FUNCTIONAL ADAPTATIONS OF FIG TREES (FICUS CARICA, L.) IN AGROECOSYSTEMS OF THE WESTERN MEDITERRANEAN DESERT OF EGYPT.

By

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ABSTRACT

The ecophysiological characteristics of fig (Ficus carica, L.) trees, growing with maximum activity during the hot and dry summer, were studied in relation to growth, carbon partitioning, nutrient balance and water use. The initiation of growth was dependent on carbohydrate reserves (estimated usage = 62%). The trees enhanced their short growth span by rapid increase in leaf area associated with high photosynthetic rate early in the season, allowing a storage of 20% of net assimilate produced for latter use. High net primary production (3200 kgDM ha⁻¹) was the result of a high relative growth rate. About 46% of this production contributes to ligneous structure of the agroecosystem.

Fig trees exhibited a positive nitrogen balance, among other nutrients, as a result of withdrawing nutrients prior to leaf abscission except for the excess calcium which is removed through litter. However, large quantities of resources are harvested within fruits, hence fertilizer application is essential for maintenance of yield. Although fig trees exhibited efficient water uptake and water use capacities, yet supplementary irrigation in years of below average rainfall is also important to maintain the relatively high transpiration rate and high annual water output.

INTRODUCTION

Fig tree (Ficus carica, L.) is deciduous subtropical and a native of arid and semi-arid Mediterranean regions. It is one of the most common fruit trees that grow successfully in the western Mediterranean desert of Egypt (Keleg et al. 1981). The area cultivated by fig in this region is estimated at about 5900 ha, with a mean expansion rate of 220 ha yr⁻¹ (Abdel-Razik et al. 1987). High planting density (190-400 tree ha⁻¹) coupled with deficiency of investigation on cultural techniques and of information about the required levels of water and fertilizer supply
Functional adaptations of fig trees constitute the major gaps of knowledge for this crop in the region.

The aim of the present study is to elucidate the main ecophysiological features of the fig agroecosystem through the intricate relationships between growth and production rates, cycling of nutrients, role of water and the biotic and physical environments. This is essential to improve our knowledge about the rates of different processes and to provide information that could be utilized in further improvement of the crop.

The study area is located at about 47 km west of Alexandria on the coastal belt of the western Mediterranean desert of Egypt. Average rainfall is 150 mm yr\(^{-1}\), and monthly average temperature ranges between 13.2\(^o\)C in January and 26.0\(^o\)C in August. Average soil measures are: pH=7.23, EC=0.46 mmhos cm\(^{-1}\), CaCO\(_3\)=4.82%, and OM.=2.17% (Abdel-Razik et al. 1984). The selected fig orchard is 30 years old, rain-fed, and with a sandy loam calcareous soil (soil depth = 50-150 cm). Planting density is about 400 trees ha\(^{-1}\) (with no intercrops), and is supplied with manure fertilizer at a rate of about 30 kg tree\(^{-1}\) yr\(^{-1}\) applied in January. The cultural practices include pruning after leaffall in autumn, ploughing during the rainy season (November-January) combined with weeding and mulching. Two or three irrigations are applied before summer.

**MATERIALS AND METHODS**

Seven trees were selected from random locations in the orchard and were used in sampling of plant material (biweekly) throughout the study period. Litter samples were collected using litter traps while composite soil samples were collected at one meter distance from the trunk underneath the selected trees. All plant and soil samples were prepared and analysed for the determination of their nutrient contents (Allen et al. 1974). The total non-structural carbohydrate (TNC) was also estimated in plant samples as well as the leaf chlorophyll content (Vernon 1960).

Variations in the number of each of the current year organs per tree were recorded each sampling date. Samples of these organs were also collected from adjacent trees for biomass determination to avoid destruction of the trees. The average leaf area and weight was measured for the three size classes (small, medium and large). Measures on each organ were then integrated over its total number per tree. A destructive harvesting of the selected trees was carried out by the end of sampling period and used to correct for the estimated biomass retrogressively, and to evaluate the standing phytomass of the orchard.

