Resource use efficiency of field-grown sunflower, sorghum, wheat and chickpea

II. Water use efficiency and comparison with radiation use efficiency

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Abstract

Water use efficiency ($w$) is a crop parameter of outstanding importance in crop simulation models, derived here as the slope of the relationship linking crop carbon gain to cumulative transpiration. This study aims at: (i) evaluating $w$ of field-grown sunflower, sorghum, wheat and chickpea, at three levels of aggregation—day-time net assimilation ($A$), daily net carbon gain, as difference between $A$ and night-time dark respiration ($R$), and biomass; (ii) assessing the robustness of $w$ parameter in terms of ability to discriminate between C_3 and C_4 species, pre- and post-anthesis, impact of nitrogen status; (iii) investigating the opportunity to normalize $w$ by climate, using FAO-Penman-Monteith reference evapotranspiration ($E_{ref}$) or atmospheric saturation vapour pressure deficit ($D$); (iv) comparing $w$ with the corresponding radiation use efficiency ($e$) results presented in the companion paper. Field experiments were conducted in 1998 and 1999 in southern Italy. All crops were well watered. Sunflower and sorghum had two nitrogen application treatments: wheat had only one and chickpea had no added nitrogen. Closed-system canopy chambers, automated for continuous measurements, were used to monitor gas-exchanges at the canopy scale, in terms of both carbon exchange rate (CER) and evapotranspiration $E$, and the cuvette method to monitor gas-exchange at the leaf scale. $w$, expressed in terms of $A$, $A - R$, or above-ground biomass, was linear over the entire cycle of sorghum and wheat, and up to anthesis in sunflower and chickpea, independent of temperature, vapour pressure deficit and radiation regimes. In sunflower, deviation from linearity was observed after anthesis due to higher carbon cost in yielding oil seeds. No conclusions could be drawn for post-anthesis chickpea due to the destruction of the crop by a thunderstorm. The overall response patterns were common to $w$ and $e$. Nevertheless, $w$ proved to be more robust than $e$ due to its high capacity to discriminate between species groups (C_3 from C_4) and its effectiveness in normalizing the values for climate, provided it is implemented through $E_{ref}$ rather than $D$. All the above confers larger extrapolative ability to $w$-based crop models.

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1. Introduction

Water use efficiency \((w)\) assumes different definitions depending on the time and space scales of the processes and system aggregation it refers to (Steduto, 1996). Here, we define \(w\) as the slope of cumulative carbon gain versus cumulative transpiration of a crop canopy.

More specifically, we qualify \(w\) as: \(w_A\) (g m\(^{-2}\) mm\(^{-1}\)), when the carbon gain is expressed by the day-time canopy net assimilation \((A)\); \(w_{A-R}\) (g m\(^{-2}\) mm\(^{-1}\)), when the carbon gain is expressed by the daily difference between \(A\) and the night-time canopy respiration \((R)\); and \(w_b\) (g m\(^{-2}\) mm\(^{-1}\)), when the carbon gain is expressed by the above-ground biomass. All three expressions have the unit of g m\(^{-2}\) mm\(^{-1}\), with the only difference that \(g\) refers to CO\(_2\) in the case of \(w_A\) and \(w_{A-R}\), and to biomass in the case of \(w_b\). An additional expression is also \(w_\gamma\), when it refers to harvestable yield.

Investigations of \(w_b\) and \(w_\gamma\) have a long history. Nevertheless, since the early reviews and studies of Briggs and Shantz (1913a, 1913b, 1914), Kiesselbach (1916), de Wit (1958) and Viets Jr. (1962), until the more recent ones of Doorenbos and Kassam (1979), Taylor et al. (1983), Stanhill (1986), and Steduto (1996), no paradigm changes have been introduced in the \(w\)-related scientific literature. This is not surprising, since the link between biomass and transpiration is extremely conservative (Hsiao and Bradford, 1983), i.e., \(w\) tends to remain constant under a wide range of conditions.

Notwithstanding the limited progress on \(w\), the subject has recently received increasing interest, both in rain-fed (e.g., Angus and van Herwaarden, 2001; Hatfield et al., 2001) and irrigated agriculture (e.g., Howell, 2001), due to the increasing concern about water supply limitations, increasing demands and inter-sectoral competition and because of declining water quality (Rosegrant et al., 2002). Moreover, the \(w\) concept has evolved towards “water productivity” due to the implications of water use on world food security (Kijne et al., 2003).

The significant features of the \(w\) relationship can be summarized as follows: (i) it tends to remain linear under both well-watered and water-deficit conditions (Hsiao and Bradford, 1983; Hsiao, 1993); (ii) it is relatively insensitive to variation in soil nutrient status (Stanhill, 1986); (iii) it may vary with climatic conditions, and hence, normalization approaches have been proposed to compare and extrapolate results from different years and/or locations (de Wit, 1958; Tanner and Sinclair, 1983).

Interestingly, the amount of data, level of insight and degree of structural analysis for water use efficiency are substantially lesser than that found in the literature for radiation use efficiency \((\varepsilon; \text{g MJ}^{-1})\), i.e., the relationship of either above-ground biomass or harvestable yield and cumulative solar radiation intercepted by crops \((\Sigma R_{\text{Si}})\). In fact, the \(\varepsilon\) concept, formalized by Monteith (1977) on experimental and theoretical grounds, represents the core feature of many crop-model “growth-engine”, such as CERES (e.g., Jones and Kiniry, 1986), EPIC (Jones et al., 1991), STICS (Brisson et al., 2003) and CROPSYST (Stöckle et al., 2003).

