# Dew is a major factor affecting vegetation water use efficiency rather than a source of water in the eastern Mediterranean area

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Received 28 September 2008; revised 8 January 2010; accepted 29 March 2010; published 21 October 2010.

[1] The purpose here is to reexamine the ecological importance of dew in arid and semiarid regions with a focus on the eastern Mediterranean area. This reevaluation is of particular importance under the controversial perspective that dew is insufficient as a source of water for plants but is sufficient to promote the spread of plant diseases. Adana, Turkey, was selected as an appropriate semiarid test ground with well-documented meteorological data and a newly developed photosynthesis and transpiration rate monitor (PTM), which was used to detect the response of transpiration and photosynthesis to the presence of dew on the leaves. A convolution theoretical model was used to simulate no-dew days; simultaneously, PTM measurements were used to obtain actual situations with dew. Contrary to expectations, we detected separate, early peaks of photosynthesis and late peaks of transpiration, leading to an average ratio of about 2:1 units of water use efficiency (WUE) for dew-affected versus no-dew conditions. The impressive performance of the dew-affected WUE was explained by a synergy between (1) low transpiration during dew-affected morning hours and (2) high CO<sub>2</sub> gradient toward the canopy. The first resulted from dew formation that created a humid environment in the near vicinity of the leaf followed by a low leaf to air vapor pressure deficit, which minimized transpiration. The second resulted from night respiration that induced a high CO<sub>2</sub> gradient from the air toward the canopy. This synergy resulted in intensive carbon intake at a low water cost and explained the ecological importance of dew.

**Citation:** Ben-Asher, J., P. Alpert, and A. Ben-Zvi (2010), Dew is a major factor affecting vegetation water use efficiency rather than a source of water in the eastern Mediterranean area, *Water Resour. Res.*, *46*, W10532, doi:10.1029/2008WR007484.

# 1. Introduction

# 1.1. Controversial Perspective: Dew as a Major Ecological Factor

[2] Modern science has shown that the amount of water from dew for plant water budgets is negligible but that it is sufficient to promote the spread of plant disease. It is for this reason that dew has been recently described mainly as a source of inspiration for poets rather than as something beneficial for plants. In contrast, in ancient times, dew was believed to be a source of great blessing. Pioneering dew research in the late 1950s and early 1960s emphasized the inspiration of dew upon poets as opposed to its impact on plant water status [*Monteith*, 1957, 1963]. These quantitative studies of *Monteith* [1963] criticized the descriptive studies on dew with sentences including: "Every poet who has sung the beauties of Nature has added his tribute to the sparkling dew drops ... and ecological investigations of dew have strayed into descriptions which belong to poetry."

[3] New studies have found that for purely physical reasons dew is unlikely to support the water budget of plants

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since the ratio of potential condensation to potential evaporation is roughly 1:7 in humid climates and 1:14 in arid climates. This was further supported by measurements of dewfall in the Negev desert of Israel showing that maximum total dewfalls do not exceed 0.2 mm/d in any case, whereas actual evaporation of about 5-6 mm/d is not uncommon. Other reports counted 100-200 dew nights, which amounted to 50-100 mm/yr [Zangvil, 1996; Goldreich, 2003]. Today, citations regarding the role of dew are mostly negative. Plant pathologists emphasize the negative role played by dew in the promotion of plant diseases [Santos et al., 2008]. The entry in the Encyclopedia Britannica reads: "From the biological viewpoint, the usefulness of dew is doubtful, as dew may stimulate the growth of fungi harmful to plants" (Encyclopedia Britannica, 2007, entry on Dew, available at http://www.britannica.com). Another study states, "Dew plays an important role in the propagation of certain plant pathogens" [Huschke, 1991]. Amazingly, nothing is mentioned about the benefit of dew to the plant water regimen.