The calculated daily increment of the orchard’s TNC content is divided by the standard conversion efficiency (0.761) of primary assimilate (CH\(_2\)O) into carbohydrate to evaluate the equivalent increment in primary photosynthate production. Similarly, the calculated net photosynthetic rate (NPR) in gram dry matter per unit
ground area is evaluated in CH$_2$O weight by dividing each organ’s growth increment by its conversion efficiency and sum over organs. The conversion efficiencies used are: leaves = 0.80, branches = 0.65, roots = 0.65 and reproductive = 0.55 gDM g$^{-1}$ CH$_2$O (Abdel-Razik et al. 1989). The resultant NPR is further calculated on leaf weight basis through dividing by average weight of leaves between each two successive dates. The maintenance respiration of new growth is calculated as function of protein and mineral contents in each organ (protein maintenance = 0.036 gCH$_2$O g$^{-1}$ protein d$^{-1}$ and minerals maintenance = 0.072 gCH$_2$O g$^{-1}$minerals d$^{-1}$).

RESULTS

The deciduous fig tree started active growth cycle early in spring and reached its peak vegetative activity and yield during the hot and dry summer season. The maximum standing biomass of current year’s growth (about 313 g m$^{-2}$) followed the peak of relative growth rate (about 28.3 g kg$^{-1}$ d$^{-1}$) which was attained late in May (Table 1). The average orchard’s skeletal biomass (old stems and roots) was

<table>
<thead>
<tr>
<th>Date</th>
<th>Biomass (g m$^{-2}$)</th>
<th>Necromass (g m$^{-2}$)</th>
<th>Harvested (g m$^{-2}$)</th>
<th>RGR (g kg$^{-1}$ d$^{-1}$)</th>
</tr>
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</tr>
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<td>0.0</td>
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<td>24</td>
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<td>9.100</td>
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Standing skeletal (stems + roots) biomass = 4088 g m$^{-2}$ orchard.
calculated as about 4088 g m\(^{-2}\). The relative growth rate of fresh material followed a trend of rapid increase to the maximum rate (28.3 g kg\(^{-1}\) DM d\(^{-1}\)) late in spring when the plant was developing syconia (floral parts). Temporal variations in carbon allocation to different organs (Fig. 1a) indicated higher physiological activity during the first part of the growth season (vegetative activity). Although both vegetative and floral buds start their growth simultaneously early in the season, the relative growth rate of vegetative organs decreased (maximum rates of leaves and branches were 11.7 and 5.0 mg g\(^{-1}\) d\(^{-1}\) respectively) when the total biomass was less than one third of its maximum value (Fig. 1b). Conversely, the relative growth rate of reproductive parts increased to a maximum (10.2 mg g\(^{-1}\) d\(^{-1}\)) coincident with maximum biomass, during which the root biomass was also increasing.

Fig. 1: Temporal variations in biomass of current organs (a), and the relationship between their relative growth rates and the cumulative biomass of these organs (b). L = leaves, B = branches, R = roots and P = reproductive parts. Note: points are mid-ranges of organs biomass which vary in the following ranges: L±(2.0 to 9.7), B±(1.7 to 6.3), R±(11.8 to 31.1), P±(3.3 to 12.4).
Populations of mature leaves replaced young ones through the more or less normally distributed population of leaves in the medium size class (Fig. 2a). An exponential increase in the population of young leaves during the first growth phase was associated with the increase in the average specific leaf area (SLA) for the canopy (Fig. 2b). On the other hand, the ratio of leaves in the medium size class exhibited much less variability in relation to increase in SLA compared with that of both young and fully mature leaves. Eventually, most leaves matured within a narrow range of variation in SLA that characterises this phase.

Fig. 2: Variation in the populations of leaves in different size classes, as ratios of the maximum number, in relation to time (a) and to SLA (b). S = small, M = medium and L = large size class.

The maximum leaf area index (LAI) was attained during mid summer (July) which coincided with the highest leaf chlorophyll content (annual range between 0.35 and 1.51 mg g⁻¹FW. leaves) and a relatively high total non-structural carbohydrate
(TNC) content in the plant canopy (Fig. 3). However, the maximum TNC was attained well after the peak of LAI, and concurrent with fruit maturity stage. The subsequent decline in LAI and TNC was directly related to losses due to leaf shedding and fruit harvesting operations.

Fig. 3: Temporal variations in leaf area index (solid line), leaf chlorophyll content (enclosed between brackets) and total non-structural carbohydrate content in the plant canopy (vertical bars).

