Int. J. Plant Sci. 155(4):460–466. 1994.

1058-5893/94/5504-0007$02.00

INFLUENCE OF SIMULATED DEWFALL ON PHOTOSYNTHESIS AND YIELD IN SOYBEAN ISOLINES (GLYCINE MAX [L.] MERR. CV WILLIAMS) WITH DIFFERENT TRICHOME DENSITIES

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Leaf surface wetness, e.g., dewfall, has been shown to have a strong influence on photosynthetic CO_2 exchange in native plants. The important influence of trichomes on leaf surface wettability has also been established. We evaluated the effect of leaf surface wetness on photosynthesis and yield in soybeans (*Glycine max*) for five isolines that varied in trichome density. Artificial misting was used to simulate the influence of natural dewfall as well as spray irrigation. Leaf trichomes had an important influence on droplet formation and the distribution and retention of liquid water on individual leaves, even though trichome densities were low compared with maximum values reported for native species. Greater water droplet formation and, thus, water repulsion occurred for isolines with greatest trichome density. Somewhat surprisingly, these isolines also have the greatest droplet retention. However, all isolines showed relatively low water repellency, along with reductions in CO_2 assimilation that averaged about 15%. Isolines subjected to misting during the morning (simulated dewfall) also had lower aboveground (15%) and seed (19%) biomass, and total leaf area (14%) compared to control plants. Thus, surface wetting, either from natural events (e.g., dewfall) or spray irrigation, may lead to significant reductions in CO_2 exchange and growth potential in agricultural species, as reported for native species.

Introduction

Leaf surface wetness, whether from natural sources (e.g., rain, ground fog, cloud mist, dewfall) or artificial sources (e.g., spray irrigation), can be almost a daily event during the growing season for many native and agricultural plants. Long periods of natural leaf surface wetness (up to 14 h for dew and longer for rain) may occur during a day (Leclerc et al. 1985; Barr and Gillespie 1987; Harrington and Clark 1989), while daily spray irrigation may substantially increase the frequency and duration of leaf surface wetness in agricultural species.

The frequent occurrence of wet leaf surfaces in agricultural areas has been the subject of considerable research. For example, widespread attention has been focused on the effect of leaf surface wetness on the efficiency of herbicide, insecticide, and fungicide applications (Fogg 1947; Bukovac et al. 1979). Also, the enhancement of pathogen invasion on wet leaves is particularly well-documented for agricultural species (Hollier 1985; Reynolds et al. 1989). Absorption of atmospheric pollutants is also known to be enhanced by leaf surface wetness (Boyce et al. 1991). However, the direct influence of leaf surface wetness on CO_2 assimilation and growth has been addressed only recently (Smith and McClean 1989; Brewer et al. 1991), despite the fact that CO_2 diffuses approximately 10,000 times more slowly through a film of water than through air (Weast 1979).

Native plants appear to have a broad spectrum of leaf surface wettability, from completely wettable leaves that become covered by a film of water to virtually nonwettable leaves that bead water into small spherical droplets (Smith and McClean 1989; Brewer et al. 1991). Films may occur as a continuous layer of water covering the entire leaf surface or as patches of water partially covering the leaf. Both adaxial and abaxial leaf surfaces are often wetted by precipitation, especially dewfall (Stone 1963; Huber and Itier 1990; Brewer 1993). Leaves with water films on their surfaces have shown major reductions in photosynthetic CO_2 uptake (Smith and McClean 1989; Brewer 1993). Also, a recent study of native plants found that trichomes appeared to have an important influence on the wettability of leaf surfaces and the tendency for leaves to retain or repel surface moisture (Brewer et al. 1991).

The purpose of the present study was to evaluate the effect of leaf surface wetness on leaf gas exchange and yield in soybeans (*Glycine max* [L.] Merr. cv Williams). Leaves were sprayed to simulate precipitation events in the field such as natural dewfall and artificial spray irrigation. The specific influence of trichomes on leaf wettability, droplet retention, and the duration of leaf wetness was evaluated by comparing near-isogenic isolines of soybean that had different trichome densities (*G. max* Clark isoline). We hypothesized that any differences in the wettability of leaf surfaces could result from different trichome densities and, thus, could also have a significant impact on photosynthetic CO_2 assimilation, plant growth, and reproduction.

