Effect of Leaf Area on Tomato Yield

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Abstract

The influence of leaf area on tomato yield was evaluated, both by simulations and experimental work. Simulated crop growth results from daily crop gross assimilation rate minus maintenance respiration rate, multiplied by a conversion efficiency factor. Dry matter partitioning is simulated based on the relative sink strengths of the plant organs. Within the plant, individual fruit trusses and vegetative units are distinguished. Leaf area increase is calculated based on temperature, unless a maximum specific leaf area is reached. In the standard situation leaves from a vegetative unit are removed one week before the truss above this unit is harvest ripe. Leaf removal could also be based on maintaining a desired leaf area index (LAI).

Measurements at 7 farms showed that in the summer season light interception was on average 90%, with values varying between 86% and 96%. Three different LAI treatments were tested by picking different numbers of old leaves. Reference, high and maximum LAI resulted in average LAI of 3.3, 3.6 and 4.1 m\textsuperscript{2} m\textsuperscript{-2}, respectively, and equal yields of 66 kg m\textsuperscript{-2}. The model predicted a yield increase of 1.5% for the maximum LAI treatment compared to the reference, with LAI being input to the model. Simulated yield when leaf picking was based upon a desired LAI of 4, was 4% higher than for a desired LAI of 3, with hardly any effect at higher LAI. Simulations showed that removal of young leaves favored partitioning to the fruits but decreased LAI and total yield. However, if removal of old leaves was delayed such that an LAI of 3 m\textsuperscript{2} m\textsuperscript{-2} was maintained, removal of every second young leaf improved yield by 10%. Methods of optimizing yield by controlling LAI are discussed.

INTRODUCTION

Many factors influence tomato yield (Heuvelink, 2005), of which radiation is the most important one, as it supplies the energy for photosynthesis, the basic production process in plants. For example, Cockshull et al. (1992) observed over the first 12 weeks of harvest (from February until May) that 2 kg fresh weight of tomato fruit are produced per 100 MJ of incident solar radiation. Only radiation that is intercepted by the crop can contribute to photosynthesis. Light interception shows a saturating response to LAI, with about 90% of the incident light intercepted at an LAI of 3.0 (Heuvelink, 1996b). LAI in tomato is influenced by stem density, number of leaves on a stem and individual leaf size.

In greenhouse tomato production, using the high wire system, plants are allowed to grow vertically up to a 3.5-4.0 m high horizontal wire. Plants produce about 3 leaves and 1 truss every week (De Koning, 1994). All side shoots are removed except for a few (e.g. one or two on each four plants) to increase stem density towards summer (Heuvelink, 2005).

Removal of full-grown leaves from below and from just above the harvest-ripe truss is common practice in greenhouse tomato cultivation. The main reasons for leaf removal are prevention of diseases, especially as in the high wire system older leaves would touch the ground surface when not removed, obtaining faster fruit ripening and easier harvest as trusses are no longer hidden by leaves. Old leaves are also believed not to contribute to the crop photosynthesis anymore. Leaf removal reduces LAI and may...
therefore reduce light interception and consequently yield. In addition, tomato growers sometimes remove young leaves. This favours dry matter partitioning towards the fruits, but decreases LAI, which makes the effect on yield uncertain (Xiao et al., 2004). In this paper, the influence of LAI on light interception and on tomato yield is evaluated, both by simulations and experimental work. LAI was manipulated by varying the rate of removal of old and young leaves.

