D tree structures suitable for light interception computations (Sonohat et al. 2006). Digitizing at the shoot scale allowed measurement of the 3D structure of 18 trees in 2004 and 2005, which in comparison with other studies with virtual plants, is a large number (cf. Thanisawanyangkura et al. 1997, Willaume et al. 2004). However, the sample size was insufficient to show statistically significant combined effects of cultivar, training and year over two years at the tree scale (Table 1). The small number of individuals allowed only one-way ANOVAs, where the separate effects of cultivar, training and year were analyzed. At the shoot scale, however, the number of individuals,
i.e., shoots, was sufficient and analysis showed significant differences among cultivars and between training systems (Table 3 and Figure 5).

Cultivar and training effects on canopy structure and light interception

At the tree scale, differences in structural parameters and interception properties can be related to the typology of the cultivars: Type II for ‘Scarletspur’, Type III for ‘Golden’ and Type IV for ‘Granny’ (Lespinasse 1992). Type II cultivars show more short shoots and fewer long shoots, as shown by Stephan et al. (2007) for ‘Scarletspur’. This leads to smaller canopy volume, leaf area and total light interception (PLA). Moreover, the display of foliage mainly in short shoots may explain the high foliage clumping (µ and ξ) in ‘Scarletspur’. Small internode length, which is a characteristic of dwarf or compact scion cultivars (Rusholme et al. 2004), has been shown to increase foliage clumping (Takenaka 1994). Leaf dispersion values were not in complete agreement with those reported by Cohen et al. (1995): ‘Smoothee’ trees (Type III) were clumped, whereas ‘Top Red’ trees (Type II) showed random leaf dispersion. Leaf irradiance (STAR) at the tree scale did not differ significantly between cultivars, although values tended to be lower for ‘Scarletspur’ and higher for ‘Granny’. The equations relating LAI to PLA and STAR have been established and discussed previously (Sinoquet et al. 2007).

Partitioning leaf area between FS and VS revealed differences among cultivars, with much more VS leaf area compared with FS leaf area in ‘Scarletspur’ and ‘Golden’, and similar leaf area for the two shoot types in ‘Granny’ (Table 2). Although STAR values were higher in VS than in FS for the three cultivars, the sunlit leaf area (PLA) was similar in both shoot types for ‘Granny’ whereas it was significantly higher in VS than in FS for the other cultivars. Because fruit yield is related to light interception by spurs (Wünsche et al. 1996, Lakso et al. 1999), the greater sunlit leaf area in FS of ‘Granny’ likely explains the higher regularity of bearing of this cultivar (Lauri et al. 1997, Stephan et al. 2007).

We found no significant effect of training system at the whole-tree scale for any leaf canopy or light interception parameter or for any combination of them. However, an effect of training was observed at the within-canopy scale. First, STAR values of individual shoots, whether VS or FS, increased more in C-trained trees than in L-trained trees (Figure 5). This is likely related to the lower LAD values in C-trained trees compared with L-trained trees (Figures 2–4). Second, L-trained trees consistently had increased VS leaf area (total and sunlit) compared with FS leaf area, whereas leaf areas of both shoot types were similar for C-trained trees (Table 2). From a physiological viewpoint, the greater sunlit leaf area proximal to the fruit is known to be an important positive factor for yield (Wünsche and Lakso 2000). We showed that the training system may significantly change the balance between the leaf areas of each shoot type (TLA) as well as their spatial distribution and access to light (PLA). However, comparison with other studies is difficult, because few data obtained at the individual shoot scale have been published.

Another effect of the training system was observed on the type of long vegetative shoots that developed either from an existing shoot (T-LVS) or from a latent bud (R-LVS). A previous analysis of the same experiment showed that pruning of branches included in the Central Leader system led to strong reiterative phenomena (Stephan et al. 2007). For ‘Golden’ and ‘Granny’, T-LVS of L-trained trees had significantly higher LA, STAR and PLA than T-LVS of C-trained trees, suggesting that at the tree scale, pruning trunk and scaffold branches stimulated growth (LA) and light interception (STAR, PLA) of individual vegetative shoots (Table 3A). We have now shown that these shoots (R-LVS) had similar LA and significantly lower STAR values than T-LVS on both cultivars. Although PLA was lower in R-LVS compared with T-LVS, the difference was significant only for ‘Golden’. This could be explained by the location of R-LVS on scaffold branches below the pruning cuts, i.e., within the canopy where there was less light penetration. Therefore R-LVS were not expected to contribute strongly to the carbon budget of the tree although they bear much of the leaf area of long vegetative shoots, i.e., 53% and 88% for L-trained trees of ‘Golden’ and ‘Granny Smith’ respectively (Table 3).

The interest in adapting training to tree architecture has often been emphasized (Lauri and Laurens 2005, Costes et al. 2006, Robinson 2007). In particular, the agronomic interest in minimal pruning strategies adapted to the cultivar (Robinson 2007) as opposed to pruning strategies based only on heading or shortening cuts, i.e., reducing the length of current-season or older wood of scaffold branches, has been demonstrated. We have now shown that manipulations of tree architecture through the training system and pruning strategies also affect light interception. For example, we found that Centrifugal Training enhanced light interception by fruiting shoots and reduced the amount of less fruit-feeding vegetative shoots (R-LVS). These results serve to guide a further study on the influence of plant structure on photosynthesis and transpiration at the fruiting branch and tree scales (Massonnet et al. 2008). Our findings contribute to the overall physiological interpretation of the positive effects of minimal pruning on fruit growth and quality, and regularity of yield across consecutive years (Lauri et al. 2007).

Acknowledgments

We thank the American University of Beirut, and especially Dr. Mohamed Farran, for orchard monitoring and availability, and the students Dahlia Mansour, Gebran Nassif, Marica Abi Nader and Majed Feghali for tree digitizing.

References


TREE PHYSIOLOGY ONLINE at http://heronpublishing.com


