Short communication

Effects of leaf to fruit ratios on fruit growth in chestnut

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Abstract

In \textit{Castanea sativa} Mill. cv. Santa Restituta, 10 days after full bloom, defoliation to give leaf-to-husk ratios of 2/1, 4/1, 7/1, 10/1 and 14/1 was performed on both girdled and ungirdled shoots fully exposed to the sun. The results showed that assimilates can be easily translocated and it is necessary to have about 10 leaves well exposed to light per husk (about five leaves per fruit) to ensure normal fruit development. Fruit is a stronger sink than shoot reserve tissues. A feedback inhibition of photosynthesis at high leaf-to-husk ratios is suggested. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: \textit{Castanea sativa} Mill.; Source–sink relationships; Photosynthesis; Fruit size

1. Introduction

The favourable chestnut market has been stimulating efforts to both renew traditional chestnut groves and to establish new intensive ones. To intensify cultivation, a good knowledge of the physiological aspects related to production is required, but up to now very little information has been available on photosynthesis and on source–sink relationships (Biricolti et al., 1993; Palliotti et al., 1997; Proietti et al., 1999). No information is available on relationships between fruit growth and leaf area. This would be very useful for a better
understanding of the biological and physiological processes controlling cropping and for optimising cultural practices, such as pruning.

In this study the effects of different leaf-to-husk ratios and girdling (which blocks the translocation of assimilates by eliminating the phloem bundles) of shoots on chestnut fruit growth were investigated, in order to obtain information on relationships between leaf area and fruit growth and related processes such as translocability of assimilates within the tree and regulation of the leaf photosynthetic process.

2. Materials and methods

The trial was carried out in 1997 in a non-irrigated adult chestnut orchard in Central Italy, of the species Castanea sativa Mill. cv. Santa Restituta. The trees had a good balance between vegetative and reproductive activities and did not show any stress symptoms. Ten days after full bloom (mid-July), defoliation to give leaf-to-husk ratios of 2/1, 4/1, 7/1, 10/1 and 14/1 was performed on girdled and ungirdled shoots fully exposed to the sun. Fifteen shoots, distributed in five trees, were used as replicates. The girdles, about 0.5 cm wide, were performed at the base of the shoots, at about 1 cm from their insertion on the branches, by removing the whole ring of bark with a grafting knife. The girdles were maintained for the entire growing season by removing any scar tissue at 2 week intervals.

On ungirdled and girdled shoots with a leaf-to-husk ratio of 4/1, 7/1 and 14/1, starting 2 weeks after treatments until September, on cloudless days, around mid-day the net photosynthesis, stomatal conductance and intercellular CO2 concentration were measured periodically (about every 15 days) on middle leaves of the shoots (10 replications per treatment), by using a portable open-system infrared gas analyser, as described in Proietti et al. (1999).

At harvest, the number of fruit per husk and fruit and husk weights and dry matter content were determined. Moreover, shoot dry matter, soluble carbohydrate and starch contents and endosperm cyto-histo-anatomical characteristics were also evaluated on ungirdled and girdled shoots with a leaf-to-husk ratio of 4/1, 7/1 and 14/1. The methods used for carbohydrate measurements and for cyto-histo-anatomical investigations are described in Proietti et al. (1999). Measurements of cell size were made using a light microscope (×1000 magnifications); the values reported are the average of 20 observations.

3. Results

The number of fruits per husk was not affected by the treatments (Table 1). The different leaf-to-husk ratios did not affect the fruit/husk + fruits ratio and fruit and husk growth in ungirdled shoots (Fig. 1). Conversely, it affected these
parameters in girdled shoots, with the 10/1 ratio showing values similar to those of ungirdled shoots; a quadratic regression curve fit the relationships between leaf-to-husk ratio and fruit and husk weight at harvest. Fruits grown on girdled shoots with a low leaf-to-husk ratio (2/1 and 4/1) had a lower dry matter content than the others, which were not significantly different from one another.