**MATERIAL AND METHODS**

**Experimental Work**

At a modern commercial tomato farm three treatments for picking of old leaves were applied (reference LAI, high LAI and maximum LAI). The crop (cv. Cedrico, Rijk Zwaan) was planted on 5 December 2002 and was ended at 13 November 2003. Plant density was 2.3 plants m\(^{-2}\). On 9 March as well as 6 April one additional side shoot was retained on 1 out of 4 plants, resulting in a final density of 3.4 stems m\(^{-2}\). On 6 October the stems were topped. Climate control and culture measures were all according to commercial practice. In the reference treatment picking of old leaves was done as usual by the grower. Leaves were removed weekly from bottom up to 3 to 4 leaves above the coloring truss. In the high LAI treatment a LAI of 3.5 m\(^2\) m\(^{-2}\) was aimed at (19-22 leaves on the plant). In the maximum LAI treatment leaves were only picked when they started to touch the floor. Each treatment was applied in 3 plots of 8 rows of plants each. Fruit production (fresh weight harvested fruits) was continuously registered by the grower. LAI and leaf weight were measured periodically. Light interception was determined at the same time (usually under dull weather conditions) by measuring the photosynthetically active radiation (PAR) on top of the canopy and just underneath the canopy using Sunscan PAR sensors (AT Delta-T Devices Cambridge England). Measurements underneath the canopy were done by a PAR stick of half the length of the average distance between two rows of plants. In July and September 2003 additionally at 7 farms growing round tomato cultivars, the light interception of the canopy was measured with the Sunscan device.

**Simulation Model**

The model is described by Marcelis et al. (2000) and is based on INTKAM (Gijzen, 1994) and TOMSIM (Heuvelink, 1999). Global radiation outside the greenhouse, inside temperature and CO\(_2\) concentration are model inputs. The model consists of modules for greenhouse radiation transmission, radiation interception by the crop, leaf and canopy photosynthesis, dry matter production, dry matter partitioning among plant organs (roots, stem, leaves and trusses of fruits), fruit harvest and leaf picking.

Greenhouse radiation transmission, radiation interception and photosynthesis are calculated with time intervals of half an hour. The time step of the modules for dry matter production, dry matter partitioning, fruit harvest and leaf picking is one day.

Assimilate partitioning between vegetative parts and individual fruit trusses is simulated on the basis of sink strengths, as described by Heuvelink (1996b). Computation of leaf area increase follows the approach given by Gary et al. (1995). Leaf area increase is potential if the average specific leaf area (SLA) of the whole canopy is smaller than the parameter SLA\(_{\text{max}}\). Potential leaf area increase is computed as the product of the potential weight of new leaf material and the parameter SLA\(_{\text{min}}\). If SLA is greater than SLA\(_{\text{max}}\) (if the leaf is thinner than permitted), leaf area increase is equal to the product of the weight of new leaf material and SLA\(_{\text{max}}\). SLA\(_{\text{max}}\) is a constant, and SLA\(_{\text{min}}\) was made dependent on the day of the year in accordance with the sinusoid function described by Heuvelink (1999). Computations are conducted daily for each vegetative section (section consists of 3 leaves and 3 internodes). Appearance rate of new sections and trusses depends on temperature alone (De Koning, 1994).

Dry matter production of the organs is calculated as the amount of assimilates partitioned into each organ divided by the assimilate requirements for dry matter production. Fresh tomato yield is obtained by dividing the dry weight of the organs by the
dry matter content. In the standard setting leaves from a section are removed when the corresponding truss above this section has reached developmental stage 0.9, which means at 20°C about 6 days before the truss is harvest ripe. Leaf removal could also be based on maintaining a desired leaf area index (LAI). In that case, when simulated LAI exceeds a threshold value, leaves from the oldest vegetative section are removed.

Comparison of Measured and Simulated LAI and Yield
For comparison with experimental data, simulations were conducted with measured outside radiation, inside temperature and CO₂-concentration, plant density, and dates of retaining side-shoots and topping stems as model input. To predict the effect on yield of the three leaf removal treatments measured LAI and leaf dry weights were also inputs to the model.

Simulation Study on Picking of Old Leaves and Removal of Young Leaves
For these studies two series of simulations were conducted, starting at December 1 (day of year 335) and finishing at November 26 (day of year 330). Global radiation data of SELYEAR (Breuer and Van de Braak, 1989) were used as model input. This so-called ‘selected year’ results in the same average irradiance as observed for the 30-year average global radiation in De Bilt (The Netherlands), however, it contains a representative variability in radiation.