The \(\varepsilon\) concept was conceived as a robust and appropriate modelling approach to describe crop growth, and as far as we know, only CROPSYST (Stöckle et al., 2003) and PARCH (Azam-Ali et al., 2001) models have a dual “growth-engine” incorporating in parallel, both the \(\varepsilon\) and the \(w\) approach, although with an emphasis on the former. Most likely, the initial formalization of the \(\varepsilon\) concept in radiation-limited rather than water-limited environments and the relatively easier determination methods of \(\varepsilon\), as compared to \(w\), have boosted the application of \(\varepsilon\)-based against \(w\)-based crop-models.

Despite the preference for \(\varepsilon\)-based growth-engines, they still suffer from many drawbacks (Kiniry et al., 1989; Sinclair and Muchow, 1999; Albrizio and Steduto, 2005). Criticisms include: inconsistent and variable estimates of \(\varepsilon\) within and between crop species, and even between C\(_3\) and C\(_4\) crop groups; unpredictable \(\varepsilon\) between locations and years; and unreliable attempts to normalize \(\varepsilon\) for climate. Furthermore, \(\varepsilon\) often loses its linearity under water stress (Azam-Ali et al., 1984) and nutrient deficit conditions (Muchow and Davis, 1988; Hall et al., 1995, O’Connell et al., 2004), whereas \(w\) appears to be more conservative, at least under less than severe water stresses (Hsiao, 1993; Steduto et al., 1997). The possible effects on linearity due to changes in biomass composition are common to both \(\varepsilon\) and \(w\).

In our companion paper (Albrizio and Steduto, 2005), \(\varepsilon\) was investigated in well-watered field crops...
(sunflower, grain sorghum, wheat and chickpea) differing in photosynthetic pathway (C\textsubscript{3}, C\textsubscript{4}) and major biomass composition (carbohydrates, proteins, lipids). The present work aims at: (i) investigating the water of these same crops, under the same experimental conditions, with observations at both leaf and canopy scale, and (ii) comparing the advantages and disadvantages, robustness and reliability of ε and w as “growth-engines”. Furthermore, two most commonly used approaches to normalize w for climate (reference evapotranspiration – \(E_{\text{ref}}\) and atmospheric saturation vapour pressure deficit – D) are examined.

2. Materials and methods

2.1. Location and field trials

The experiments were conducted in 1998 and 1999 at the experimental field of the Mediterranean Agronomic Institute (IAMB) located in Valenzano (Bari), southern Italy (41°03′N, 16°52′E, 72 m above sea level).

All the details about the experimental design, the soil characteristics, and the cultural practices in terms of the utilized cultivars, the sowing dates, the inter-row distance, the plant density, the emergence date, the type of fertilizer and the amount of nitrogen applied for sunflower (Helianthus annuus L.), grain sorghum (Sorghum bicolor L. Moench.), durum wheat (Triticum durum L.) and chickpea (Cicer arietinum L.) were reported in the first paper of this series (Albrizio and Steduto, 2005). Both sunflower and sorghum were differentially supplied with nitrogen; N\textsubscript{1} was the well-fertilized treatment, while N\textsubscript{0} was the unfertilized control. Due to the anticipated difficulties in controlling nitrogen in relation to water regimes in a winter crop, wheat had only treatment N\textsubscript{1}. No nitrogen fertilization was applied to chickpea because of its ability to fix nitrogen.

During the whole season, all crops were drip-irrigated, except wheat, which was irrigated by mini-sprinklers. The drip lines, with 2 l h\textsuperscript{-1} drippers 0.5 m apart, were laid along each plant row and wetted a soil strip never exceeding a width of about 0.30 m. This corresponds to 25, 37 and 42% wetted soil surface for sunflower, sorghum and chickpea, respectively. The mini-sprinklers wetted the whole soil surface of wheat.

Crop water requirements for each investigated species were determined through reference crop evapotranspiration (\(E_{\text{ref}}\)) estimated by the FAO–Penman–Monteith method (Allen et al., 1998) and the crop coefficients obtained from local information (Tarantino and Onofri, 1988). A relatively constant irrigation interval (about 4–5 days) was employed to restore water lost by evapotranspiration. Measurements began only after a uniform ground cover was achieved.

2.2. Canopy gas-exchange measurements

Daily evapotranspiration (E) and carbon exchange rate (CER) were measured in a closed-system canopy chamber automated for day and night monitoring. The automated system enables the chamber to keep the top wall closed during measurements and to hold it open in-between consecutive measurements. Measurements were taken at 0.5 s intervals for 15 s, 5 s after chamber closure. Measurements were repeated every 15 min for 2–3 days.

The short-term CER and E values (taken every 15 min) were integrated over time to obtain daily CER and E averaged over 2–3 day periods. CER was differentiated in terms of net assimilation (A) and dark respiration (R), with A being calculated during daytime hours (from sunrise to sunset) and R during nighttime hours (from sunset to sunrise). Calculation of cumulative fluxes required estimates of CER and E during the days between measurement sets, i.e., when the chambers were not mounted. The daily A and E of each interval were both derived using a correlation with the daily \(S_{\text{SR}}\), while the night-time R of each interval was derived using a correlation between the night-time R and the biomass.