Material and methods

Plants

Seeds of the soybean isolines with different trichome densities were obtained from the U.S. De-

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Manuscript received November 1993; revised manuscript received February 1994.

partment of Agriculture, Northern Soybean Germplasm collection in Urbana, Illinois. Seeds of glabrous (no trichomes) (L62-1385), plus sparse (L63-2999), semisparse (L62-314), wild-type (L88-1718), and dense (L62-1686) pubescence isolines were planted on November 21, 1991. Prior to planting, seeds were dipped in a fungicide (captan) and then transferred to germination paper. Seedlings were grown on germination paper under 24 h light, 24°C, and 90% humidity in a growth chamber until the appearance of the first true leaves. Twenty healthy plants were selected arbitrarily from 50 seedlings of each isoline (100 seedlings total) and transplanted to plastic cone-shaped containers filled with sterilized sand. After 6 wk, 15 healthy plants from each isoline were transplanted into 10-in-diameter plastic pots filled with a mixture of 1 : 1 : 1 peat, sand, and topsoil. Ten plants from each isoline were assigned to the misting experiment described below (five misted, five nonmisted controls), while remaining plants were used for measurement of photosynthesis and leaf surface features.

All plants were transferred to a temperature controlled greenhouse on December 18, 1991, where they were grown under ambient light at a temperature of 21°–25°C. Plants were rotated weekly to minimize the effect of position in the greenhouse and to minimize mutual shading. Plants were watered thoroughly each day and fertilized with a 1 : 50 solution of 20-20-20 N,P,K approximately once per week. Insecticides (Avid, Enstar, Orthane, or Malathion) were applied as needed (approximately every 2 wk) to control pests.

Misting treatment

Five plants from each isoline were misted within ± 30 min of dawn every morning from December 11, 1991, until they were harvested in mid-March 1992. We have observed that dew occurs commonly on leaf surfaces in both natural and agricultural species. Because soybeans are amphistomatous, both adaxial and abaxial leaf surfaces were spray misted. To simulate the deposition of advective and distillation dew (Monteith and Unsworth 1990), and intensive spray irrigation, we sprayed with a fine mist nozzle as well as a hand-held spray bottle to ensure that both adaxial and abaxial leaf sides were wetted. This procedure took approximately 1 h each morning. The experimental spray misting technique used in the greenhouse resulted in dew droplet formation that was similar to natural leaf wetting following dewfall in the field. Droplet sizes on leaves in the field ranged from approximately 90 μm to over 6 mm in diameter (Brewer et al. 1991) and were similar to experimentally misted leaves. The duration of leaf surface wetness was monitored once per week throughout the experiment by visual inspection and was found to be similar to the duration of leaf surface wetness measured in the field (up to 5 h after dawn [C. A. Brewer and W. K. Smith, unpublished]).

Leaf surface characteristics

Morphological and anatomical characteristics known to be important to leaf surface wettability, including trichome and stomatal density, contact angles of water droplets on the leaf surface (θ), and droplet retention, were measured. Both adaxial and abaxial leaf surfaces from five leaves of each isoline were measured. Measurements were made on leaves that had been cut from plants. Average trichome density was calculated by counting the number of trichomes within a micrometer grid (2.5 mm × 2.5 mm) for five leaves with five replicates per leaf surface for each isoline. Surface casts were made from each leaf surface using enamel (Neill et al. 1990), and stomatal density was also estimated by counting the number of stomatal impressions for five replicates per leaf surface on five leaves of each isoline.

The degree of water repellency of the leaf surface was quantified by measuring the contact angle (θ) of a 5 μL droplet placed upon the leaf surface with a micropipette (Adam 1963; Crisp 1963). The angle, θ, of a line tangent to the droplet through the point of contact between the droplet and leaf surface was measured relative to the epidermis for horizontally positioned leaves, even when droplets rested above the leaf surface on trichomes. Five replicates per leaf were measured on both leaf surfaces from five leaves for each isoline. In general, wettable leaf surfaces ($\theta < 110°$) do not generate spherical droplets, while nonwettable surfaces ($\theta > 130°$) generate distinct droplet formation.

Droplet retention was measured by placing 50 μL droplets on leaves oriented horizontally and then measuring the angle of leaf inclination at which the droplet first began to move. Higher inclination angles before droplets moved indicated a greater tendency to retain them. Five replicates per leaf surface for five leaves were measured for each isoline.