Effect of picking of old leaves was studied as picking of all 3 leaves from the oldest section on the plant, when LAI exceeded a threshold of 1 up to 8. Effect of removal of young leaves was simulated for the following treatments: 0 (control), 1, 2, or 3 leaves out of 6 leaves removed. This removal was simulated by reducing the sink strength of the leaves proportionally, while keeping the sink strengths of the other organs unchanged. The treatments for removal of young leaves were combined with two strategies for picking of old leaves, i.e. (1) standard, old leaves were removed from a section when the corresponding truss has reached developmental stage 0.9, which means at 20°C about 6 days before the truss is harvest-ripe, and (2) old leaves were removed from the oldest section each time when LAI exceeded 3.

RESULTS

Observed LAI and Light Interception
In summer, commercial crops intercept 90% light on average, values varying between 86% and 96% (Table 1). Heuvelink (1996a) reported for measurements during the season in a tomato crop grown at 3 plant densities (LAI range from 0.7 up to 3.1) a negative exponential relationship between LAI and the fraction intercepted light, according to the Lambert-Beer law (Monsi and Saeki, 1953) with an extinction coefficient (k) of 0.75. Our measurements in the leaf picking experiment at a commercial farm throughout the season, agreed reasonably well with this relationship (Fig. 1). Nevertheless, the increase in light interception with increasing LAI tended to be less strong in the measurements, than suggested by the exponential relationship. This apparent decrease in k with LAI was also observed by Heuvelink (1996a) and results from leaf angle distribution (not all leaves horizontal) as discussed theoretically by Goudriaan (1988).

Observed and Simulated Effect of Removal of Old Leaves
Measured LAI, averaged over the period mid March till mid August was 3.3, 3.6, 4.1 m² m⁻², for reference, high and maximum LAI leaf pruning treatment, respectively. Validation of the model for the reference leaf pruning treatment resulted in good agreement between measured and simulated LAI (Fig. 2). Observed tomato, yields did not differ between treatments and were 66.4±0.4, 65.8±1.0, and 66.0±1.2 kg m⁻², respectively. Simulated yield (67 kg m⁻²) of the reference treatment corresponded well with the measurements. With LAI and leaf dry mass per m² as input to the model simulated yields
were 68.3, 68.8 and 69.2 kg m\(^{-2}\). These values are in agreement with measured values, as a predicted yield increase of 1.5% when maximum LAI is compared with reference LAI is too small to prove experimentally. This makes the model a useful tool for evaluation of a much wider range of leaf pruning strategies. Simulation of leaf picking based upon a desired LAI, showed that yield increased up to an LAI of 4 with hardly any effect at higher LAI; the response curve showed a saturation type of curve rather than an optimum response curve.

Simulated Effect of Removal of Young Leaves

Weekly removal of some young leaves increased partitioning to the fruits (Table 2). When every second young leaf was removed, 77% of dry mass was partitioned to the fruits, whereas this was 69% for the control treatment where no young leaves were removed. Despite this positive effect on partitioning, removal of young leaves resulted in reduction of fruit yield because of reduced LAI (Table 2). Average LAI dropped from 2.5 for the control, to only 1.2 when every second young leaf was removed. Reduced total dry mass production as a result of reduced LAI had a larger effect on fruit yield than increased dry matter partitioning towards the fruits. When reduction in LAI through removal of young leaves was largely compensated by delayed leaf picking aiming at a LAI of 3, total dry mass production was hardly affected (4.18 to 4.25 kg m\(^{-2}\)). Hence, in that case a yield increase resulted from pruning of young leaves (Table 2). This increase was 3% when 1 out of 6 leaves was removed in an early stage, whereas it was 10% when every second leaf was removed (Table 2). For treatments where removal of old leaves was started only when LAI of 3 was reached, this moment was day 70, 78, 88 or 104, for control, removal of every sixth, third or second leaf, respectively.