Timing of CER and E measurements along the cycle of the four crops is given in the companion paper (Albrizio and Steduto, 2005). Detailed descriptions of the automated canopy-chamber system, tests and operations are reported in Steduto et al. (2002).

2.3. Leaf gas-exchange measurements

Leaf gas-exchanges were measured by using a portable photosynthesis open system (LiCor Inc.,
Lincoln, Nebraska, USA, model Li-6400). Measurements were taken around noon-time (from 11:00 to 15:00 h), on the exposed uppermost leaves over a clipped leaf surface of 6.0 cm². Because of the small size of chickpea leaves, the actual leaf area was determined after the measurement, drawing the leaf shape on graph paper. The gas-exchange parameters were then recalculated.

Measurements were taken from 23 May up to 10 July (from 52 to 101 days after planting – DAP) for sunflower, from 17 June up to 29 August (76–149 DAP) for sorghum, from 27 April up to 31 May (130–164 DAP) for wheat, and from 16 May up to 14 June (76–104 DAP) for chickpea.

Leaf assimilation and transpiration were analysed to derive water use efficiency, while intercellular air space CO₂ concentration was derived as an expression of optimal stomatal behaviour (Cowan, 1982; Farquhar and Sharkey, 1982).

2.4. Water use efficiency

At the canopy scale, the measurements of water transpired in conjunction with above-ground biomass determinations or canopy CO₂ gas-exchanges, were used to calculate the canopy water use efficiency (w) through the “cumulative approach” (e.g. Steduto and Hsiao, 1994).

In this study, the relationship between above-ground biomass and the amount of water transpired (wᵦ; g m⁻² mm⁻¹) was investigated, taking into account different levels of aggregation, i.e., net assimilation (A) and net carbon gain (A – R). When considering ΣA versus ΣE (wᵦ; gCO₂ m⁻² mm⁻¹) all CO₂ assimilated is included, irrespective of its organ utilization and allocation. When considering Σ(A – R) versus ΣE (wᵦ–R; gCO₂ m⁻² mm⁻¹) net carbon assimilation of the whole plants, irrespective of the final composition, is included. These responses at gas-exchange scale may indicate to the extent the linearity of w can actually be reliable and accurate. To minimize the contribution of soil evaporation to water consumption, w was determined for all the crops beginning with full ground cover. However, since E includes the soil evaporation (Eₛ), a proper calculation of the water use efficiencies wᵦ, wᵦ–R, and wᵦ requires a separation of Eₛ from E. Using the Ritchie approach (Ritchie, 1972) and the actual values of the wetted fraction of the soil surface, along with the actual leaf area index (L) and the corresponding transmitted solar radiation to the ground, the calculated Eₛ ranged between 5 and 8% of E during the canopy gas-exchange measurement period. The range of Eₛ values being close to the degree of accuracy expected from canopy chamber measurements of E in experimental fields (Steduto et al., 2002), it was decided to neglect Eₛ and to accept the uncertainty possibly, introduced by using E as such.

Analogous concerns about the soil contribution of CO₂ to CER were already expressed in the companion paper (Albrizio and Steduto, 2005).

In order to normalize wᵦ for climate variability, two different approaches are attempted:

(i) Dividing E by day-time vapour pressure deficit D (wᵦ; g m⁻² mm⁻¹ kPa) calculated on 12 h basis (from 6:00 to 18:00), i.e.,

\[
wᵦ = \frac{\text{biomass}}{\sum_{i=1}^{n}(E/D)_i}
\] (1)

(ii) Dividing E by the FAO–Penman–Monteith reference evapotranspiration Eᵦ (wᵦₑ; g m⁻²), referred to the same time period, i.e.,

\[
wᵦₑ = \frac{\text{biomass}}{\sum_{i=1}^{n}(E/Eᵦ)ᵦₑ}_i
\] (2)

At the leaf scale, normalized photosynthetic water use efficiency (wᵦₑ; μmol mmol⁻¹ kPa) was calculated directly from gas-exchange measurements as the ratio of net photosynthesis to transpiration rate, normalized for leaf-to-air water vapour pressure difference (D).

The Student’s t-test was used to evaluate the least significant differences between treatments and regression slopes.

3. Results

3.1. Canopy evapotranspiration

Daily integrals of evapotranspiration (E) for sunflower, sorghum, wheat and chickpea during the whole crop cycle are shown in Fig. 1a–d. E initially increased quite steeply for all the crops, reaching a maximum of: 12 mm day⁻¹ for both N₀ and N₁
treatments of sunflower; 7 and 7.5 mm day\(^{-1}\), for \(N_0\) and \(N_1\) treatments of sorghum, respectively; 4.4 mm day\(^{-1}\) for wheat and 10.4 mm day\(^{-1}\) for chickpea. Peak values of \(E\) occurred before anthesis (3 June, 63 DAP) for sunflower, at the full flowering stage (12 July, 102 DAP) for sorghum, at the end of the vegetative stage for wheat (7 April, 110 DAP) and at the end of flowering for chickpea (4 June, 94 DAP). \(E\) tended to decline at the onset of the reproductive stage, following the progressive reduction in leaf area (Albrizio and Steduto, 2005), and reached the minimum values at the end of the measurement time for all the crops. As explained earlier, chickpea was not monitored until the end of its cycle. \(E\) was higher in \(N_1\) treatment of sorghum than in \(N_0\), from the beginning of fertilization to the end of the season. In sunflower, however, the situation was reversed during the entire growing season.