Fruit weight was related to size; both maximum and minimum diameters were modified by treatments (Table 2). The different leaf-to-husk ratios did not cause any difference in endosperm cell size in ungirdled shoots, whereas they caused significant differences in girdled shoots, with the 14/1 ratio having cells as large as those of the ungirdled shoots.

### Table 1
Effect of leaf-to-husk ratio and girdling on some fruiting characteristics

<table>
<thead>
<tr>
<th>Shoot</th>
<th>Leaf/husk ratio</th>
<th>Fruits/husk (no.)</th>
<th>Fruits/(husk + fruits) (%)</th>
<th>Fruit dry matter content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ungirdled 2/1</td>
<td>2.2 a</td>
<td>38.9 cd</td>
<td>43.0 c</td>
<td></td>
</tr>
<tr>
<td>Girdled 2/1</td>
<td>2.3 a</td>
<td>25.0 a</td>
<td>38.0 a</td>
<td></td>
</tr>
<tr>
<td>Ungirdled 4/1</td>
<td>2.3 a</td>
<td>40.4 cd</td>
<td>43.0 c</td>
<td></td>
</tr>
<tr>
<td>Girdled 4/1</td>
<td>2.3 a</td>
<td>35.0 b</td>
<td>41.1 b</td>
<td></td>
</tr>
<tr>
<td>Ungirdled 7/1</td>
<td>2.3 a</td>
<td>39.4 cd</td>
<td>43.1 c</td>
<td></td>
</tr>
<tr>
<td>Girdled 7/1</td>
<td>2.4 a</td>
<td>35.6 bc</td>
<td>42.5 bc</td>
<td></td>
</tr>
<tr>
<td>Ungirdled 10/1</td>
<td>2.2 a</td>
<td>39.8 cd</td>
<td>42.8 c</td>
<td></td>
</tr>
<tr>
<td>Girdled 10/1</td>
<td>2.3 a</td>
<td>40.1 cd</td>
<td>42.7 c</td>
<td></td>
</tr>
<tr>
<td>Ungirdled 14/1</td>
<td>2.4 a</td>
<td>41.5 d</td>
<td>42.4 bc</td>
<td></td>
</tr>
<tr>
<td>Girdled 14/1</td>
<td>2.3 a</td>
<td>41.1 d</td>
<td>42.9 c</td>
<td></td>
</tr>
</tbody>
</table>

*Data were submitted to analysis of variance and means separation was performed using the Student–Newman–Keuls test. In each column, means followed by the same letter are not significantly different at \( P \leq 0.05 \).*

### Table 2
Effect of leaf-to-husk ratio and girdling on fruit dimension and endosperm cell size

<table>
<thead>
<tr>
<th>Shoot</th>
<th>Leaf/husk ratio</th>
<th>Maximum fruit diameter (mm)</th>
<th>Minimum fruit diameter (mm)</th>
<th>Endosperm cell size</th>
<th>External zone (( \mu m^2 ))</th>
<th>Internal zone (( \mu m^2 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ungirdled 4/1</td>
<td>31.0 c</td>
<td>19.1 c</td>
<td>1545 c</td>
<td>1976 bc</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Girdled 4/1</td>
<td>25.1 a</td>
<td>13.1 a</td>
<td>974 a</td>
<td>1506 ab</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ungirdled 7/1</td>
<td>32.0 c</td>
<td>19.6 cd</td>
<td>1420 bc</td>
<td>1783 bc</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Girdled 7/1</td>
<td>27.3 b</td>
<td>16.3 b</td>
<td>1011 a</td>
<td>1272 a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ungirdled 14/1</td>
<td>29.9 c</td>
<td>17.0 c</td>
<td>1455 bc</td>
<td>1898 bc</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Girdled 14/1</td>
<td>36.4 d</td>
<td>21.2 d</td>
<td>1119 ab</td>
<td>1996 c</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Data were submitted to analysis of variance and means separation was performed using the Student–Newman–Keuls test. In each column, means followed by the same letter are not significantly different at \( P \leq 0.05 \).*
In all treatments, as expected, fruit weight was also affected by the number of fruits per husk (1, 2 or 3), with a negative correlation between number and weight (data not shown). The slope (b) of the regression lines was $-1.2$ for ungirdled shoots (with no differences due to leaf-to-husk ratios) and $-1.8$, $-1.6$ and $-1.0$ for girdled shoots with a leaf-to-husk ratio of 4/1, 7/1 and 14/1, respectively.