[4] On these grounds, it has been argued that the contribution of dew to the overall vegetation water regimen is negligible. Current dew research is dominated by phytopathologists who are concerned with the calculation of leaf wetness duration that is related to plant disease occurrence [Sentelhas and Gillespie, 2008] and plant protection against the negative role played by the dew in the promotion of plant diseases.

[5] Contrary to the above we found that dew formation serves as an integral part in the general strategy of vegeta-

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		Crop	Temperatures (C)				
Date <sup>a</sup>	Time		DPT	Leaf	Air	Relative Humidity	
16/06/03	3:30	Cotton	20.2	20.0	21.3	93.2	
16/06/03	4:00	Cotton	20.1	19.8	21.7	96.2	
16/06/03	5:30	Corn	20/4	20.1	21.5	93.3	
16/06/03	5:30	Soybean	20.9	20.6	21.7	95.4	
16/06/03	5:30	Lemon	20.6	20.8	21.4	95	
16/06/03	5:30	Oak, pine, and pistachio	20.4	20.7	22.9	85.6	

Table 1. Dew Point, Leaf, and Ambient Temperatures During the Measuring Period at Times of Maximum Relative Humidity

<sup>a</sup>Date is given as day/month/year.

tion water economy in arid and semiarid zones. The significant contribution of dew to the plant water economy will be explained and demonstrated below.

# 2. Materials and Methods

[6] A field study was carried out in the Chukurova basin near Adana, Turkey (~37°01'N, 35°21'E; elevation 10-150 m). This site was selected as an appropriate test ground after thorough analysis of meteorological data [Kimura et al., 2007; Kitoh, 2007] from 1994 to 2003 showed that every summer, throughout  $330 \pm 70$  h, the dew point temperature was higher than or equal to the air temperature, and the relative humidity during these hours varied between 99% and 100%, thus, satisfying the necessary conditions for dew formation. The basin is situated in the Mediterranean region surrounded by the Taurus Mountains. The Mediterranean climate is hot and dry during the summer and mild and rainy during winter.

#### 2.1. Experimental Approach

#### 2.1.1. Meteorological Measurements

[7] Over a period of 5 days, we measured and calculated the relevant meteorological variables including PIR-1, a Photosynthesis Radiation Sensor that measured photosynthesis photon flux density (PPFD). Air temperature and humidity (ATH) measured ambient temperature and relative humidity from which vapor pressure deficit (VPD) and dew point temperature (DPT) were determined using one of the dew point calculators (http://www.decatur.de/javascript/dew/ index.html) when relative humidity (RH) was at its maximum. The measured DPT and associated climatic conditions are given in Table 1.

[8] Within the Chukurova basin, maximal relative humidity (RH) ranged between 93% and 99%, and on the Taurus Mountains, it was about 10% less. Minimal ambient temperature varied between 21°C and 23°C, and minimal leaf temperatures varied between 19°C and 21°C. In the early morning hours, canopy temperature was below the DPT of the surrounding air and leaves were covered with dew during four nights on three crops. Dew formation was not detected when leaf temperature was slightly higher than the DPT.

#### 2.1.2. Plant Physiological Measurements

[9] The measurements of photosynthesis and transpiration were taken with a PTM-48 photosynthesis and transpiration monitor [Bio Instruments, 2007]. The combined measurements of leaf temperature measured with leaf temperature (LT) sensors and RH enabled the monitor's software to determine the leaf to air VPD. Photosynthesis and transpiration data from the leaf chambers as well as data from the additional sensors were automatically recorded every 30 min around the clock. Considering Fick's first law, the leaf conductance was obtained from the ratio  $g_1 = TR/VPD$  (TR units). Leaf hydraulic conductance  $(g_1)$  is a coefficient of proportionality between transpiration flux density (converted to  $H_2O$  volume area<sup>-1</sup> time<sup>-1</sup>) and its driving force VPD in terms of partial vapor pressure [Alessio et al., 2004].