Table 1 reports total \(E\) values obtained at the end of each crop season. The \(N_0\) sunflower treatment had the

<table>
<thead>
<tr>
<th>Crop</th>
<th>Treatments</th>
<th>Total (E) (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunflower (20 May–21 August)</td>
<td>(N_0)</td>
<td>891</td>
</tr>
<tr>
<td></td>
<td>(N_1)</td>
<td>837</td>
</tr>
<tr>
<td>Sorghum (11 June–15 September)</td>
<td>(N_0)</td>
<td>485</td>
</tr>
<tr>
<td></td>
<td>(N_1)</td>
<td>510</td>
</tr>
<tr>
<td>Wheat (25 March–29 May)</td>
<td>(N_1)</td>
<td>230</td>
</tr>
<tr>
<td>Chickpea (29 April–15 June)</td>
<td>–</td>
<td>320(^*)</td>
</tr>
</tbody>
</table>

\(^*\) Incomplete cycle due to thunderstorm.
highest total $E$ (891 mm, 6% higher than $N_1$), followed by treatment $N_1$ of sorghum (510 mm, 5% higher than $N_0$), chickpea (320 mm) and wheat (230 mm). The corresponding average ratio of the seasonal crop evapotranspiration to the seasonal reference evapotranspiration was around 1.3 and 1.2 for sunflower $N_0$ and $N_1$, respectively, 0.9 for both N treatments of sorghum, 1.1 for wheat and 1.2 for chickpea.

3.2. Water use efficiency at the canopy scale

Water use efficiency ($w$) was measured not only in terms of above-ground biomass ($w_b$), but also as daytime net assimilation ($A$) and whole-day net carbon gain ($w_{A-R}$). Cumulative net assimilation $\Sigma A$, cumulative net assimilation minus dark respiration $\Sigma (A - R)$ and above-ground biomass are plotted against cumulative evapotranspiration $\Sigma E$, for all the crops and treatments in Fig. 2a–i. The corresponding slopes and determination coefficients ($R^2$) values of the regressions are reported in Table 2.

Except for sunflower, the three variables were linearly correlated with $\Sigma E$ for all the crops and during the whole season. As in the investigation (Albrizio and Steduto, 2005), consistency in the response of the two carbon balance components ($A$ and $\Sigma (A - R)$) supports the strength of $w$ for predictions of biomass production.

In sunflower, for both nitrogen treatments, the three relationships linearly increased at pre-anthesis and
linearly declined at post-anthesis. Between pre- and post-anthesis, w decreased for N₀ and N₁, respectively, by 40 and 45% as wₐ, by 90 and 74% as wₐ₋ᵣ, and by 76 and 89% as wₕ (Table 2). For each of the three w relationships, no significant differences were established between N₀ and N₁ treatments, both at pre- and post-anthesis. In contrast to the sunflower results, wₕ, wₐ and wₐ₋ᵣ were constant during the whole crop cycle in both nitrogen treatments of sorghum (Fig. 2d–f), wheat and chickpea (Fig. 2g–i).

Higher R² values (Table 2) were found for the regressions of both $\Sigma A$ and $\Sigma A - R$ versus $\Sigma E$ of all crops, except for wₐ₋ᵣ of post-anthesis sunflower with treatment N₀, as compared to the corresponding regression of above-ground biomass versus $\Sigma E$, as a consequence of a larger variability in biomass sampling than in CER sampling.

The relationship between above-ground biomass and $\Sigma E$ for all crops and treatments (Fig. 3a) shows a range of slopes with no distinctive pattern. Only the fertilized treatment N₁ of sorghum is different from that of the other crops, with a slope value of 5.7 g m⁻² mm⁻¹, while wheat and the unfertilized treatment of sorghum have a very similar slope (4.5 and 4.4 g m⁻² mm⁻¹, respectively). These results indicate large variability in w, and no apparent distinction between C₃ and C₄ species, similarly to that observed for $\varepsilon$ in the companion paper (Albrizio and Steduto, 2005). However, since growth cycles of these crops do not occur in the same season and/or

Table 2
Slopes and determination coefficients ($R^2$) of the regressions, for all the crops and treatments, between: cumulative assimilation and cumulative evapotranspiration ($wₐ$); cumulative assimilation minus dark respiration and cumulative evapotranspiration ($wₐ₋ᵣ$); above-ground biomass and cumulative evapotranspiration ($wₕ$).