Temporal variations in the orchard’s TNC content, its daily increments, the biomass increment, the net photosynthetic rate and the maintenance respiration (Table 2) indicate that early in the season (February) a growth increment (NPP) of 0.33 gDM m⁻² d⁻¹ was produced when no photosynthesis occurred and TNC increment was nil. Accordingly, this initiation stage was completely dependent on carbohydrate reserves, and when the maintenance need was added, a daily usage can be estimated as about 5.5% of TNC reserves during this stage. The orchard’s NPR increased gradually to its peak (6.12 gCH₂O m⁻² d⁻¹) attained at maximum vegetative activity and was associated with increasing the increments to TNC and to growing plant tissues. However, NPR per unit leaf weight exhibited the reverse trend; the highest value was attained at the beginning of the growth period after self sufficiency of growing buds.

Although maintenance demand for assimilate increased dramatically during peak activity of the plant, which coincided with the sharp decline in orchard’s NPR, yet a measurable TNC increment to its reserves occurred and a maximum content of about 101 g m⁻² was attained in summer. The maximum ratio of assimilate
Temporal variations in the orchard’s content of total non-structural carbohydrate (TNC), its daily increment (TNCI), net primary productivity (NPP), net photosynthetic rate (NPR) and maintenance respiration (MR).

<table>
<thead>
<tr>
<th>Date</th>
<th>TNC (g m⁻²)</th>
<th>TNCI (gCH₂O m⁻² d⁻¹)</th>
<th>NPP (gDM m⁻² d⁻¹)</th>
<th>NPR (gCH₂O leaves d⁻¹)</th>
<th>MR (gCH₂O m⁻² d⁻¹)</th>
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<tr>
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<td>1.738</td>
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<tr>
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<td>0.154</td>
<td>0.152</td>
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<td></td>
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<td>0.070</td>
<td>0.097</td>
<td>0.002</td>
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<tr>
<td>O</td>
<td>42.90</td>
<td>0.0</td>
<td>0.092</td>
<td>0.117</td>
<td>0.003</td>
</tr>
<tr>
<td>N</td>
<td>36.91</td>
<td>0.0</td>
<td>0.025</td>
<td>0.034</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Allocated to TNC reserves was attained during the early vegetative activity (about 34%) and declined to lower value (about 16%) at peak vegetative activity. A calculated ratio of about 36.5% of maximum TNC reserves attained during the season was speculated to be the stored amount for maintenance use during dormancy period and for initiation of growth for next season.

The reproductive parts of fig trees had the highest average concentrations of nitrogen, phosphorus and potassium, in contrast to calcium, as compared to their concentrations in the other organs and in litter which was particularly rich in Ca (Fig. 4). The ash content, as an indication of total minerals, was high in leaves and reproductive parts compared to branches and roots. Carbohydrate reserves were more variable especially in young branches and in fruits which contained the highest concentrations compared to leaves and roots.

Leaves had the highest protein to carbohydrate (P/C) ratio followed by reproductive parts (annual average of 0.94 and 0.62 respectively) compared to those of branches and roots (0.24 and 0.26 respectively). The general trend of temporal changes in P/C ratio was a decline for leaves and reproductive parts which
Fig. 4: Average concentrations of selected nutrients and of ash in the different organs, and the associated contents of TNC (confidence intervals are indicated).
M. S. ABDEL-RAZIK and S. EL-DARIER

contrasted the increase in the ratio for the other organs. The overall P/C ratio for the tree was increasing from 0.21 to 0.84 along the growth season with an annual average ratio of about 0.43.

The quantity of the reproductive parts produced at time of peak growth activity was relatively high and exceeded the sum of leaves and current branches (Fig. 5).

Fig. 5: The state of fig agroecosystem at time of peak growth activity. Each component includes biomass in g m\(^{-2}\) and concentrations of nitrogen (N), phosphorus (P), total minerals (TM) and TNC in mg g\(^{-1}\)DM. All flows and retained amounts are in g m\(^{-2}\) yr\(^{-1}\). The uptake is the magnitude of change in nutrient content at successive points of time. The translocation is the amount to flow after decrementing retained amounts in the successive organs.
Reproductive parts were also more rich in all their contents of nutrients that reflected the high translocation rate into this component. The skeletal parts were considered mediators in translocation processes. The concentration of nutrients, except for N, in the litter component was very close to that in leaves. The integrated content of each nutrient over organs' components (biomass times concentration) was lower than annual translocation by the amount translocated post peak activity (which is not presented in the diagram). This also applied to translocation to roots. Some reproductive parts were lost to litter during the season which increased litter nutrient concentrations. However, the high ash content in litter was due to accumulation of especially Ca, while other nutrients were withdrawn prior to senescence. The TNC annual increment in the orchard (106.8 g m\(^{-2}\)) was considered to be the net assimilate reserves and was distributed among the different components starting with leaves.

