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Environmental factors affecting the life tables of *Tetranychus urticae* KOCH (Acarina). II. Host plant water stress

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Small micro-propagated apple trees were exposed to different water supply treatments. The induced changes in leaf surface temperatures and in leaf nitrogen and sugar content were related to the life tables of the twospotted spider mite *Tetranychus urticae*. Water deficiency increased stomatal diffusive resistance, inducing higher leaf temperatures and thus shortening immature developmental time. Fecundity and longevity were also impaired, presumably by the declining leaf N content. Therefore, the growth of a mite population, expressed as the intrinsic rate of natural increase (r_m), turned out to be the result of a subtle balance between leaf quality and temperature: at slight stress, poor (or unaffected) leaf quality was outweighed by the acceleration of development from increased temperature. At severe stress, poor leaf quality limited reproduction outstripping the favorable effects of higher temperatures. Temperature seemed to be a key factor since at compensated leaf temperatures oviposition rate did not differ between water stress treatments.

INTRODUCTION

It is well known that hot and dry weather conditions favor the outbreak of spider mites (MATTSON & HAACK, 1987). Besides direct environmental influences such as ambient temperature and humidity, indirect, plant-mediated factors also affect the development of herbivorous populations. Such effects can be best investigated in a plant-herbivore-system under natural or artificial stress conditions.

In a previous paper the direct effect of ambient temperature on spider mite life tables was discussed (WERMELINGER *et al.*, 1990a). While the existing literature on water stress – herbivore interactions has generally focused on either biophysical or biochemical aspects, the present work investigates short term changes in both aspects of host plant condition at water shortage, and the consequences for the life tables of the twospotted spider mite *Tetranychus urticae* KOCH. The term “water stress” used hereinafter will always signify water deficiency.

LITERATURE REVIEW

Response of the host plant to water stress

Some crucial arthropod-relevant effects of water stress on plant physiology and morphology are summarized below (according to HSIAO, 1973; MATTSON & HAACK, 1987; HOLTZER *et al.*, 1988a):

Attractiveness – Water stressed host plants may become more attractive to arthropods by changing colors, acoustical attractants (JONES & PENĀ, 1986), production of kairomones or phagostimulants like proline.

Microclimate – Closed stomata lead to lower evapotranspiration and hence to less efficient cooling of the plant, raising the temperature of the leaf surface by 2–4 °C, to the extreme of 15 °C above ambient temperature. This means an acceleration of the development of poikilothermic herbivore. Because leaf temperatures and water supply are closely correlated, canopy temperature was also used to evaluate water stress (e.g., JACKSON, 1982). In addition, relative humidity in the microenvironment inhabited by spider mites is influenced as well. The microclimate mainly affects herbivore development.

Growth – Cell division and enlargement are hindered, the cell walls grow thicker and more fibrous generally rendering food uptake more difficult. Stomatal closure hampers CO₂ uptake and with it photosynthesis. Eventually, the biosynthesis systems are impaired (LAWLOR, 1983) reducing food quantity available to herbivores.

Turgor pressure – The osmotic potential decreases, i. e., it becomes more negative, whether by passive concentration of the cell sap (DAVIES & LAKSO, 1978) or by active accumulation of solutes. Through the latter mechanism the plant tries to maintain its turgor potential to keep stomata open (osmotic adjustment). At severe stress the turgor pressure eventually declines, thus augmenting the effort of sucking arthropods to acquire food. A lower water content (water potential) seems to impair the efficiency of foodplant biomass assimilation of chewing insects (SCRIBER, 1977).

Nutritive value – Stress reduces synthesis of proteins and enhances their degradation (cf. WHITE, 1984), resulting in an accumulation of soluble nitrogen (amino acids, mainly proline) and of soluble sugars, which improve the dietary quality for spider mites. On the other hand, high availability of carbohydrates and nitrogenous compounds promotes the formation of secondary metabolites acting as defensive compounds against insects. Nutrient uptake is limited under water stress, but since growth is reduced as well, nutrient concentration may even increase. The concentration of the nutrients and also their balance play an essential role: in general, water stress seems to improve the dietary composition for herbivores.