<table>
<thead>
<tr>
<th>Crop</th>
<th>Treatments</th>
<th>$wₐ$</th>
<th>$wₐ₋ᵣ$</th>
<th>$wₕ$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Slope</td>
<td>Slope</td>
<td>Slope</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$gCO_2$ m⁻² mm⁻¹</td>
<td>$gCO_2$ m⁻² mm⁻¹</td>
<td>($g$ m⁻² mm⁻¹)</td>
</tr>
<tr>
<td>Sunflower (pre-anthesis)</td>
<td>N₀</td>
<td>5.1</td>
<td>0.999</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td>N₁</td>
<td>6.1</td>
<td>0.998</td>
<td>3.3</td>
</tr>
<tr>
<td>Sunflower (post-anthesis)</td>
<td>N₀</td>
<td>3.0</td>
<td>0.957</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>N₁</td>
<td>3.3</td>
<td>0.984</td>
<td>0.9</td>
</tr>
<tr>
<td>Sorghum</td>
<td>N₀</td>
<td>8.2</td>
<td>0.999</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>N₁</td>
<td>10.6</td>
<td>0.998</td>
<td>6.0</td>
</tr>
<tr>
<td>Wheat</td>
<td>N₁</td>
<td>8.5</td>
<td>0.999</td>
<td>6.0</td>
</tr>
<tr>
<td>Chickpea</td>
<td>–</td>
<td>7.5</td>
<td>0.983</td>
<td>4.8</td>
</tr>
</tbody>
</table>

Fig. 3. Regressions between (a) above-ground biomass and cumulative evapotranspiration ($\Sigma E$), and (b) above-ground biomass and cumulative evapotranspiration normalized by mean day-time vapour pressure deficit D ($\Sigma (E/D)$), during the crop cycle of sunflower, sorghum, wheat and chickpea. In (a), the regression line of wheat overlies the regression line of sorghum N₀. In (b), the regression line of chickpea overlines the regression line of sunflower N₁.
year, climatic conditions may differ, thus making any comparison difficult. Generally, for a proper comparison among experiments carried out in different years and/or locations, it is necessary to normalize \( E \) for evaporative demand of the atmosphere, which can be obtained dividing \( E \) either by the atmospheric vapour pressure deficit (\( D \)) or by the evapotranspiration from a reference crop (\( E_{\text{ref}} \)).

In Fig. 3b, above-ground biomass is plotted against \( \Sigma(E/D) \) for the same time period for all the crops and treatments. The corresponding slopes (\( w_D^b \)) and determination coefficients (\( R^2 \)) values of the regressions are reported in Table 3. In this case, greater \( w_D^b \) of sorghum (\( C_4 \)) is evident, as compared to other crops (all \( C_3 \)), with \( w_D^b \) values of 8.5 and 11.3 g m\(^{-2}\) mm\(^{-1}\) kPa for \( N_0 \) and \( N_1 \) treatments, respectively. Nevertheless, the \( C_3 \) species show some degree of variability and apparent inconsistency. Chickpea, in fact, has the highest \( w_D^b \) value (3.8 g m\(^{-2}\) mm\(^{-1}\) kPa), followed by sunflower \( N_1 \) (3.5 g m\(^{-2}\) mm\(^{-1}\) kPa), sunflower \( N_0 \) (3.1 g m\(^{-2}\) mm\(^{-1}\) kPa), and lastly by wheat (2.2 g m\(^{-2}\) mm\(^{-1}\) kPa).

Alternatively in Fig. 4, above-ground biomass is plotted against \( \Sigma(E/E_{\text{ref}}) \) for the same time period for all the crops and treatments. The corresponding slopes (\( w_{E_{\text{ref}}}^b \)) and determination coefficients (\( R^2 \)) of the regressions are reported in Table 4. In this case, greater \( w_{E_{\text{ref}}}^b \) of sorghum (\( C_4 \)) is evident, as compared to other crops (all \( C_3 \)), with \( w_{E_{\text{ref}}}^b \) values of 8.5 and 11.3 g m\(^{-2}\) mm\(^{-1}\) kPa for \( N_0 \) and \( N_1 \) treatments, respectively. Nevertheless, the \( C_3 \) species show some degree of variability and apparent inconsistency. Chickpea, in fact, has the highest \( w_{E_{\text{ref}}}^b \) value (3.8 g m\(^{-2}\) mm\(^{-1}\) kPa), followed by sunflower \( N_1 \) (3.5 g m\(^{-2}\) mm\(^{-1}\) kPa), sunflower \( N_0 \) (3.1 g m\(^{-2}\) mm\(^{-1}\) kPa), and lastly by wheat (2.2 g m\(^{-2}\) mm\(^{-1}\) kPa).

### Table 3

<table>
<thead>
<tr>
<th>Crop</th>
<th>Treatments</th>
<th>( w_D^b ) Slope (g m(^{-2}) mm(^{-1}) kPa)</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunflower</td>
<td>( N_0 )</td>
<td>3.1</td>
<td>0.978</td>
</tr>
<tr>
<td></td>
<td>( N_1 )</td>
<td>3.5</td>
<td>0.921</td>
</tr>
<tr>
<td>Sunflower</td>
<td>( N_0 )</td>
<td>1.1</td>
<td>0.819</td>
</tr>
<tr>
<td></td>
<td>( N_1 )</td>
<td>0.5</td>
<td>0.408</td>
</tr>
<tr>
<td>Sorghum</td>
<td>( N_0 )</td>
<td>8.5</td>
<td>0.958</td>
</tr>
<tr>
<td></td>
<td>( N_1 )</td>
<td>11.3</td>
<td>0.994</td>
</tr>
<tr>
<td>Wheat</td>
<td>( N_1 )</td>
<td>2.2</td>
<td>0.906</td>
</tr>
<tr>
<td>Chickpea</td>
<td></td>
<td>3.8</td>
<td>0.899</td>
</tr>
</tbody>
</table>

Regressions of sunflower are distinguished between pre- and post-anthesis stages.