# 2.1.3. PTM

Tama and tama (QC)

[10] This is a new portable device equipped with a fourchannel automated system for monitoring CO<sub>2</sub> exchange and transpiration of leaves. Each of the four chambers is a self-clamping leaf chamber, operating one-by-one in such a manner that one of the leaf chambers is closed at a time while all others remain open. Thus, most of time, the sample leaves are not disturbed. The CO<sub>2</sub> exchange is determined by decrement of  $CO_2$  concentration at the outlet of the leaf chamber, which is compared with the concentration of incoming ambient air. Transpiration rate is determined in much the same way using the absolute concentration of water vapor in the air. To shorten the measurement cycle, the absolute humidity is computed during a transient period between the 20th and 30th s after closing the chamber. The calculation algorithm takes into account the rising humidity inside the chamber and, hence, allows determining the initial transpiration rate at the ambient air humidity. Note that the PTM provides the unique capability of continuous measurement of undisturbed gas exchange by a single leaf. Other available devices for measurements of leaf gas exchanges are capable of manual sampling and hence require special efforts and arrangements to observe the early morning dew formation (as opposed to monitoring), whereas the PTM provides automated long-term monitoring of fluxes at the leaf level. Additional details on the PTM and the organization of the records were given by Ben-Asher et al. [2008]. It should be mentioned here that eddy covariance is another useful method for simultaneous monitoring of photosynthesis and transpiration [Mildenberger et al., 2009], but unlike the ordinary diffusion theory, the diffusion coefficients of H<sub>2</sub>O and CO<sub>2</sub> are the same. In the eddy covariance theory, a small packet of air moves more or less as a unit carrying with it all the H<sub>2</sub>O and the CO<sub>2</sub> molecules that it contains, and hence, photosynthesis and transpiration are linked to each other such that separation between them under dew and no-dew conditions is not possible.

#### 2.1.4. Soil Variables

[11] Only three (of the four) leaf chambers were used to monitor leaf gas exchange. The fourth chamber was used to monitor soil respiration. Three soil moisture sensors (time domain reflectometry) were used to determine the water content as supplemental data. These supporting sensors were used to compare soil water content and soil respiration of

**Table 2.** Average of Maximum Values of Photosynthesis Measured at About 9:00 A.M. and the Maximum Transpiration That was Measured at About 2:00 P.M.<sup>a</sup>

	Units	Cotton	Corn	Soybean
Photosynthesis Transpiration	$\mu$ mol m <sup>-2</sup> s <sup>-1</sup> mmol m <sup>-2</sup> s <sup>-1</sup>	$\begin{array}{c} 14.1 \pm 2.5 \\ 5.2 \pm 0.5 \end{array}$	$\begin{array}{c} 16.2 \pm 1.0 \\ 2.5 \pm 0.5 \end{array}$	$14.1 \pm 1.6$ $4.1 \pm 0.1$

<sup>a</sup>The data were used to calculate the dimensionless display in Figure 1a.

the irrigated crops and the nonirrigated natural vegetation in order to characterize the differences between the two habitats.

# 2.1.5. Crops and Mediterranean Vegetation

[12] The field crops were cotton (*Gossypium hirsutum*), soybean (*Glycine max*), and maize (*Zea mays*). One orchard plantation of lemon (*Citrus limon*) was studied in addition to a group of natural Mediterranean vegetation species: pine (*Pinus pinea*), pistachio (*Pistacia terebinthus*), and oak (*Phyllyrea media*). This group was located on the slope of the Taurus Mountains, some 150 m above sea level. Measurements conducted on 16–22 June 2003 and a summary of important data are given in Table 1.

[13] Each day, a different crop was equipped with the measuring system for at least 24 h, hoping to detect dew formation. On the nights of 16–19 June, the dew point temperature was higher than the leaf temperature and dew was detected on the leaves. On the nights of 20 and 21 June, the dew point temperature was below the leaf temperature and dew was not formed.