DISCUSSION

Removal of Old Leaves

Current commercial crops show a much higher LAI and hence light interception than reported in the early nineties. Both De Koning (1993) and Heuvelink (1999) reported LAI values as low as 1.5 or 2.0 in summer. Because observed commercial crops had LAI values greater than 3 during summer, a large part of yield increase as a result of better light interception has already been obtained. For LAI at 3 the amount of intercepted light is 15% higher than for a LAI of 2 (Fig. 1; Heuvelink, 1996a). Increased LAI is probably the result of a larger number of stems per m\(^{2}\) as extra side shoots are retained from spring onwards. The use of plants grafted on a rootstock is also reported to result in more vigorous, vegetative plant growth (Heijens, 2004), which may contribute to the current higher LAI in summer.

Reference, high and maximum LAI leaf pruning treatments did not differ in yield and this was also predicted by the model, presumably because of the high LAI levels (3.3 to 4.1 m\(^{2}\) m\(^{-2}\)) in all three pruning strategies. Which LAI should be maintained is an important question in tomato cultivation. This is even more so for crops supplemented with artificial radiation, a common situation in Scandinavian countries and Canada, and becoming increasingly popular in The Netherlands to obtain year-round production (Marcelis et al., 2002). The use of assimilation light is expensive and light not intercepted by the crop contributes to the costs, but not to yield. Increased LAI results in higher light interception (Fig. 1) and therefore higher gross photosynthesis. A higher LAI implies a higher biomass as more leaf weight is present and hence a higher maintenance respiration is required. However, in the model, specific maintenance respiration, i.e. respiration per unit biomass, depends on crop metabolic activity, quantified by the relative growth rate of the crop (RGR). With the same growth rate, higher biomass reduces RGR and hence maintenance per unit biomass. This leads to no clear optimum for LAI, as above an LAI of 4 both gross photosynthesis and crop maintenance hardly change (not shown).

Our model calculations show that maintaining LAI at 4 results in a 4% yield increase compared to LAI at 3, whereas maintaining LAI at 5 increases yield by only 1%
compared to LAI at 4. This 4% yield increase when LAI is kept at 4 instead of 3 is substantial, yet difficult to prove in experiments. In the Netherlands, 4% yield increase represents €36,000 to €44,000 per grower, assuming a tomato greenhouse of 2 ha. This estimated yield increase of 4% has some uncertainties. It was assumed that all leaves have identical photosynthetic characteristics, whereas older leaves are adapted to low light intensities and hence are expected to have a lower maximum photosynthetic rate. Furthermore, specific maintenance respiration of all organs is reduced in the model at lower RGR. However, only for the leaves one can imagine a lower specific maintenance respiration because of lower average light level received by the leaves at higher LAI and hence lower metabolic activity.

It should be mentioned that retaining extra leaves has practical implications in the common high-wire system, as in low greenhouses it may imply that leaves touch the ground with extra risks for diseases (e.g. Botrytis) and making leaf removal later on virtually impossible. Furthermore, fruit harvest is more difficult when the trusses are hidden by leaves, and delayed leaf removal may delay fruit ripening.

It was expected that yield would show a clear optimum response to LAI, as above a certain LAI the increase in maintenance respiration would be larger than the increase in gross photosynthesis with LAI increase. However, this was not observed in our simulations, as specific maintenance respiration rate decreased with LAI. The importance of maintenance respiration in our findings, and the uncertainty in simulation of maintenance respiration (Marcelis et al., 1998), stresses the need for more experimental work in this field.

Buitelaar and Janse (1987) studied the effect of removing 3, 6, 9 or 12 leaves above the truss being harvested, and found that yield was reduced only when removing 12 leaves above the truss being harvested. This treatment also reduced the shelf life and refraction index of the fruits. Buitelaar (1989) observed in a similar experiment that yields, as well as the internal and external fruit quality, were adversely affected only by the most severe defoliation treatments. In several trials (harvest until 7 Oct.) with round and beefsteak tomato this author observed no significant differences in yield and average fruit weight when comparing different intensities of weekly leaf removal, such that 15, 18, 21 or 24 leaves remained per plant. These results seem to conflict with our simulation results, although we can not be certain as LAI was not recorded. However, it seems unlikely that removal of 6 or 9 leaves above the truss being harvested still results in LAI values above 3. One reason for the possibly conflicting findings may be that in experiments yield differences of less than 10% are difficult to prove statistically significant, although they may be highly important commercially.