Biomass

After seed pod formation was well underway but before leaf senescence (to get a realistic estimate of leaf area), all plants in the misting experiment were harvested. Shoots were cut at the soil surface and total leaf area for each plant was measured for detached, flat leaves using a video leaf area meter (Decagon Instruments, Pullman, Wash.). Fresh leaves, stems and petioles, flowers, and seed pods were sorted and weighed separately, dried at 80°C to a constant weight, and then reweighed. Within-treatment means were compared with a one-way analysis of variance,

Table 1

Leaf surface characteristics for five isolines of soybeans

Isoline/leaf side	Stomatal density (no./mm²)	Trichome density (no./mm²)	θ (degrees)	Retention angle (degrees)
Glabrous:				
AD...	80 (8.9)	.1 (.04)	71 (1.0)	17 (1.2)
AB...	187 (12.9)	.2 (.11)	72 (.7)	14 (.8)
Sparse:				
AD...	18 (9.8)	.3 (.08)	78 (1.0)	18 (1.1)
AB...	155 (11.9)	1.0 (.19)	77 (1.0)	13 (.9)
Semisparse:				
AD...	27 (7.2)	.6 (.07)	86 (1.7)	20 (.7)
AB...	182 (14.0)	1.2 (1.2)	83 (.8)	18 (.6)
Wild:				
AD...	102 (16.3)	1.4 (.09)	117 (1.4)	55 (3.9)
AB...	231 (18.5)	2.9 (.08)	116 (1.4)	20 (1.2)
Dense:				
AD...	62 (13.6)	8.0 (.45)	128 (1.3)	34 (1.7)
AB...	169 (16.6)	10.3 (.68)	130 (.6)	20 (1.5)

Note. Data for each leaf side are presented separately (AD is the adaxial surface and AB is the abaxial surface). Values are for stomatal density, trichome density, contact angle of water droplets (θ), and droplet retention. Values in parentheses are standard errors: $n = 5$ for each average.

while between-treatment means were compared with Student's t-test.

Photosynthetic CO_2 exchange

Net photosynthetic CO_2 assimilation was measured for dry leaves and compared with the identical measurements for leaves that had been misted to simulate dew formation and spray irrigation. Prior to misting treatments, photosynthetic CO_2 uptake was measured on three leaves each from the glabrous, semisparse, and dense isolines. Two of these leaves were misted on both leaf surfaces while the other leaf was not misted. Photosynthesis was monitored periodically until the misted surfaces were completely dry. Data for stomatal conductance to water vapor and, thus, internal CO_2 concentration were not considered because of the presence of moisture on the leaf surfaces. Measurements were made between 1000 hours and 1500 hours under clear skies to avoid potentially strong influences of variable light levels.

A fast response, closed-flow portable infrared gas analyzer system (model LI-6200, Li-Cor, Lincoln, Nebr.) was used, which also measured leaf temperature and incident PPFD (Li-Cor 190S quantum sensor). Measurements were made on individual attached leaves (leaf area of 12 cm²) sealed in a gas exchange cuvette (1-L volume) in their natural orientation to the sun. Measurements were made on leaves of the same age (each 4 wk old), and CO_2 was not depleted by more than 25 μL/L for each measurement period. The PPFD sensor was oriented in the same plane as the leaf and all values for net photosynthesis (A) are expressed as μmol CO_2 m^{-2} s^{-1} on a silhouette leaf area basis (Smith et al. 1991).

Results

Leaf surface characteristics and water repellency

Stomatal density on adaxial surfaces was lowest for the sparse ($\overline{X} = 17.8$ stomates mm^{-2}) and semisparse ($\overline{X} = 26.6$ stomates mm^{-2}) isolines. Stomata were most numerous on the abaxial surfaces of all isolines examined, although numerous stomata also occurred on adaxial surfaces (table 1). The greatest adaxial and abaxial stomatal densities occurred in the wild-type isoline (102 mm^{-2} and 231 mm^{-2}, respectively).

Trichomes were rarely observed on glabrous leaves (table 1). Sparse and semisparse isolines had very similar trichome numbers (≤ 1.2 trichomes mm^{-2}) on the abaxial surface, but there were twice as many adaxial trichomes on the semisparse isoline ($\overline{X} = 0.6$ mm^{-2}) as the sparse isoline ($\overline{X} = 0.3$ mm^{-2}). The wild isoline was intermediate in trichome number ($\overline{X} = 2.9$ mm^{-2}), while the dense isoline had the most trichomes for both adaxial ($\overline{X} = 8.0$ mm^{-2}) and abaxial ($\overline{X} = 10.3$ mm^{-2}) surfaces. For all isolines, the abaxial surfaces had the highest number of trichomes as well as stomata (table 1).