#### 2.1.6. Data Analysis

[14] We should emphasize that there is low probability of finding a day in which two fields of the same crop and environmental conditions differ from one another only by the presence of dew. Thus, simple comparison between crops' response to dew and no-dew conditions is impossible de facto. In order to overcome this problem, we characterized leaf properties by two empirical dimensionless parameters: unit photosynthesis and unit transpiration. It was assumed that  $CO_2$  uptake is accompanied by water efflux through the stomata and both are generated only by PPFD. Consequently, proportions of transpiration and photosynthesis change diurnally in concert with PPFD. Another generality that will be discussed in more detail in the theory section is that unlike dew-affected leaves, in dry leaves, the two processes are linked linearly to PPFD. Thus, to separate dew from no-dew conditions, we developed a convolution model that was based on empirical data. This was solved in Excel [Olsthoorn, 2008] and represented the no-dew situation during the daylight hours.

# 2.1.7. Statistical Considerations

[15] The diurnal evolution of transpiration and photosynthesis of the different plants was unified by presenting the measured values in terms relative to the maximum fluxes. We presented the data in relative terms because it allows combining many values and processes in a concise manner; representation of a large group in this way is easier to comprehend than a large mass of actual data. Furthermore, the diurnal evolution of gas exchange can be extracted for each crop from the product of maximum fluxes and the relative value at any given time. The maximum fluxes of cotton, corn, and soybean are given in Table 2. [16] The dimensionless data are thus an average of actual values from three dew-affected plants with three replications such that each data point represents a population of nine plants. The standard deviation (SD) of ambient  $CO_2$  was determined with four probes. Average SD of the normalized values was 0.13 for both photosynthesis and transpiration.

#### 3. Results and Discussion

#### 3.1. Experimental Observations

[17] The results in Figure 1a display the lag time between peak photosynthesis and peak transpiration of the dew-affected crops (three crops with three replications each, n = 9, 1 standard deviation, SD = 0.13).

[18] From Figure 1a, maximum photosynthetic rates were measured several hours earlier than the maximum transpiration rate. The same trend with actual fluxes of  $H_2O$  and  $CO_2$  for cotton leaves is shown in Figure 1b.

[19] Separate early peaks of photosynthesis and late peaks of transpiration are contrary to expectations because the pathway for diffusion of  $CO_2$  into leaves is similar to the pathway for diffusion of  $H_2O$  out of leaves. Both are strongly linked to stomatal conductance and solar radiation. Thus, the two processes are expected to be in the same phase [*Slatyer*, 1960; *Fritschen and Doraiswamy*, 1973; *de Wit*,



**Figure 1.** The effect of dew formation on the diurnal course of photosynthesis and transpiration. (a) Normalized values for the three dew-affected plants: cotton, maize, and soybean. (b) Example of actual data for cotton. Photosynthesis scale is given on the left ordinate. Transpiration scale is given on the right ordinate. The double arrow line indicates 9:00 A.M., the time at which the largest difference and ratio between photosynthesis and transpiration were obtained. It thus indicates the time of maximum WUE.



**Figure 2.** The effect of dew formation on the course of canopy conductance. (a) Zoom on the early morning average of normalized canopy conductance of dew and no-dew plants (SD = 0.36). The solid straight lines show the linear correlations of dew and no-dew conductance as a function of time from 4:00 to 9:30 A.M. (b) Example of actual data and the standard deviation for cotton throughout a course of 24 h.

1978; Collatz et al., 1991; Pollard and Thompson, 1995; Nobel, 2005].