**Removal of Young Leaves**

Removal of young leaves favours partitioning to the fruits, which is the result of a higher fruit:leaf ratio. In a reference crop 69% is partitioned to the fruits and 31% to the vegetative parts (Table 2). Partitioning is based on sink strength (Heuvelink, 1996b), and hence we could assume that average total fruit sink strength (\(SS_{\text{fruits}}\)) is 0.69\(\times Z\) and average total vegetative sink strength (\(SS_{\text{veg}}\)) is 0.3\(\times Z\), with \(Z\) an unknown scaling factor. Then partitioning to the fruits will be \(SS_{\text{fruits}}/(SS_{\text{fruits}}+SS_{\text{veg}}) = 0.69\times Z/(0.69\times Z+0.31\times Z) = 0.69\), hence 69%. Partitioning within the vegetative organs of tomato between leaves, stem and roots is 7:3:1.5 (Heuvelink, 1996b). Removal of e.g. 1 out of 3 young leaves is expected to reduce leaf sink strength by one third and hence \(SS_{\text{veg}}\) by (11.5-9.2)/11.5=20%. This is expected to improve partitioning to the fruits to \(0.69\times Z/(0.69\times Z+0.31\times Z\times 0.8)=0.74\) or 74%. This is indeed the value shown in Table 2. In the model calculations of Xiao et al. (2004) a larger effect on young leaf removal on partitioning is reported, as these authors reduced total vegetative sink strength, instead of leaf sink strength, by 1/3 when 1 out of 3 leaves was removed. This was based on the assumption that this could be achieved genetically, i.e. 2 leaves between trusses instead of 3 leaves, and hence also no third internode would be formed.
Removal of young leaves to favour partitioning towards the fruits appears a valuable measure for yield improvement, as long as LAI is kept at a sufficiently high level. This can be done by delayed leaf picking (Table 2) or by increased plant (or stem) density (Xiao et al., 2004). Removal of every second young leaf improved yield by 10%, when removal of old leaves was delayed such that an LAI of 3 m² m⁻² was maintained (Table 2).

Starting removal of young leaves immediately after anthesis of the first truss leads to a delay in LAI development. This delay can be avoided by starting removal of young leaves only after a desired LAI has been reached, e.g. 3. In that case an even larger increase in yield as a result of removal of young leaves is expected, as the drop in average LAI (Table 4, lower half) would disappear. Breeding could positively contribute to yield by developing cultivars that genetically limit the number of leaves and internodes between two trusses to e.g. two instead of three. The impact would be even higher as in our calculations, since in such a cultivar also investment in stem material would be reduced by one third as opposed to no reduction in stem weight when leaves are removed manually. Breeding would also overcome a possible practical problem, as compensation for removal of young leaves by retaining older leaves for a longer time may result in leaves lying on the ground. When through breeding not only leaves between trusses disappear, but also internodes, still the same total number of leaves on the plant can be obtained in the same plant length as before. Manual removal of young leaves means extra labour requirement, which could be avoided when cultivars with less leaves between trusses would be available.

Concluding Remarks
Yield can be optimized by controlling LAI. Our calculations show that retaining a LAI up to 4, obtained by delayed picking of old leaves, results in improved yield. Compared to LAI of 3, aiming at LAI of 4 improves yield by about 4%. Partitioning to the fruits is favoured by pruning of young leaves. This is a promising way to improve yield, as long as LAI is kept at a sufficiently high level. If removal of old leaves was delayed such that an LAI of 3 m² m⁻² was maintained, removal of every second young leaf improved yield by 10%.

Literature Cited

Tables

Table 1. Fraction intercepted light measured on two dates in summer at 7 tomato growers in the Netherlands.