Response of spider mites to water stress

A number of studies have investigated the influence of host plant water stress on spider mites. Both low and very high ambient humidities generally have a negative effect on spider mites (VAN DE VRIE *et al.*, 1972; HAZAN *et al.*, 1973; FERRO & CHAPMAN, 1979; BOYNE & HAIN, 1983; PERRING *et al.*, 1984a,b; CROOKER, 1985; VAN DER GEEST, 1985). A study by HOLTZER *et al.* (1988b) demonstrated in more detail the effect of the microenvironmental humidity relevant to spider mite population development.

On *Chrysanthemum* the density of *T. urticae* was inversely related to the water supply (PRICE *et al.*, 1982), and on peppermint it was higher in the water stress treatment (HOLLINGSWORTH & BERRY, 1982). Water stressed almond foliage promoted the development of two tetranychid species compared with unstressed leaves (YOUNGMAN & BARNES, 1986). With *Oligonychus pratensis* (BANKS) on corn, FEESE & WILDE (1977) reported higher oviposition at the low water treatment, and out of three different stress levels applied on corn, the inter-

mediate one developed the highest number of this species (PERRING *et al.*, 1986), which was attributed to higher canopy temperatures and adequate host quality. YOUNGMAN *et al.* (1988) found total egg production of *Tetranychus pacificus* MCGREGOR to differ more between two kinds of water stress than between stressed and nonstressed almond trees: at intermittent stress females deposited more eggs than at continuous water stress. Water shortage seemed to bias the sex ratio in favor of the females. Stressed leaves had higher temperatures and lower total nitrogen.

On the other hand, SPECHT (1965) found retardations in *Panonychus ulmi* KOCH population growth on water stressed apple trees, depending on the soil type. Water stress was reported to improve the resistance of a cucumber variety to the twospotted spider mite (GOULD, 1978). Survivorship of the mites was reduced at constant stress compared to the no-stress and late stress treatments. Developmental rates, however, generally increased with stress intensity. Regularly irrigated field corn had lower numbers of *O. pratensis* and *Tetranychus cinabarinus* (BOISDUVAL) than plants with a water shortage (CHANDLER *et al.*, 1979). On soybeans the abundance of *T. urticae* was reduced (MELLORS *et al.*, 1984; OLOUMI-SADEGHI *et al.*, 1988), however the MELLORS experiments were conducted at the extreme temperature range of 20–45°C. In recent works, ENGLISH-LOEB (1989, 1990) described a non-linear response of *T. urticae* to water stress. Their abundance and fecundity decreased at mild and at severe stress, while they increased at moderate stress. The effect of plant-mediated micro-environmental conditions on a spider mite population could be simulated by a computer model (TOOLE *et al.*, 1984).

The opposite stress, i. e. flooding, appears to increase herbivory. LOUDA (1986) found chewing, sucking and mining insects to cause more damage on root-severed, flooded *Cardamine* plants.

The controversy of the above results may be explained by different intensities and durations of water stress besides the general environmental conditions under which the studies were made (for more details see the discussion section).

MATERIAL AND METHODS

Apple trees

Young apple trees of the variety “Glockenapfel” were cloned by tissue cultures (WERMELINGER, 1985). At a height of 25 cm, two trees at a time were potted in a mixture of soil, sand and peat (10:1:1) in 20-liter containers. The experiments were started at a plant height of approximately 50 cm. The pots were placed in a growth chamber at 24/18°C day/night temperatures, 70% rH and a photoperiod of 16 h.

The water stress levels resulted from the different frequencies of irrigation (see below) and were monitored by two tensiometers per container. Irrigation was applied such that soil water potentials lower than – 800 hPa (– 0.8 bar) were avoided. The characteristics measured on the plant were leaf water potential Ψ , osmotic potential Ψ_{π} , diffuse resistance, leaf temperature T, nitrogen concentration and sugar content of the leaves. The water potential Ψ of leaves was measured by the pressure-bomb method (PMS Instruments). For the determination of the osmotic potential Ψ_{π} , leaf samples were immediately frozen in liquid nitrogen to interrupt the metabolism and to destroy the membranes. Plant sap

squeezed from these samples was analyzed in an osmometer (Wescor). From the osmolality readings, Ψ_{π} was calculated as

$$\Psi_{\pi} = -C_s R T \text{ (van't Hoff)} \quad [1]$$

where Ψ_{π} = osmotic potential [MPa], C_s = osmolality [Os m⁻³], R = gas constant (8.314 J mol⁻¹ K⁻¹) and T = (leaf) temperature [K]. From the water and the osmotic potential, the turgor potential Ψ_P can be approximated as