[20] In Figure 1, however, photosynthesis in the early morning hours was weakly linked or not linked at all to transpiration. We argue here, and later demonstrate experimentally, that, thanks to the dew, this weak linkage is an inherent part of a strategy aimed at maximizing water use efficiency (WUE), which is most important in habitats where water supply is limited. The presence of dew on the leaves creates temporary humid conditions in the leaf-air boundaries, followed by a reduction of the driving force for transpiration, thus, increasing stomata aperture [Mott and Parkhurst, 1991; Monteith, 1995; Jarvis et al., 1999]. The biophysical basis for the results is shown in Figure 2, presenting the stomatal conductance resulting in response to low transpiration in the morning (Figure 1). Concurrently, high transpiration at noon resulted in low canopy conductance. This result was explained theoretically by a reanalysis of the stomata response [Monteith, 1995]. The conclusion of this reanalysis was that stomatal conductance and the equivalent canopy conductance (g) respond to the rate of transpiration rather than to humidity per se. In general, dg/dTr is negative. That is, when dew covers the leaves, the hydraulic conductivity of the canopy is high, and at noon when transpiration is at its peak, the hydraulic conductivity is low.

[21] In Figure 2a it is most important to note that canopy conductance is greatest during the most effective photosynthetic hours (4:00–10:00 A.M.), with dew in the morning. At 9:00 A.M., it was about 1.5 times that of no-dew plants. This resulted from the presence of dew on the leaves, which caused a temporary reduction in VPD associated with relatively high stomatal conductance. Figure 2b is the actual canopy conductance of cotton. As an example of its diurnal cycle, it shows typical bimodal midday depression in the cotton field. The main peak in the morning is affected by the dew. It then displays the midday depression and a second small peak in the afternoon that is unaffected by the dew.

[22] In terms of the molecular diffusion equations (Fick's first law), any increase in canopy conductance will cause a linear increase in the assimilation rate of  $CO_2$ . Thanks to the dew, transpiration will not increase in proportion because stomata are open early in the morning when the water vapor gradient is minimal and the evaporative ability of the atmosphere is also small. Moreover, as shown in Figure 3, night respiration dramatically increased  $CO_2$  concentration in the air.

[23] At 5:00–6:00 A.M., the CO<sub>2</sub> gradient is at its maximum. Thus, with high potential for CO<sub>2</sub> intake and low potential for transpiration, each unit of fixed CO<sub>2</sub> requires less water. The difference between Mediterranean vegetation and cultivated crops was studied by *Evrendilek et al.* [2005], who concluded that net ecosystem emission (NEE) increased as photosynthesis decreased, and soil respiratory loss of CO<sub>2</sub> to the atmosphere increased. Our measurements indicated that soil respiration was the dominant contributor to NEE. Soil respiration of the Mediterranean vegetation was only about 20  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. Thus, the natural vegetation suppressed the contribution of Mediterranean ecosystems to NEE and CO<sub>2</sub> concentration as shown in Figure 3.



**Figure 3.** The effect of night respiration on the diurnal course of  $CO_2$  concentration in the air. Lines are the moving average of four sampling channels. An example of extreme data and the standard deviation of the average are shown for the mature corn. It shows that at 6:00 A.M.  $CO_2$  concentration was 460 ppm, and at 12:00, it was only about 320 ppm.



**Figure 4.** The course of PPFD transpiration and photosynthesis in lemon. Measurements were taken under no-dew conditions to demonstrate the signal (PPFD) that results in a simultaneous response in gas exchange ( $CO_2$  and  $H_2O$ ), as opposed to the dew conditions shown in Figure 1.

#### 3.2. Modeling the No-Dew Conditions

#### **3.2.1.** Biophysical Considerations

[24] The usual case that causes a loss of water from the leaf during daylight hours (from late morning to early afternoon) requires the vapor pressure of the leaf to be greater than that in the surrounding air and the stomata to be open. However, in the early morning hours when vapor pressure in the air is greater than that in the leaf, a net diffusion of water vapor occurs toward the leaf. This can increase the vapor pressure at the leaf surface to saturation value and form dew or even intake of water into the leaf. Stomata control the exit of water vapor from leaves and the entry of CO<sub>2</sub> into them. Upon illumination, stomata are open through a well-known [Nobel, 2005] set of biophysical processes. In the usual case above, stomata openings lead to the CO<sub>2</sub> intake that is necessary for photosynthesis, resulting in an inevitable loss of water for which the driving force is the availability of irradiative energy. Our results (Figure 4) corroborated many others [for example, Mildenberger et al., 2009] and showed that during a no-dew testing day the transpiration and photosynthesis started at sunrise and both reached the sinusoidal peak shortly after the peak of the PPFD.