### Table 4

<table>
<thead>
<tr>
<th>Crop</th>
<th>Treatments</th>
<th>( w_{A_{\text{ref}}}^E ) Slope (gCO(_2) m(^{-2}))</th>
<th>( R^2 )</th>
<th>( w_{A \rightarrow R}^E ) Slope (gCO(_2) m(^{-2}))</th>
<th>( R^2 )</th>
<th>( w_{E_{\text{ref}}}^b ) Slope (g m(^{-2}))</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunflower</td>
<td>( N_0 )</td>
<td>29.7</td>
<td>0.952</td>
<td>17.9</td>
<td>0.940</td>
<td>13.4</td>
<td>0.974</td>
</tr>
<tr>
<td></td>
<td>( N_1 )</td>
<td>29.7</td>
<td>0.952</td>
<td>17.9</td>
<td>0.940</td>
<td>13.4</td>
<td>0.974</td>
</tr>
<tr>
<td>Sunflower</td>
<td>( N_0 )</td>
<td>16.9</td>
<td>0.943</td>
<td>1.4</td>
<td>0.659</td>
<td>3.1</td>
<td>0.804</td>
</tr>
<tr>
<td></td>
<td>( N_1 )</td>
<td>18.9</td>
<td>0.975</td>
<td>4.8</td>
<td>0.827</td>
<td>1.5</td>
<td>0.442</td>
</tr>
<tr>
<td>Sorghum</td>
<td>( N_0 )</td>
<td>47.0</td>
<td>0.991</td>
<td>27.0</td>
<td>0.985</td>
<td>25.0</td>
<td>0.985</td>
</tr>
<tr>
<td></td>
<td>( N_1 )</td>
<td>61.2</td>
<td>0.990</td>
<td>34.7</td>
<td>0.989</td>
<td>32.9</td>
<td>0.996</td>
</tr>
<tr>
<td>Wheat</td>
<td>( N_1 )</td>
<td>29.7</td>
<td>0.952</td>
<td>17.9</td>
<td>0.940</td>
<td>13.4</td>
<td>0.974</td>
</tr>
<tr>
<td>Chickpea</td>
<td></td>
<td>29.7</td>
<td>0.952</td>
<td>17.9</td>
<td>0.940</td>
<td>13.4</td>
<td>0.974</td>
</tr>
</tbody>
</table>

Regressions of sunflower are distinguished between pre- and post-anthesis stages.
regressions are reported in Table 4. The same table also reports the normalized \( w \) values expressed in terms of both day-time net assimilation \( \left( w_{A}^{\text{E ref}}; \text{E CO}_2 \text{m}^{-2} \right) \) and whole-day net carbon gain \( \left( w_{A \rightarrow R}^{\text{E ref}}; \text{E CO}_2 \text{m}^{-2} \right) \). Focusing on \( w_{A}^{\text{E ref}} \), both treatments of the C_4 crop are very clearly separated (25.0 and 32.9 g m\(^{-2}\) for N_0 and N_1 treatments, respectively) from the others, with the C_3 crops grouping together in a single slope of 13.4 g m\(^{-2}\). Furthermore, the effect of nitrogen supply is much more evident on sorghum than on sunflower (at least pre-anthesis), consistently with the leaf area index development (Albrizio and Steduto, 2005) and leaf assimilation rates (Albrizio and Steduto, 2003).

3.3. Water use efficiency at the leaf scale

As expected, the normalized photosynthetic water use efficiency \( (w_i^1) \) and the intercellular air-space CO_2 concentration \( (c_i) \) of sorghum (the only C_4 species) differ from the other C_3 crops (Fig. 5). \( w_i^1 \) was 10.5 ±0.9 \( \mu \text{mol mmol}^{-1} \text{kPa} \) for both treatments of sorghum and 4.8 ±1.1 \( \mu \text{mol mmol}^{-1} \text{kPa} \) for the C_3 species (Fig. 5a). All four crops maintained a similar \( w_i^1 \) throughout the season, confirming the conservative behaviour of \( w_{A}^{\text{E ref}} \) of sorghum, wheat and chickpea, observed at the canopy scale (Fig. 4). In contrast to differences in \( w_{A}^{\text{E ref}} \) observed at the canopy scale between pre- and post-anthesis of sunflower, no variations in \( w_i^1 \) were found at the leaf scale for both nitrogen treatments. This can be explained taking into account day-time respiration of the reproductive organs, which is included in the gas-exchange at the canopy scale, but excluded from the observations at the leaf scale.

Following the \( w_i^1 \) trend, also the \( c_i \) values (Fig. 5b) were well differentiated between C_3 \( (221 \pm 24.2 \mu \text{mol mol}^{-1}) \) and C_4 species \( (63 \pm 16.8 \mu \text{mol mol}^{-1}) \). The value of \( c_i \) tended to remain about constant during the season of the C_3 species, with no difference between treatments, while it showed a tendency to increase from 50 to 80 \( \mu \text{mol mol}^{-1} \) for sorghum.