The different leaf-to-husk ratios did not influence the dry matter, soluble carbohydrate and starch contents of ungirdled shoots, but it affected those of girdled shoots (Table 3).

Fig. 1. Relationship between leaf area, fruit and husk weights on ungirdled (linear) and girdled (quadratic) shoots. Bars represent standard error. Leaf-to-husk ratios are shown in the parentheses.
Table 3
Effect of leaf-to-husk ratio and girdling on shoot dry matter and carbohydrate contents

<table>
<thead>
<tr>
<th>Shoot ratio</th>
<th>Dry matter (%)</th>
<th>Soluble carbohydrates (mg gf w⁻¹)</th>
<th>Starch (mg gf w⁻¹)</th>
<th>Total carbohydrates (mg gf w⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Un-girdled 4/1</td>
<td>47.5 b</td>
<td>41.1 c</td>
<td>35.2 c</td>
<td>76.3 c</td>
</tr>
<tr>
<td>Girdled 4/1</td>
<td>44.0 a</td>
<td>21.4 a</td>
<td>22.2 a</td>
<td>43.6 a</td>
</tr>
<tr>
<td>Un-girdled 7/1</td>
<td>47.8 b</td>
<td>44.4 cd</td>
<td>33.8 c</td>
<td>78.2 c</td>
</tr>
<tr>
<td>Girdled 7/1</td>
<td>45.1 a</td>
<td>26.6 b</td>
<td>26.4 b</td>
<td>53.0 b</td>
</tr>
<tr>
<td>Un-girdled 14/1</td>
<td>46.7 b</td>
<td>41.1 c</td>
<td>34.4 c</td>
<td>75.5 c</td>
</tr>
<tr>
<td>Girdled 14/1</td>
<td>49.9 c</td>
<td>46.0 d</td>
<td>40.0 d</td>
<td>86.0 d</td>
</tr>
</tbody>
</table>

Data were submitted to analysis of variance and means separation was performed using the Student–Newman–Keuls test. In each column, means followed by the same letter are not significantly different at \( P \leq 0.05 \).

Fig. 2. Effect of leaf-to-husk ratio and girdling on leaf gas exchange parameters (seasonal average values). A = net photosynthesis; gs = stomatal conductance; Ci = intercellular CO₂ concentration. Bars represent standard error.
The leaf photosynthetic rate, stomatal conductance and intercellular CO₂ concentration were similar in all the ungirdled shoots and the girdled ones with a ratio of 4/1 and 7/1, whereas the girdled shoots with a ratio of 14/1 showed lower net photosynthesis and stomatal conductance and higher internal CO₂ concentration (Fig. 2).

4. Discussion

The alteration of the assimilate availability for fruits starting 1–2 weeks after bloom did not affect the number of chestnuts per husk; this means that this important production factor is mainly influenced up to the time of fruit-set.

The lack of differences in the growth of fruits and in the shoot dry matter and carbohydrate content in ungirdled shoots with different leaf-to-husk ratios indicates ready translocability of assimilates within the tree, so that the growth of fruits and the accumulation of dry matter in shoots with a low leaf-to-husk ratio can be sustained. This result is similar to that obtained in other fruit species such as *Actinidia deliciosa* (Snelgar and Thorp, 1988; Famiani et al., 1997).