The highest transpiration rate on leaf area basis (0.174 g dm\(^{-2}\) h\(^{-1}\)) was attained in April (Figure 6) when leaves were young and had the highest water content (3.84 g g\(^{-1}\)DM) and maximum specific leaf weight (0.055 gFW cm\(^{-2}\)). Conversely, the highest transpiration rate on fresh weight as well as on dry weight basis (50 and 196 g 100g\(^{-1}\) h\(^{-1}\) respectively) was attained in August (fruit maturity) when leaf margin started dissection.

The daily average water output on soil surface area basis was calculated using the daily average transpiration rates and the corresponding leaves biomass. It exhibited a gradual increase from 0.012 mm d\(^{-1}\) early in the season to a maximum value of 1.765 mm d\(^{-1}\) at time of peak vegetative activity, then declined gradually in response to reduction in leaf area upon their death. This was associated also with gradual decrease in soil moisture content. The annual water output was estimated as 175.44 mm yr\(^{-1}\) which was calculated by integration of daily output over the growth period.

**DISCUSSION**

This intensive study on the important cash crop of fig in arid coastal land of Egypt provides perspectives for improvement of its cultural development. The growth pattern of deciduous fig trees and their peak summer activity causes the ecophysiological responses and adaptations to come into prominence.

The net primary productivity was calculated as about 3203 kg DM ha\(^{-1}\) when the standing crop biomass was 40.88 tonnes ha\(^{-1}\). About 20% of this productivity was lost to litter (mostly due to leaf shedding) while about 34% was due to harvesting operations. Consequently, a relatively high ratio (about 46%) contributed to the growth of skeletal structures (ligneous plant parts) of the orchard; conservation of
Fig. 6: Temporal variations in the transpiration rate on fresh weight (F), dry weight (D) and leaf area basis (L), in relation to leaf water content (hatched bars) and to soil moisture content at different soil depths. The standard error for (F) varied between 2.12 in March and 6.98 in July, between 8.51 in June and 26.97 in August for (D), between 0.011 in May and 0.022 in August for (L) and between 0.015 in July and 0.077 in April for leaf water content.
Functional adaptations of fig trees

resources for positive net ecosystem productivity (Melillo 1985). The root ratio (about 41% of total biomass) is within the range characterising many of desert perennial vegetation (e.g. Wallace et al. 1974, Abdel-Razik et al. 1988) and is very close to the ratio for olive trees in the same region (Ayyad et al. 1985). Maximum relative growth rate was attained during late spring (28.3 g kg\(^{-1}\) new tissues d\(^{-1}\)) which coincided with the middle of an exponential growth phase of current year organs and resulted in attaining the maximum production rate during mid summer (about 40.7 kg ha\(^{-1}\) d\(^{-1}\)) corresponding to the peak reproductive activity.

The initiation of growth by the expanding buds generally depends on the carbohydrate reserves which concurrently decline to their lowest level. Importing carbohydrate from storage tissues shortly after bud break (Moorby 1977) and drainage of carbohydrate stores for use of new shoot (Larcher 1975, Tateno and Watanabe 1988) is well documented for deciduous trees. The estimated usage of carbohydrate reserves during leafing out activity in fig trees in the present study was about 62% of its content (in excess of maintenance needs of average 0.2 gCH\(_2\)O m\(^{-2}\) d\(^{-1}\)) during dormancy period.