<table>
<thead>
<tr>
<th>Grower</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 July</td>
<td>0.94</td>
<td>0.96</td>
<td>0.90</td>
<td>0.91</td>
<td>0.87</td>
<td>0.86</td>
<td>0.89</td>
</tr>
<tr>
<td>10 Sept.</td>
<td>0.92</td>
<td>0.93</td>
<td>0.91</td>
<td>0.89</td>
<td>0.88</td>
<td>0.86</td>
<td>0.92</td>
</tr>
</tbody>
</table>
Table 2. Simulated cumulative fruit dry weight (\(DW_{\text{fruit}}\)), total dry weight (\(DW_{\text{total}}\)), fraction partitioned to the fruits (\(F_{\text{fruits}}\)), average LAI (\(\text{LAI}_{\text{av}}\)), day of year when LAI value 3 was first reached (\(\text{LAI}_{\text{3,day}}\)) and average LAI after this date (\(\text{LAI}_{\text{av3}}\)) for a tomato crop grown from 1 Dec. till 26 Nov. In the control treatments no young leaves were pruned, whereas three other treatments were applied: removal of every sixth (1 out of 6), third (1 out of 3) or second (1 out of 2) leaf at appearance starting when the first truss reached anthesis.

<table>
<thead>
<tr>
<th>Number of young leaves removed</th>
<th>Timing of old leaf removal</th>
<th>(DW_{\text{fruit}}) (kg m(^{-2}))</th>
<th>(DW_{\text{total}}) (kg m(^{-2}))</th>
<th>(F_{\text{fruits}})</th>
<th>(\text{LAI}_{\text{av}}) (m(^2) m(^{-2}))</th>
<th>(\text{LAI}_{\text{3,day}})</th>
<th>(\text{LAI}_{\text{av3}}) (m(^2) m(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>standard(^{x})</td>
<td>2.93</td>
<td>4.26</td>
<td>0.69</td>
<td>2.48</td>
<td>96</td>
<td>3.14</td>
</tr>
<tr>
<td>1 out of 6</td>
<td>standard(^{x})</td>
<td>2.90</td>
<td>4.08</td>
<td>0.71</td>
<td>2.06</td>
<td>106</td>
<td>2.61</td>
</tr>
<tr>
<td>1 out of 3</td>
<td>standard(^{x})</td>
<td>2.79</td>
<td>3.79</td>
<td>0.74</td>
<td>1.63</td>
<td>(___)</td>
<td>(___)</td>
</tr>
<tr>
<td>1 out of 2</td>
<td>standard(^{x})</td>
<td>2.54</td>
<td>3.30</td>
<td>0.77</td>
<td>1.19</td>
<td>(___)</td>
<td>(___)</td>
</tr>
<tr>
<td>Control</td>
<td>delayed(^{y})</td>
<td>2.92</td>
<td>4.25</td>
<td>0.69</td>
<td>2.41</td>
<td>70</td>
<td>2.83</td>
</tr>
<tr>
<td>1 out of 6</td>
<td>delayed(^{y})</td>
<td>3.01</td>
<td>4.24</td>
<td>0.71</td>
<td>2.38</td>
<td>78</td>
<td>2.86</td>
</tr>
<tr>
<td>1 out of 3</td>
<td>delayed(^{y})</td>
<td>3.11</td>
<td>4.22</td>
<td>0.74</td>
<td>2.33</td>
<td>88</td>
<td>2.89</td>
</tr>
<tr>
<td>1 out of 2</td>
<td>delayed(^{y})</td>
<td>3.22</td>
<td>4.18</td>
<td>0.77</td>
<td>2.25</td>
<td>104</td>
<td>2.92</td>
</tr>
</tbody>
</table>

\(^{x}\) standard: removal of old leaves according to developmental stage of the corresponding truss  
\(^{y}\) delayed: removal of leaves from oldest vegetative unit every time LAI>3  
\(^{z}\) treatment did not reach LAI of 3

Figures

Fig. 1. Fraction intercepted light as function of measured leaf area index (LAI), determined once per month starting from mid-March until mid-August for three leaf picking strategies: (●) reference, (Δ) high and (▲) maximum LAI. Curve equation:

\[\text{fract. intercept.} = 1 - e^{-0.75 \text{LAI}}\]

Each data point based on 3 plots.

Fig. 2. Measured (●) reference, (Δ) high and (▲) maximum LAI leaf pruning treatment and simulated (—— reference) LAI throughout the season for commercial tomato crops.