[25] In Figure 4 the growth of CO<sub>2</sub> fixation by the leaves is seen to be large and transpiration from the leaves is large when PPFD is large and vice versa, at least over a significant part of its range. Analysis of the data in Figure 4 showed that both photosynthesis and transpiration responded linearly to changes in PPFD with correlation coefficients of  $r^2 =$ 0.72 and 0.86 for transpiration and photosynthesis, respectively. This linearity means that the flows of the  $CO_2$  are controlled by its own concentration gradients and the flow of H<sub>2</sub>O is controlled independently by the vapor pressure gradients. For example, the concentration and gradient of  $CO_2$ , and hence, the photosynthetic flux are affected only by  $CO_2$  gradients and not at all by the dew. Thus, when modeling it as a function of PPFD, the model is a no-dew model. One way to describe such behavior is with the convolution type of expression that will be given in the mathematical consideration.

#### 3.2.2. Mathematical Consideration

[26] Convolution is a form of superposition that efficiently deals with input varying arbitrarily in time or space. PPFD in this case is the energy input that varies with time. Even though convolution has been well known since the 19th century, to our knowledge, the method has not been used extensively or used at all in micrometeorology. It works whenever superposition is applicable, that is, for linear systems. As shown above in no-dew systems, photosynthesis and transpiration are the impulses that responded linearly to the pulse of energy input (PPFD). This linearity implies that the response of photosynthesis and transpiration to PPFD is unique, and it has a unique "unit step" response. This unit step response contains all the dynamic information of the system, but dew is not included because, as previously stated, the calculated photosynthetic flux is affected linearly by PPFD, and dew does not take part in the calculated process. For this reason we provided the convolution model as an indication for no-dew conditions to compare with the actual measurements during the dew hours when dew is effective.

[27] Development of the convolution model was based on actual sets of continuous measurements of photosynthesis and transpiration and PPFD as a driving force. We extracted unit step responses that were marked: UTr for unit transpiration (Tr) and UPn for unit photosynthesis (Pn) using the practice of deconvolution.

[28] A simple way to express the convolution that was carried out in the study is in the form of a matrix:

$$[Tr] = [PPFD][UTr]$$
(1a)

$$[Pn] = [PPFD][UPn], \tag{1b}$$

where UTr and UPn are matrices of dimensionless units of photosynthesis and transpiration that are produced by one unit of PPFD.

[29] Equation (1) is a discrete convolution equation, and following the biophysical considerations, it allows the computation of transpiration and photosynthesis without dew. Given the measured PPFD, the unknown unit transpiration and photosynthesis UTr and UPn, were determined by the reverse process (deconvolution) from the ratios [Pn]/ [PPFD] and [Tr]/[PPDF]. This was needed in order to derive continuous processes of transpiration and photosynthesis that are strongly affected by PPFD and less or not affected by dew formation. We now have two expressions for WUE:

$$WUE_{WD} = Pn(t)/Tr(t)$$
(2a)

$$WUE_{WOD} = [PPFD][UTr]/[PPFD][UPn],$$
(2b)

where the subscripts of the WUE are with dew (WD) and without dew (WOD).

# 3.2.3. Using Measured and Convoluted WUE

## for Comparison of Dew and No-Dew Conditions

[30] The results of calculated WUE are displayed in Figure 5.