Experimental misting generated water films, not droplets, on both surfaces of the glabrous and sparse isolines, as well as on the adaxial surface of the semisparse isoline. For the two isolines with the greatest density of trichomes (wild type and dense), misting resulted in large and small water patches as well as in single droplets on both leaf surfaces. There were no large differences (<2%) in leaf wettability (θ) between adaxial and abaxial surfaces within any isoline (table 1). The glabrous, sparse, and semisparse isolines were wettable on both leaf surfaces ($\theta < 110°$) while the wild-type isoline was less wettable ($\overline{X}$ for θ approximately $115° \pm 1.4°$). The dense isoline was relatively nonwettable ($\overline{X}$ for $\theta = 129° \pm 0.6°$) on both leaf sides (table 1).

For all isolines, the adaxial leaf surface had the highest droplet retention (16°–55°), while abaxial surfaces had somewhat lower mean retention (13°–20° [table 1]). Glabrous and sparse isolines had the least tendency to retain droplets (retention typically <20°), while semisparse, wild-type, and dense isolines retained droplets on the leaf surface to a much steeper angle of inclination (retention typically >20°).

Biomass

Total leaf area and total aboveground biomass did not vary significantly between the five different isolines within each misting treatment. Because there was little within-treatment variation between isolines (except for glabrous plants), data from all isolines were pooled to examine overall effects of the misting treatment. Leaf and flower weight did not vary significantly between misted and nonmisted plants, although average biomass was higher by about 10% in nonmisted plants (table 2). However, stem ($P \leq .01$) and seed ($P \leq .05$) biomass were significantly greater by nearly 20% in nonmisted plants. Both the number of seed pods produced ($P \leq .001$) and seed weight ($P \leq .05$) were also significantly greater by about 16% and 19%, respectively, in nonmisted plants (table 2). Nonmisted plants had 14.4% more leaf area ($\bar{X}$ = 3,184 cm^2) than misted plants ($\bar{X}$ = 2,725 cm^2) by the end of the experiment ($P \leq .01$). Overall, plants that were not misted had substantially greater total aboveground production ($\bar{X}$ = 48.4 g) than misted plants ($\bar{X}$ = 41.7 g; $P \leq .01$), a net increase of almost 14% (table 2).

Photosynthesis

Stomata of nonmisted (dry) soybean leaves were generally open in the morning and afternoon, and the highest rates of net photosynthesis (A) and stomatal conductance (g) were achieved by late morning. During a typical day with little cloud cover, A for dry leaves did not decline substantially until late afternoon. Highest A occurred at about 1100 hours ($\bar{X}$ = 20.4 μmol m^{-2} s^{-1}; $\bar{X}$ stomatal conductance = 270 mmol m^{-2} s^{-1}; n = 9). Late in the afternoon, average A declined to about 11.0 mmol m^{-2} s^{-1} and stomatal conductance was only 180 mmol m^{-2} s^{-1} (n = 6).

There was a substantial and immediate reduction in A following misting (fig. 1). Typically, A decreased 1%–15% and then returned to ±3% of premisting levels within 30–40 min (fig. 1). During the same time intervals, A varied by only about ±6% for untreated control leaves. For all isolines, A declined by 3%–46% after misting compared with unmisted control leaves, with an average decline of ca. 15% (table 2). The average decline for glabrous leaves was 10%, compared with an 11.5% decline for semisparse leaves and a 15% decrease for dense leaves.