In girdled shoots, fruit and husk growth is strictly dependent on the leaf-to-husk ratio. Ten leaves well exposed to light per husk were necessary to ensure fruit development similar to that observed in ungirdled shoots. Since the weight of fruit grown on such shoots was within the range considered normal for the examined cultivar (Antognozzi, 1986), it can be deduced that 10 leaves per husk (about five per fruit) is the leaf surface area (about 630 cm²) that is required for normal fruit development. The quadratic regression curves, which represent the relationships between leaf area, fruit and husk weight, showed that the production of both fresh and dry matter per unit leaf area decreased as the leaf-to-husk ratio increased. On a seasonal basis 1 cm² of leaf produced 320–250 mg of fresh and 70–90 mg of dry matter (fruits + husk) when the leaf-to-husk ratio ranged from 2/1 to 4/1 and 120–90 mg of fresh and 40–30 mg of dry matter when the ratio ranged from 10/1 to 14/1. The productivity obtained with low leaf to fruit ratios is high with respect to studies carried out on other crops, such as apple, grape, grapefruit, kiwifruit and pecan (Marquard, 1987; Snelgar and Thorp, 1988 and references in it; Famiani et al., 1997). Kiwifruit, which among the other crops showed the highest values, had higher values on fresh weight basis (470–880 mg of fresh matter per cm² of leaf), but similar or lower values on dry matter basis (50–80 mg of dry matter per cm² of leaf), even though its fruiting season was longer. The lower leaf productivity observed in girdled shoots with a high leaf-to-husk ratio is consistent with the lower net photosynthesis observed in these shoots; the low photosynthetic activity in the presence of a high CO₂ intercellular concentration, in spite of the low leaf stomatal conductance, suggests that the reduced photosynthesis is due to a feedback inhibition, which has also been observed in some other fruit species (Flore and Gucci, 1988). This effect was not
observed on ungirdled shoots with a high leaf-to-husk ratio, probably because of
the demand for assimilates by other sinks, such as fruits on other shoots, roots,
shoot apices and reserve tissues. The photosynthetic rate values are similar to
those reported by other authors for other chestnut cultivars (Biricolti et al., 1993;
Palliotti et al., 1997).

The strong effect of the different leaf-to-husk ratios on carbohydrate content of
girdled shoots can be explained by the observation that in deciduous trees during
the time of application of treatments (from summer to autumn), accumulation of
reserves takes place in shoots and branches (Dickson, 1991). In girdled shoots,
the amount of carbohydrates augmented by about 21% as the leaf-to-husk ratio
increased from the 4/1 to the 7/1 and by about 62% from the 7/1 to the 14/1.
Whereas fruit dry weight increased by about 85% from the 4/1 to the 7/1 ratio and
by about 46% from the 7/1 to the 14/1 ratio. This shows that, when the assimilate
availability is low most of the assimilates are allocated to fruits and only when
there is a surplus is there a remarkable increase in carbohydrate concentration
in shoot reserve tissues.

The microscopic observations indicated that assimilate availability still affected
endosperm cell division 1–2 weeks after bloom. The larger size of fruits on
girdled shoots with a leaf-to-husk ratio of 14/1 must be due to a higher cell
number in the endosperm as cell size was similar to that of fruits on ungirdled
shoots. Moreover, assimilate availability affects cell size which was greatly
reduced (up to 30%) when the leaf-to-husk ratio was low. This demonstrates that
all the phases of fruit growth are affected by assimilate availability.

The regression lines fitted to evaluate the relationships between the number of
chestnuts per husk and their weight show that the degree (slope of line) of
decrease in weight with increase in fruit number was higher when assimilate
availability was low and vice versa. Therefore, when the tree is able to guarantee
a large amount of assimilates it is possible to reach a good fruit size even with
three fruits per husk.

Since we report a single season’s and cultivar’s results, further investigations will
be necessary to define the extent of influence of seasonal trend and cultivar on
relationships between leaf area and fruit growth and shoot reserve accumulation.

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