[31] On the left side of Figure 5, WUE that was affected by dew and obtained from the actual measurements (equation 2a) is compared to the ratio that was convoluted (equation 2b) and linked to PPDF with weak or no effect of



**Figure 5.** The course of WUE during daylight hours. The dew-affected lines (marked with WD) are results of measurements, while the no-dew lines (marked with WOD) were derived from the convolution model. Note that measurements of WUE on the right side of Figure 5 were taken under no-dew conditions, as specified in Table 1, but are included in the text as dew in order to make a consistent distinction between measured and convoluted lines.

dew. Clearly, until late morning, WUE with dew based on actual data ranged between 0.010 and 0.014 WUE units, while WUE in the afternoon was about 1 order of magnitude smaller and ranged between 0.002 and 0.004. It can also be seen that the afternoon values of WUE<sub>WD</sub> were very close to the low WUE<sub>WOD</sub> of the simulated no-dew conditions. On the right side of Figure 5, the actual measurements of WUE<sub>WD</sub> (equation 2a) were practically the same as the modeled value (WUE<sub>WOD</sub> in equation 2b) throughout the

entire day and ranged between 0.0 and 0.004. This result emphasizes the situation when the major factor affecting WUE is solar radiation (in its PPFD form) and not the presence of dew. Here both the measured and the simulated WUE with no-dew conditions are lower than that on the left side when dew was a dominant factor affecting WUE.

[32] The strength of this convolution analysis is in its ability to approximate properly what would be the WUE under no-dew conditions. It was formulated to demonstrate

Table 3.	Water Use	Efficiency of	f Three Crops	Measured in the	• Morning and	the Afternoon <sup>a</sup>
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	Units	Corn	Cotton	Soybean
CO <sub>2</sub> intake early hours of the day	g CO <sub>2</sub> m <sup><math>-2</math></sup> (leaf) h <sup><math>-1</math></sup>	2.2	2.2	3.2
CO <sub>2</sub> afternoon	$g CO_2 m^{-2}$ (leaf) $h^{-1}$	1.2	1.7	1.4
Transpiration early hours of the day	$g H_2 O m^{-2}$ (leaf) $h^{-1}$	103.5	112.3	116.9
Transpiration afternoon	g H <sub>2</sub> O m <sup>-2</sup> (leaf) $h^{-1}$	227.5	291.6	151.2
$CO_2$ assimilation at high light intensity	g CO <sub>2</sub> m <sup><math>-2</math></sup> (leaf) h <sup><math>-1</math></sup> [van Keulen and Wolf, 1986]	1.5-5	1.5-5	3–9
WUE early hours of the day	$g CO_2$ intake per kg water	21.3	19.6	27.4
WUE afternoon	$g CO_2$ intake per kg water	5.3	5.8	9.3
Integrated daily WUE	$g CO_2$ intake per kg water	6.9	7.7	11.2

<sup>a</sup>Measured when PPFD was 1000  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. In the morning, it approximated dew, and in the afternoon, it approximated the no-dew conditions. The last row presents the integrated effect of dew and no-dew conditions over a day.

the difference between  $WUE_{WD}$  and  $WUE_{WOD}$ , and as such, it strengthens the experimental data obtained from a large group of plants and crops that suggested that the presence of dew improved water use efficiency.

[33] In order to further verify the data in Figure 5, we used a comprehensive energy balance model [*Kim and Leith*, 2003] and calculated the ratio Tr/PPFD for two plants (maize and soybean) that are specified both in their model and in our measurements. In both calculations, we obtained the same values for the deconvolution term UTr (0.004 mmol m<sup>-2</sup> s<sup>-1</sup> µmol m<sup>-2</sup> s<sup>-1</sup>) and the energy balance model of *Kim and Leith* [2003] under steady state for maize and soybean when PPFD was 1500 µmol m<sup>-2</sup> s<sup>-1</sup>. For the photosynthesis in the maize and soybean energy balance model, they obtained 0.03 and 0.01 µmol m<sup>-2</sup> s<sup>-1</sup> of CO<sub>2</sub> µmol m<sup>-2</sup> s<sup>-1</sup> of PPFD for maize and soybean, respectively, while the equivalent values obtained by deconvolution calculations were about the same (Upn  $\approx$  0.01).