$$\Psi_P = \Psi - \Psi_{\pi} \quad [2]$$

Leaf surface temperatures were measured by a hand held infrared thermometer (Telatemp) which allowed remote detection of temperatures. An automatic porometer (Delta-T Devices) determined the diffusive resistance of leaves. Dried (48 h at 65 °C) and ground leaf material was analyzed volumetrically for nitrogen in an automatic N analyzer (Heraeus). Sorbitol, glucose, fructose and sucrose were analyzed enzymatically by UV-test combinations (Boehringer Mannheim). These sugars will be collectively referred to as carbohydrates. For more details on the experimentation theory the reader is referred to SCHNIDER (1989).

Spider mites

A culture of *Tetranychus urticae* KOCH was maintained on leaf disks of bush beans in plastic trays. The conditions in the growth chamber were typically 24 °C/18 °C at a photophase of 16 h, however temperature was used to regulate developmental speed, if required, to synchronize the stage of mites and plants.

Experiments

A first experiment was conducted to determine the dynamics of the plant potentials, diffuse resistance and leaf temperatures at two water stress treatments with eight plants each. The control was watered daily, while the irrigation of the stressed plants was interrupted after the plants had established. The changes over time of the previously described parameters were recorded 1, 4, 7, 10 and 13 days from the beginning of water withdrawal.

In the second experiment the effect of three different water stress levels on the development of *T. urticae* was tested on 12 plants per treatment. The plants of the control treatment (treatment C) were irrigated daily, the irrigation of the other two treatments was discontinued 5 days (treatment S I) and 8 days (treatment S II) before the infestation with spider mite eggs. On days 3 and 7 each container of the two stress treatments received 1 liter of water to prevent too severe desiccation. On day 0 a one-day-old egg was placed on each of three similar leaves per plant, totalling 36 eggs per treatment. The development of the mites was monitored until oviposition at 3 h intervals. Leaf temperatures were recorded three times a day, soil water potential daily, and leaf N content was determined at the end of the experiment.

The third experiment evaluated the oviposition and the longevity of adult females at three different water supply levels (C, S I, S II). Three days (S I) and 5 days (S II) before the beginning of the experiment irrigation was interrupted for the stressed plants, the control (C) continued to be watered daily. Due to the longer duration of the experiment, S I was watered every 3 days and S II every 5 days with 1 liter of water, while the control was irrigated daily. Per treatment, two leaves of each of 12 trees were infested with a newly emerged female which was

confined to the leaf with a clip cage. Every two days the cages were moved to another spot on the leaves, and the survival and egg production of the females were checked. The eggs were removed after counting. Leaf temperatures inside the cages were recorded daily by thermocouples.

To assess the role of leaf temperature, three water supply treatments (C, S I, S II) of eight trees each were tested in a fourth experiment. The control was watered daily, S I and S II were stressed by discontinuing irrigation 2 and 4 days respectively before the beginning of the experiment. On day 4 each pot received 1.7 liter of water. The plants of the different treatments were staggered in height such that the proximity to the chamber illumination compensated for different leaf temperatures (radiation intensity). Three to four leaves of equal age per plant were infested with young females (28 mites per treatment). After 4 and 8 days the females were transferred to new leaves and the eggs were counted. Measurements of soil water potential and leaf temperatures were made daily, carbohydrate and nitrogen analyses on day 4 and 8.

Life table analysis

From the above experiments life tables for three treatments were constructed assuming a sex ratio of 0.75 (CAREY & BRADLEY, 1982; WERMELINGER & DELUCCHI, 1990) and an immature mortality of 20% (HERBERT, 1981). The tables were analyzed using a computer program that computed iteratively the intrinsic rate of natural increase (r_m) from the equation

$$\sum e^{-r_m x} l_x m_x = 1 \quad [3]$$

where l_x = probability of survival to age class x and m_x = age specific fertility (SOUTHWOOD, 1978). Net reproductive rate (R_0) and mean generation time (G) were computed as well.