Reduction in leaf area is normally an important morphological adaptation in desert plants. However, the leaf area index (LAI) of fig trees reached its maximum value together with peaks of specific leaf area and of leaf chlorophyll content during mid summer when the soil was virtually dry. Such LAI of fig trees is comparable to many wild and cultivated plants in less stressful environments (cf. Whittaker and Likens 1975, Tanner 1980, Fitter and Hay 1981). Therefore, the interplay between leaf area and resource allocation is an important criterion. The early vegetative stage was characterised by the expansion of leaf area via increasing leaf population as well as SLA, hence most resources were used in building up of new tissues. This was followed by an intermediate phase characterised by less variability in leaf population while resources were monopolized for increasing SLA through leaf maturation process. Finally leaf maturity stage exhibited minor changes in SLA and coincided with the period of fruit maturity and material storage in roots. Therefore, we assume an active translocation of resources from leaves to the other organs takes place during this later stage.

The fig trees enhanced their short growth period and the acquired storage of energy reserves through a relatively high net photosynthetic rate (NPR) early in the season. The average NPR during spring was about 0.255 gCH\(_2\)O g\(^{-1}\)leaves DM. d\(^{-1}\), which is equivalent to net assimilation rate (NAR) of about 23 mgCO\(_2\) g\(^{-1}\) h\(^{-1}\) as average for day time. In comparison, Larcher (1975) reported values for maximum NAR between 15 and 25 mgCO\(_2\) g\(^{-1}\) h\(^{-1}\) for winter-deciduous trees and shrubs in tropics and subtropics. About 20% of the total net assimilate produced during vegetative activity was allocated to TNC increments, while the remainder was used in building up of the plant tissues (structural carbohydrates). The stored
TNC was partially used latter in the season to support fruit yield especially with the much lower NPR during late reproductive activity. Accordingly, replenishment of carbohydrate reserves occurred early in the season.

The characteristic positive N-balance in fig trees is essential (annual uptake exceeds total restitution to litter and harvested fruits) since deciduous fruit trees may make little growth and bear little or no fruit when N supply is low (Chandler 1951). Consequently, protein was building up in the new tissues of fig trees which resulted in an increase in protein/carbohydrate ratio (P/C) from about 0.21 at the initiation of vegetative growth to about 0.84 at reproductive stage, although TNC content in these tissues was also increasing. However, the annual average P/C ratio was about 0.42 which is a relatively low value and may reflect a dominating role of TNC storage in the fig tree. McNoughton (1966) suggested that lower P/C ratio for a plant population would indicate that the plant is operating on more of a carbohydrate economy; it converts proportionally more of the incoming energy into readily utilizable energy stores. This was more evident in roots of fig trees, assuming meta-populations of individual plant organs, with annual average P/C ratio of about 0.26 compared to 0.94 and 0.62 for leaves and reproductive parts respectively. This may be attributed to the higher requirements of leaves and fruits for building up of tissues within shorter period. Furthermore, the roots are not exposed to fluctuations in climate as great as those to shoot, hence active translocation of TNC for storage in root result in low P/C ratio.

Small proportions of the uptaken quantities of N, P and total minerals were retained in perennating organs (about 10, 39 and 28% respectively) compared to those allocated to deciduous organs. This coincided with accumulation of TNC in perennating organs up to about 34% of its total annual increments. On the other hand, the release from nutrient deficiency by manure addition led to higher concentrations of N and total minerals in leaves associated with reduced concentration of TNC compared to those in ligneous parts. This is consistent with observations of Chapin (1980) and Van Soest (1982), and to the assertion that carbohydrate accumulation leads to substantial investment in fibre (Chapin et al. 1986).

The edible fruits constituted about one third of the annual dry matter production of the fig orchard, and accumulated relatively high ratios of the annual supply of N, total minerals and TNC at peak growth (about 60, 40 and 52% respectively). Therefore, fruit harvesting was a major constraint on the ecosystem, yet harvesting of N and total minerals were eventually made up for by manure fertilization. Conservation of meagre nutrients was also recorded. For example, Ca accumulation in litter to high concentration (annual average 1.5 folds that in leaves) contrasts to the lower concentrations of N and K in litter (annual averages at most one half those in leaves).
Functional adaptations of fig trees

The annual mean transpiration rate (about 36 g 100g⁻¹FW h⁻¹) was very close to previous records in the region (El-Shourbagy 1967). This rate is relatively high compared to that of deciduous almond trees (31 g 100g⁻¹ h⁻¹) and is four folds that of evergreen olive trees (10 g 100g⁻¹ h⁻¹) as measured by Abdel-Rahman et al. (1966) in the region. However, the annual total water output by fig orchard (about 175 mm yr⁻¹) was intermediate in quantity when compared with outputs by almond and olive (216 and 72 mm yr⁻¹ respectively). The relatively high root to shoot ratio in fig trees (1:1.44) coupled with the extension of roots to a distance nearly twice as that of top spread (Keleg et al. 1981) would have a prominent role in providing the plant with its need of water and nutrients during the summer activity.