#### **3.3. Examining Special Cases of WUE**

[34] In Table 3, the average CO<sub>2</sub> assimilation in the early hours of the day (approximating wet dew-affected leaves) was 80% larger than that of the afternoon (approximating no-dew conditions) in spite of the fact that both were taken when PPFD was about 1000  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>.

[35] The maximal assimilation rate was that of corn, which amounted to 3.2 g  $CO_2 m^{-2} h^{-1}$  (about the potential production rate of C4 plants) [*van Keulen and Wolf*, 1986], whereas dry leaves produced only 1.4 g  $CO_2 m^{-2} h^{-1}$ , a ratio of more than 2:1 wet-dry leaf assimilation under the same environmental conditions. In terms of WUE, the results are even more convincing. Average transpiration of plants covered with dew was 111 compared to 223 g H<sub>2</sub>O m<sup>-2</sup> h<sup>-1</sup> from dry plants. The combination of high photosynthetic rate and low transpiration on dew-affected leaves led to an average WUE of 24.6 compared to 6.6 g CO<sub>2</sub> per kg water for unaffected plants. Thus, the synergistic contribution of dew to WUE was clearly demonstrated.

[36] It should be mentioned that while Figure 1 shows that photosynthesis leads transpiration during morning hours, at the end of the day, the trend is reversed by the extended transpiration in the afternoon. In Figure 5 the WUE of dew-affected plants was greater than that of the no-dew plants in the morning and about the same later during the day. As a result, the integrated effect over a day remains very positive, but it contributes only 20%–40% to WUE as shown in Table 3.

#### 3.4. Concluding Comments and Related Issues

[37] Modern growers and ecologists with sharp senses for natural phenomena detected the blessings of dew. In biblical times, also, the dew blessing was considered to be similar or even larger compared to rainfall but without proper scientific documentation [Monteith, 1957, 1963]. Our study with modern instrumentation provides for the first time the experimental picture of the interaction between dew and plant growth, illustrating how the dew plays an important role in biomass production at low water cost. Moreover, the consequences of this study are independent of the dispute regarding the role of dew as a water source. On one hand, preliminary estimations based on global warming output suggest reductions in the dew frequencies with a potential significant effect on the WUE, a fact not yet considered in the vast literature on global warming impacts. Prediction of regional warming [Kimura et al., 2007; Kitoh, 2007] for 2070-2080 indicate a clear decline of relative humidity in the region from 100% to  $64\% \pm 18\%$  during the best hours for dew formation in the summer. If the predicted regional warming of the eastern Mediterranean area becomes a reality, natural vegetation and agricultural crops will likely display reductions in WUE and increased water demand in order to maintain the current biomass production. On the other hand, elevated CO<sub>2</sub> may result in significant increase of plant growth. Prediction of the impact of these two contradictory directions requires a more comprehensive model that is currently under study and a different set of measurements. It can possibly be obtained by the approximated relationship WUE  $\approx$  atmospheric CO<sub>2</sub> concentration/ VPD [Kefi et al., 2008]. As a first approximation, our convolution model assumed that the major and the only driving force for photosynthesis and transpiration is the PPFD. Under this assumption, atmospheric CO<sub>2</sub> concentration does not significantly affect the two functions. According to this approximation, the response of the stomata to the environmental conditions in their near vicinity is hidden within the UPn, which provides the photosynthetic rate per unit PPFD and the UTr, which provides the transpiration rate per unit PPFD.

[38] Acknowledgments. This study was funded by the GLOWA Jordan River grant from the Ministry of Science Israel, and the Bundesministerium fuer Bildung und Forschung (BMBF), the ICCAP project (Impact of Climate Change on Agriculture Productivity) of the Research Institute for Humanity and Nature (RIHN) in Kyoto, Japan, and TUBITAK, the Ministry of Science and Technology, Turkey.

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