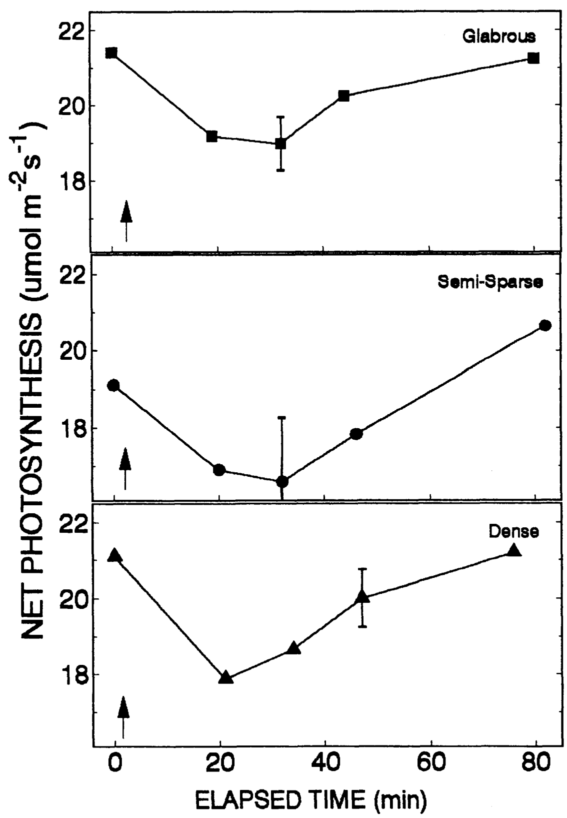

Fig. 1 Representative response of net photosynthesis of soybean leaves from three isolines to misting treatment. Responses to misting are shown for glabrous leaves (top), semisparse leaves (middle) and dense leaves (bottom). The arrow indicates the time of application of misting treatment. Bars represent ± the maximum standard error for n = 4.

Discussion

Trichomes and leaf surface wettability

Leaf trichomes have an important influence on leaf wettability in a variety of native plant species. Brewer et al. (1991) reported that dense trichome canopies held droplets above the leaf surface so that contact with the leaf surface and, thus, interference with stomatal pores was minimized. More intermediate trichome densities tended to segregate water into patches that were retained until they evaporated. In both cases, the amount of surface area beneath liquid water was substantially reduced because of trichomes. In some species, high water repulsion resulted in very spherical droplets (high θ), yet droplet retention was also high, creating moist air next to the leaf surface (Brewer et al. 1991). A higher vapor pressure next to the leaf surface could stimulate greater stomatal opening and CO_2 uptake at a much lower transpiration rate and higher water use efficiency (Smith and McClean 1989; Brewer et al. 1991).

In the present study, droplets tended to coalesce on both leaf surfaces of glabrous and sparse isolines and on the adaxial surface of the semisparse isoline and then roll off (low droplet retention). In contrast, trichomes on the abaxial surface of the semisparse isoline and on both surfaces of wild-type and dense isolines appeared to have a strong influence on the location of surface water. According to the classification of Brewer et al. (1991), the semisparse, wild-type, and dense isolines of soybeans have trichome arrangements that may enhance retention of droplets on the leaf surface. In this case, water droplets with relatively high θ tended not to be shed, even at steep leaf angles (table 1), but remained on the leaf surface for several hours until they evaporated. None of the isolines tested had great enough trichome densities to suspend droplets above the leaf surface. Suspension of water droplets appears to require a minimum of 20–30 trichomes mm^{-2} (Brewer et al. 1991).

Duration of leaf wetness

The duration of leaf surface wetness we observed in the greenhouse (up to 5 h after sunrise) was similar to that observed in the field for dew-generated leaf wetness in maize (Barr and Gillespie 1987), as well as for native plants in the central Rocky Mountains of the United States (Smith and McClean 1989; Brewer 1993). In agricultural systems and natural habitats, the duration of leaf wetness is dependent upon a host of environmental variables including total absorbed radiation, wind speed, air temperature, and vapor pressure (Butler 1986). In addition, leaf surface features such as trichomes, waxes, or other surface irregularities may alter the susceptibility to, and duration of, leaf surface wetness (Leclerc et al. 1985). The combination of trichome densities greater than 40 mm^{-2}, low surface wettability (high θ), and low droplet retention has been shown (Brewer et al. 1991; Brewer 1993) to enhance the shedding of water droplets and reduce the formation of surface films of water in both greenhouse and field conditions. The duration of leaf surface wetness may be shortened substantially by wind if water droplets are displaced from leaves as they flutter. Within a canopy, sun-exposed leaves probably dry most quickly, while surface wetness may persist much longer for shaded leaves. Although small droplets evaporate rapidly because of a higher surface-to-volume ratio, larger droplets and water patches may persist for several hours (Brain and Butler 1985). Furthermore, as drying proceeds, droplets often tend to flatten, resulting in lower θ (Leclerc et al. 1985; Brewer et al. 1991, and unpublished data). Consequently, the extent of leaf surface area, and, thus, the number of stomatal pores affected by droplets, may increase slightly as evaporation occurs without any addition of surface water.