RESULTS

Since soil water potentials are very difficult to maintain at a constant level, the *first experiment* evaluated the response of various plant parameters to increasing water stress. The soil water potential of the watered control ranged near the saturation level between -5 and -80 hPa, while in the stress treatment the potential decreased from -75 to -670 hPa over a period of 13 days. Water potential, osmotic potential and turgor potential of the leaves were consistently lower in the stress treatment than in the control and the difference between treatments increased with time (Fig. 1). Because the osmotic potential compensated for the decreasing leaf water potential (cf. eqn. 2), turgor pressure remained fairly constant (osmotic adjustment). Diffuse resistance and leaf surface temperature showed a similar response to the soil water potential in the stress treatment (Fig. 2). With increasing stress intensity the stomata closed and evapotranspiration and cooling of the leaf surface were diminished, causing leaf temperature to rise. During this 13-day-period temperature increased by about 3.5°C at water stress and only 1°C in the control. N content of stressed leaves was 13% lower after 13 days (3.1%), but carbohydrate concentration remained the same in both treatments (13%).

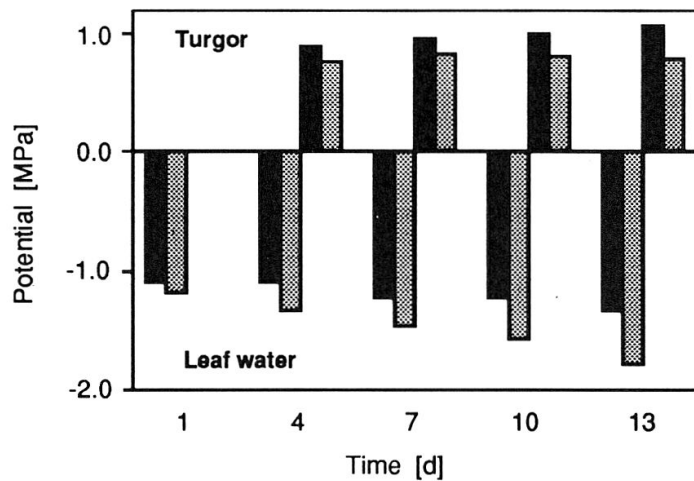


Fig. 1. Temporal development of turgor and leaf water potential of apple leaves at stressed (shaded columns) and non-stressed (black columns) conditions.

The results of the *second experiment* on the development of the twospotted spider mite are listed in Tab. 1. The differences within the two stress treatments S I and S II in terms of soil water potential, plant and mite characteristics were not substantial, while between control and stress treatments significant differences were observed. Leaf N concentration and egg to egg developmental time of *T. urticae* were lower and leaf temperature higher at water stress than in the control. Embryonic development differed between S I and S II. All differences were however relatively minor. The observed immature developmental times were compared with the values that were expected based on the temperature-dependent development described in a previous paper (WERMELINGER *et al.*, 1990a). That paper enabled us to calculate the effect of stress induced temperature increase on developmental rates and consequently the duration of the develop-

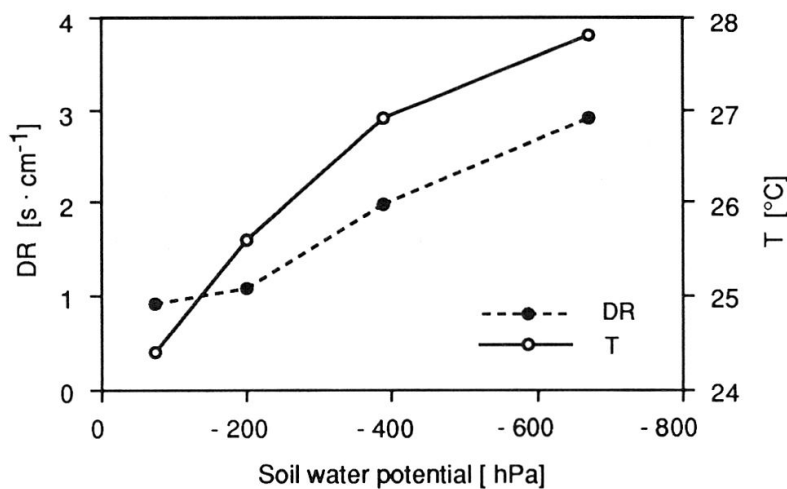


Fig. 2. Development of diffusive resistance (DR, ●) and leaf surface temperature (T, ○) at increasing water stress.