4. Discussion

4.1. Canopy evapotranspiration

The \( E \) values between initial and final measurements (Fig. 1a–d) essentially followed leaf area development during the crop cycle (Albrizio and Steduto, 2005). N_1 treatment of sunflower showed a lower \( E \) than N_0. This may be due to reduced plant-size development of sunflower N_0 that favoured greater light penetration into the canopy and higher inter-row advection, with an overall result of slightly higher \( E \) than in N_1. It is important to highlight that the \( E \) measurements during the various crop seasons were always carried out at a relatively high ground cover percentage. Therefore, the transpiration component greatly exceeded soil evaporation, thus making water consumption more closely related to physiological responses of the crops. Daily peaks (Fig. 1) and total \( E \) values (Table 1) are consistent with typical water consumption of these crops in the Mediterranean climates (Tarantino and Onofrii, 1988).

4.2. Water use efficiency and its normalization for climate

The strict link observed between the three levels of carbon aggregation \( (A, A \rightarrow R, \text{above-ground biomass}) \) and \( \Sigma E \) (Fig. 2), strongly confirms the conservative relationship between assimilation and dark respiration at the canopy scale. Such conservative behaviour was observed by the same authors in a previous study.
under varying environmental conditions (Albrizio and Steduto, 2003).

The change in slope of sunflower at post-anthesis (Fig. 2a–c) is, instead, the consequence of the change in composition of the reproductive biomass during seed filling, when oil is the major compound being synthesized. The slope of N1 treatment at post-anthesis was lower than N0. This can be explained on the grounds that there was no change in slope between the nitrogen treatments of sunflower at pre-anthesis, that is, most of the nitrogen was used to grow more leaves (Albrizio and Steduto, 2005) rather than to increase leaf nitrogen concentration as observed in sorghum (data not shown). Therefore, a higher nitrogen sink present at post-anthesis for N1 treatment imposed a higher N translocation from the leaves to the seeds, leaving the leaves with a lower N concentration for carbon assimilation, and thus, resulting in a lower w. Though keeping linearity, the post-anthesis phase requires the determination of a different slope value when the biomass composition introduces considerable changes in the energy requirements. A rather limited number of field experiments have addressed the post-anthesis change in the CO2 assimilation–respiration relationships (e.g., Whitfield et al., 1989; Albrizio and Steduto, 2003). This applies to both e and w approaches, and definitely calls for additional information on the post-anthesis behaviour of different crops and new cultivars (Calderini et al., 1997).

A part from a few, though obvious exceptions, the prevailing constancy of e and w is strongly in support of their use as parameters for biomass prediction (Tanner and Sinclair, 1983; Monteith, 1990). Nevertheless, experimental evidence (Kiniry et al., 1989; Sinclair and Muchow, 1999; Albrizio and Steduto, 2005) furnishes arguments for indicating w as a better biomass predictor, provided normalization for climate is employed.

It is worthy noticing that the conceptual normalization of w can take two routes: (i) normalizing through the “transpiration gradient”, or (ii) normalizing through a “reference transpiration flux”.

The gradient-normalizing route is derived from the leaf-scale gas-diffusion model, where,

$$w_1 = \frac{A}{E} = \frac{g'_s \Delta C}{g_s \Delta e} \Rightarrow w'_1 = w_1 \Delta e$$

with, $g'_s$ and $g_s$ being the stomatal conductance for CO2 and water vapour, respectively; $\Delta C$ being the CO2 partial pressure gradient between air and leaf-interior air space; $\Delta e$ being the leaf-to-air water vapour partial pressure difference; $w_1$ and $w'_1$ being the leaf water use efficiencies without and with normalization for the $\Delta e$, respectively.

By analogy, and following the derivation of Tanner and Sinclair (1983), also at the canopy level, w should be normalized by multiplying by the vapour pressure gradient ($\Delta e$) that represents the driving force of the transpiration process and incorporates the climate dependency of w. At the canopy scale, $\Delta e$ represents the canopy-to-air water vapour pressure difference. However, in the absence of canopy temperature, the practical normalization of w for climate is approached by replacing $\Delta e$ by the atmospheric vapour pressure deficit (D).

This approximation has the drawback of not properly representing the actual $\Delta e$, of being inadequate to incorporate changes in sensible heat direction (Asseng and Hsiao, 2000) and of being very sensitive to low D values; in that case, the predictions of biomass become unreliable. Furthermore, it is not clear what should be the proper time-interval acceptable for D normalization, since the actual $\Delta e$ depends also on the rate of transpiration flux, so that different time periods during crop growth will have different normalizing weights (Asseng and Hsiao, 2000). Nevertheless, when the above-ground biomass versus $\Sigma E$ relationship of our crops is normalized through D (Fig. 3b and Table 3), though maintaining the ability to distinguish C3 from C4, $w'_{0D}$ values of the C3 species are displaced following the time of occurrence of the crop season, as compared to the $w_0$ values (Fig. 3a and Table 2).

These values do not compare with any of those found in the literature (e.g., Azam-Ali et al., 1994), either because of possible ineffectiveness of the normalization (e.g., Clover et al., 2001) or because of different D time interval averaging (e.g., Pilbeam et al., 1995). Only the $w'_{0D}$of chickpea (3.8 g m$^{-2}$ mm$^{-1}$ kPa) was comparable with the value reported by Tanner and Sinclair (1983) for soybean (4.0 g m$^{-2}$ mm$^{-1}$ kPa), but not quite enough to the one reported by Singh and Sri Rama (1989) for another variety of chickpea (4.8 g m$^{-2}$ mm$^{-1}$ kPa).