The transpiration coefficient for fig trees in the present study reflected a very conservative use of water (about 326 gH₂O g⁻¹DM) at time of maximum dry matter production. This coefficient indicates higher water use efficiency of fig trees compared to the cultivated herbaceous crops as wheat, barley, clover and cotton (540, 520, 640 and 570 gH₂O g⁻¹DM respectively; Stocker 1929, Polster 1967 and Black 1971). However, the C4 plants as maize have coefficients around 370 gH₂O g⁻¹DM, while an average value for deciduous trees is about 340 gH₂O g⁻¹DM produced.

CONCLUSIONS

The deciduous fig trees seem to adopt tactics that would help to sustain a relatively high yield and provide the acquired carbohydrate stores for next growth season. Of these are rapid increase in LAI, high NPR, and a positive nitrogen balance, which together support both growth requirements and storage of reserves. Indeed the exponential growth of new tissues results in a continuous increment to TNC reserves that supports maintenance needs and fruit yield demands during lower assimilation activity late in summer. While a relatively high ratio of net primary productivity is invested in long term net ecosystem production.

The ability of fig tree to remove the absorbed Ca ions in excess through dying leaves, and to conserve less available nutrients is admirable. Consequently, insignificant annual variation in nutrient concentrations (detected by their confidence intervals) may indicate the role of large reserve pool in the skeletal component of the tree. However, fruit harvesting results in constraints that can be compensated for by adequate fertilizer application, which seems to affect yield more than total primary production.

The relatively high transpiration rate of fig trees and the estimated annual water output, although indicate high water uptake and use efficiencies, yet strengthen the importance of supplementary irrigation in years of below average rainfall to meet their water demands and to prevent premature leaf drop (strike reduction in LAI). 

196
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REFERENCES


التكيفات الوظيفية لأشجار الزيتون (Ficus carcia, L.) – زراعية لصحراء الساحل الغربي للبحر المتوسط بمصر

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إنهدف البحث لدراسة الصفات البيئية - فسيولوجية لأشجار التين السلطاني والتي تتميز بأقصى نشاط لها أثناء موسم الصيف الجاف والرتفع في درجة الحرارة. وقد أمكن ربط هذه الصفات بتقديرات النمو ونسبة الأعضاء المختلفة، إلى جانب ميزانية العناصر المعدنية واستخدام الماء المتاح. وقد تبين إ komment ٍنباط في بدء نشاطه على مخزونه من الكربونات المتاحة، بينما تميزت المراحل اللاحقة من فترة النمو القصيرة نسبيًا لهذه الأشجار بزيادة سريعة لساحة أوراقها الكلية مصحوبة بإرتفاع معدل البناء الضوئي مبكراً في موسم النمو، ويسمح هذا بتوفير كمية تختلف للإستخدامات اللاحقة ترتفع ٢٠٪ من مجموع إنتاجيتها. وقد كان لإرتفاع معدل النمو النسبي للمجموع الخضري تأثيره الواضح في إرتفاع الإنتاجية الأولية الصافية لأشجار التين.

وقد أظهرت الدراسة وجود ميزان موجب للتيتوجين والذي يعزى إلى إعادة توزيعه بسحابة من الأوراق قبلي موتها مع العديد من العناصر الأخرى فيما عدا الكالسيوم الزائد والذي يتخلص منه النبات بتركيزه في النثر. وتبين الدراسة أيضاً أن كمية كبيرة من المصادر الغذائية يتم حصادها في النثر، ولذا فإنها من الهام إضافة المخصبات لهذه الزراعات لضمان إنتاجيتها بشكل جيد. ومن ناحية أخرى فإنها بالرغم من أن أشجار التين تبدي كفاءة في إمتصاص وإستخدام الماء إلا أنها تحتاج إلى إضافات مائية مقننة خلال سنوات الجفاف لموازنة احتياجاتها المائية، ومقابلة معدلات النمو المرتفعة وكمية الماء المفقودة سنوياً لهذه الأشجار.