Tab. 1. Duration of the life stages of *Tetranychus urticae* on apple trees, leaf nitrogen content (means and standard deviations), average day/night leaf temperatures and soil water potential at three water supply levels (DT = developmental time)

	Control	Stress I	Stress II
Egg [d]	4.3 ±0.14	4.3 ±0.20	4.0 ±0.21
Juvenile [d]	6.4 ±0.25	6.2 ±0.34	6.4 ±0.54
Preoviposition [d]	1.6 ±0.31	1.5 ±0.24	1.5 ±0.24
Egg to egg [d]	12.4 ±0.45	12.0 ±0.60	11.9 ±0.77
Observed/expected DT [d]	10.7 / 10.7	10.5 / 10.1	10.4 / 10.0
N content [%]	3.24 ±0.14	3.04 ±0.18	3.05 ±0.12
Leaf temp. [°C]	25.0 / 18.0	26.2 / 18.1	26.5 / 18.1
Soil water pot. [hPa]	near saturation	-300 to -820	-480 to -820

ment. The observed developmental times of the stress treatment were 4% longer than would have been expected based on the temperature effects only (Tab. 1). This suggests a slight deterioration of the food quality at water stress.

Experiment 3 on egg production and longevity revealed a moderate reduction of the fecundity at severe water stress (Tab. 2). At the same time, however, daily oviposition rate increased with increasing water stress, coinciding with a distinct reduction of the oviposition period. Day temperature of leaves differed by 1.4°C between the control and S II, the difference at night being less marked.

Tab. 2. Egg production, oviposition rate per female and oviposition period of *Tetranychus urticae* on apple trees, as well as average day/night temperatures inside clip cages at three different water supply levels.

	Control	Stress I	Stress II
Fecundity [eggs/fem.]	108.7 ±37.3	109.3 ±43.3	100.1 ±38.9
Ovipos. rate [eggs/d]	4.3 ±1.3	4.8 ±1.1	5.6 ±1.2
Oviposition period [d]	26.1 ±6.6	24.9 ±9.8	18.8 ±6.2
Leaf temp. [°C]	26.2 / 23.5	27.2 / 24.1	27.6 / 24.4

The above data on the biology of *T. urticae* formed the basis for the life tables. The results of the analysis are listed in Tab. 3. The life table characteristics were computed for three water stress treatments, the control C being near field capacity, S I corresponding to a range of around - 300 hPa and S II to - 700 hPa. Net reproductive rate R_0 peaked at S I. Generation time G slightly decreased with stress, thus raising the intrinsic rate of increase r_m under water stress. Both stress levels had similar r_m values despite different R_0 's, because the shorter generation time at stress II balanced the lower reproduction. An illustrative characteristic of the performance of a population is its doubling time DT calculated as $\ln 2/r_m$ (derived from eqn. 4) which decreased with stress according to generation time.

The experiments described above suggested increased leaf temperatures to be the predominant effect of water stress on spider mites. The *fourth experiment* largely excluded differences in leaf temperature (Tab. 4). Thus, any differences in

Tab. 3. Life table analysis of *Tetranychus urticae* feeding on apple leaves at three different water supply levels (r_m , R_0 and G see text, DT = doubling time)

	Control	Stress I	Stress II
r_m [d^{-1}]	0.229	0.249	0.251
R_0	67.7	81.5	70.1
G [d]	18.4	17.6	16.9
DT [d]	3.03	2.78	2.76

egg production should result from the nutritional quality of leaves. Average oviposition rate during this ten-day-period did not differ between treatments. It tended to be lower at S II where leaves possessed lowest N and sugar content. The latter decreased only slightly with increased water stress.

Tab. 4. Ten-day-average oviposition rate per female of *Tetranychus urticae*, average nitrogen and total sugar content of apple leaves, average leaf temperature and soil water potential at three different water supply levels with compensated leaf temperature differences

	Control	Stress I	Stress II
Ovipos. rate [eggs/d]	5.9	6.1	5.7
N content [%]	3.5	3.4	3.1
Sugars [%]	14.6	13.9	13.4
Leaf temp. [$^{\circ}C$]	24.5	24.6	24.6
Soil water pot. [hPa]	near saturation	-150 to -460	-340 to -680

DISCUSSION

Leaf surface humidity in the boundary layer inhabited by spider mites reportedly ranges between saturation when stomata are open and the humidity of the canopy with closed stomata (HOLTZER *et al.*, 1988b). Relative humidity in our growth chambers was 70%, hence microenvironmental humidity did not fall below 70% and therefore never reached critical levels (CROOKER, 1985).