The normalization approached through a “gradient” appears to be extremely effective when done at
the leaf scale (Fig. 5a), where the flux-gradient theory is properly applied and $\Delta e$ is not approximated, with a generally high level of accuracy. The normalized leaf photosynthetic water use efficiency ($w'_c$) of the C3 crops groups in one single value averaging around 4.8 ± 1.1 $\mu$mol mmol$^{-1}$ kPa, while $w'_c$ of sorghum (C4) is much higher, averaging around 10.5 ± 0.9 $\mu$mol mmol$^{-1}$ kPa. These values compare quite well with those reported by Rawson and Constable (1980) on sunflower, and Rawson and Begg (1977) on grain sorghum.

It is very important to note that $w'_c$ remained quite constant throughout the whole crop cycle, reflecting the theory of optimal stomatal behaviour (Cowan, 1982; Farquhar and Sharkey, 1982) as indicated by the tendency of the intercellular air-space CO$_2$ concentration ($c_i$) to remain equally constant over the season, as illustrated in Fig. 5b. This underlying physiological mechanism at the leaf scale is fundamental to the constancy of $w$ at the canopy level (Hsiao and Bradford, 1983).

The reference-flux normalizing route is derived from the original idea of de Wit (1958), where the evaporative demand of the climate is represented by the evaporation rate of a reference condition ($E_{ref}$), as reported in Eq. (4)

$$w = \frac{A}{E} \Rightarrow w^{E_{ref}} = wE_{ref}$$

While in the de Wit case, the reference-flux was the pan evaporation, in our case it is the reference-crop evapotranspiration ($E_{ref}$) calculated according to Allen et al.(5,2),(996,996). When normalizing through $E_{ref}$, $w^{E_{ref}}$ slopes of pre-anthesis C3 crops (Fig. 4 and Table 4), all group into one single value (13.4 g m$^{-2}$). Sorghum remains distinguishable from the other crops and maintains further difference between nitrogen treatments (25.0 and 32.9 g m$^{-2}$ for N0 and N1, respectively).

Explicit values of $w$ normalized by $E_{ref}$ are extremely difficult to be found in the literature. We are aware only of the $w^{E_{ref}}$ values reported by Asseng and Hsiao (2000) for alfalfa, and equal to almost 11 g m$^{-2}$, and of those expressed on CO2 assimilated basis ($w^{E_{ref}}_A$), reported by Steduto (1993) for maize equal to 55.4 g m$^{-2}$, and by Steduto et al. (1997) for sweet sorghum. Considering that the methods of determining evapotranspiration rate at the canopy scales were quite different, both values of 11 and 55.4 g m$^{-2}$ compare fairly well with $w^{E_{ref}}_A$ of our C3 crops (13.4 g m$^{-2}$) and with $w^{E_{ref}}_A$ of our C4 crop (54.1 gCO$_2$ m$^{-2}$), if an average between the two N treatments is considered. These outcomes clearly show that the normalization of $w$ for climate through the evapotranspiration reference-flux is much more effective than the normalization through the transpiration-gradient.

However, the normalization for climate by $E_{ref}$ is expected to be applicable to all conditions, from well watered to water stressed. Indeed, more experimental research is needed to support the conservative behaviour of normalized $w$ by $E_{ref}$ under water and/or salt stresses and nutrient deficit conditions, since some sources of variability can be introduced under these conditions (e.g., different root–shoot biomass partitioning).

One of the most important inferences is that the $w$ approach to modelling biomass production provides an effective way of extrapolating from one location to another, since it permits the normalization for climatic differences of such locations. Similarly, it allows comparability of results obtained in the same location but in different seasons. Such effectiveness of climate normalizations for $w$ does not apply to $e$. In fact, the attempts shown in the literature are rather weak on theoretical ground (Stöckle and Kiniry, 1990; Kiniry et al., 1998).

The observed results and the investigated literature confirm the expected superior robustness of a $w$-versus $e$-based crop modelling approach, provided that climate is normalized by $E_{ref}$ rather than $D$.

5. Conclusion

On the basis of our experiments with only one C4 species crop, albeit for two nitrogen treatments, the $w$ approach overcomes the disadvantages of $e$ by showing a consistent discrimination capacity between species groups (C3 versus C4). Moreover, it offers a straightforward and effective way of normalizing the climate through $E_{ref}$. In fact, all the investigated C3 species grouped in one $w^{E_{ref}}$ relationship (only pre-anthesis is included for sunflower) with a single value of 13.4 g m$^{-2}$, while sorghum showed distinct slopes, largely above the C3 crops, depending on the nitrogen treatments: 25.0 g m$^{-2}$ for N0 and 32.9 g m$^{-2}$ for N1.
Similar to what is observed in the ε relationship, the change in slope between pre- and post-anthesis of sunflower, due to the higher carbon cost for yielding oil-rich seeds, was evident.

Overall, crop-growth modelling, based on w is expected to be more robust than those based on ε, with w having a much higher extrapolation capability than ε, provided the normalization for climate is implemented through Eref rather than D. However, further experimental evidence on the effectiveness of climate normalization under water stress is needed.

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