Photosynthesis and biomass production

The effect of leaf surface wetness on plant growth has been discussed most often in regard to pathogen infection (Fogg 1947; Bukovac et al. 1979; Hollier 1985). In contrast, the impact of leaf surface wetness on photosynthetic gas exchange has not received widespread attention, even though dew forms most commonly during the night and early morning hours and can persist well into the morning when stomatal conductance and photosynthetic carbon assimilation should be greatest because of high tissue water potential (Schulze and Hall 1982). A few earlier studies have considered specifically the effects of early morning dewfall on transpiration and exchange of CO_2 (Stahl 1898; Stone 1957, 1963; Ghorashy et al. 1971). Dew formation was reported to cause either increased or decreased transpiration and reduced water usage in seedlings of different pine species (Stone 1963). Ghorashy et al. (1971) suggested that trichome density had a significant relationship to transpiration rate. Transpiration was substantially higher for glabrous than pubescent isolines of soybeans, and they hypothesized that trichomes increased the leaf boundary layer resistance to water vapor loss.

In the current study, the largest reductions in A occurred immediately after misting, perhaps because water physically blocked stomatal pores. We also found the least reduction in photosynthesis in the glabrous isoline. Although more stomates were initially blocked, glabrous leaves had the lowest droplet retention, and, therefore, water was effectively removed from the leaf surface after being wetted.

Smith and McClean (1989) found that leaf surface wetness caused the greatest decline in photosynthesis for the surfaces with the lowest water repulsion (lowest θ). However, the reduction we observed in soybeans was less (3%–46% reduction), in general, than for the native species (2%–95% reduction) evaluated by Smith and McClean (1989), probably because of the wider range of θ values measured for the larger number of native species. Also, neither A nor g increased immediately after artificial drying of misted leaves as Smith and McClean observed for three native species. Thus, these soybean isolines did not appear to respond to surface wetting (and increased vapor pressure at the leaf surface) by opening stomata. Regardless, the possibility that increased droplet retention may lead to increased vapor pressure at the leaf surface and, thus, increased stomatal opening deserves further study.

Decreased biomass production in soybeans also occurred in response to experimental leaf wetting early in the morning (table 2). A mean reduction in above ground production of at least 14% ($P <$ .01) occurred for plants that were artificially wetted during the morning. Egli (1988) reported that fruit and seed number were related to crop growth rate, which implied that seed number was determined primarily by current photosynthesis. Thus, any factor decreasing photosynthetic rate could also lead to reduced seed set and yield. Consequently, the frequency of occurrence of leaf wetness in natural and agricultural systems from

Table 2

COMPARISON OF MISTED AND NONMISTED PLANTS

Variable	Misting treatment	Nonmisted control	Significance
Net photosynthesis (μmol m^{-2} s^{-1})	18.1	20.6	**
Biomass (g):			
Leaf	14.8	15.4	ns
Stem	7.8	9.6	**
Flower	.15	.17	ns
Seed	18.9	23.3	*
Total reproductive tissue	19.0	23.5	*
Total aboveground biomass	41.7	48.4	**
Total belowground biomass	21.0	20.1	ns
Number of nodes per main stem	13.1	14.0	*
Number of seed pods	62.6	74.9	***
Total leaf area (cm^2)	2,725.2	3,183.7	**

Note. Values for all isolines were combined. Significant differences between groups were determined with Student's t-test. Values represent averages ($n = 5$ for all values except net photosynthesis where $n = 10$).

* $P \leq .05$.
** $P \leq .01$.
*** $P \leq .001$.

dewfall (and spray irrigation in cultivated fields) may have an important effect not only on biomass accumulation through the growing season but also on fruit and seed production. Given the reductions in A (fig. 1), it is not surprising that biomass accumulation was lower for plants experiencing long periods of leaf surface wetness. Contrary to the views of Monteith (1963), these results indicate that dew may have considerable physiological significance for plant growth and yield.

Acknowledgments

Funding was provided by National Science Foundation (BSR-89-19228) to W. K. Smith. We thank Dr. R. Groose and Dr. A. Schoettle for advice on soybean isolines and growth, and Dr. R. Groose and Dr. R. Abernethy for space and use of equipment. C. Amiand, Farhatullah, and T. Thompson provided technical assistance. We thank T. J. Gillespie and an anonymous reviewer for constructive criticism of this manuscript.

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