The soil water potentials measured by the tensiometers seem to represent a mild stress. These readings, however, are likely to underestimate stress intensity, since tensiometers are reliable only above -800 hPa and do not measure the potential actually experienced by the roots. Because water conductivity in the soil very rapidly declines in desiccating soil, the potential in the immediate vicinity of the roots may be lower than the one measured by the tensiometers at some distance.

The general pattern of plant parameters in all experiments was a slight decline in leaf N concentration and a relatively constant sugar content under water stress. However, leaf temperatures were affected very distinctly by stress as a result of changes in leaf water potential and diffuse resistance. Immature development of the twospotted spider mite tended to be less accelerated at stress than would be expected from the mere effects of increased leaf temperatures indicat-

ing a decline in food quality. In fact the difference can be explained well by a leaf N dependent developmental rate quantified by WERMELINGER *et al.* (1990b). Nevertheless, leaf surface temperature turned out to be the key factor influencing spider mite populations: mites on plants suffering from water stress but with compensated leaf temperature differences showed the same oviposition rate. The net reproductive rate R_0 was highest in the medium stress treatment, possibly resulting from higher temperatures and still good nutritional quality of the leaves. At the same time, however, generation time G declined, due to faster development resulting in a high r_m . At the second stress level, G still decreased (faster development at higher temperature), but reproductive capacity R_0 was low (poor leaf quality), thus balancing the intrinsic rate of increase, r_m . The parameter r_m determines the slope of the exponential growth at a hypothetically unlimiting environment given by the equation

$$N_t = N_0 \cdot e^{r_m t} \quad [4]$$

In the water stress range under study, leaf temperatures speeding up development outweighed the adverse effects of poor nutritional quality on reproduction and longevity. Developmental rate, which was reported to be linearly related to temperature in a range between 15 °C and 35 °C (WERMELINGER *et al.*, 1990a), would be even more affected in the field, where larger temperature differences may occur.

Presumably, at more severe water stress, plant quality (and quantity during extended stress periods) would become the prevailing limiting factor. This is in agreement with findings of ENGLISH-LOEB (1989) who found increasing development speed with increasing stress, but an optimum in oviposition at moderate stress. The r_m values found in our study compare well to findings on cotton (CAREY & BRADLEY, 1982) but differ from results on strawberries (LAING, 1969), bean (SHIH *et al.* 1976) and on apple (HERBERT, 1981).

An important aspect of water stress appears to be its duration. Short term stresses may stimulate faster development via temperature, while long term stress starts to limit mite population growth by reduction of food quality and quantity. These components may help to explain the variability of experimental results described in the literature review.

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ZUSAMMENFASSUNG

Klonierte Apfelbäumchen wurden verschiedenen Intensitäten von Wassermangel ausgesetzt. Die daraus resultierenden Veränderungen der Blattoberflächen-Temperatur und des Stickstoff- und Zuckergehalts der Blätter wurden mit den entsprechenden Lebensstafeln von darauf saugenden *Tetranychus urticae* in Zusammenhang gesetzt. Wassermangel bewirkte ein Schliessen der Stomata und eine Erhöhung der Blatt-Temperatur, was die Entwicklung der Spinnmilben beschleunigte. Gleichzeitig waren jedoch Fekundität und Lebensdauer wahrscheinlich infolge des niedrigeren Blatt-Stickstoffgehalts vermindert. Das Wachstum einer Milbenpopulation, ausgedrückt durch die spezifische natürliche Wachstumsrate r_m , wurde somit durch das Verhältnis zwischen Blattqualität und -temperatur bestimmt: Bei schwachem Wasserstress überwog der positive Effekt der höheren Blatt-Temperatur denjenigen der schlechten (oder unveränderten) Nahrungsqualität. Bei stärkerem Stress hatte die schlechte Qualität, welche die Reproduktion einschränkte, grösseres Gewicht als die günstige Wir-

kung der höheren Blatt-Temperatur. Letztere scheint aber eine Schlüsselrolle bei Wasserstress zu spielen, wies doch die Eiablage der Gemeinen Spinnmilbe keine Unterschiede auf, wenn die Blatt-Temperaturen kompensiert wurden.

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