Bundesforschungsanstalt für Rebenzüchtung Geilweilerhof, Siebeldingen, BR Deutschland

Structure and function of grapevine leaves (Vitis vinifera L.) as affected by the European red mite (Panonychus ulmi KOCH)

by

G. RILLING and H. DURING

Strukturelle und funktionelle Veränderungen an den Blättern der Rebe (Vitis vinifera L.) unter dem Einfluß der Obstbaumspinnmilbe (Panonychus ulmi Koch)

Zusammenfassung: Die durch Panonychus ulmi verursachte Schädigung der Blätter von Vitis vinifera-Sorten wurde untersucht:

- In den befallenen Blättern wurden histologische Veränderungen an Zellen der unteren und oberen Epidermis und im Schwamm- und Palisadenparenchym festgestellt. Die Schädigung reichte vom Abbau der Zellorganenellen bis zur vollständigen Zerstörung von Zellen, so daß im Mesophyllgewebe nekrotische Hohlräume entstanden.
- Die Häufigkeit und Ausdehnung dieser Nekrosen nahm mit dem Grad der Blattverfärbung durch Spinnmilbenbefall ("Bronzierung") zu.
- Der Chlorophyllgehalt der befallenen Blätter verringerte sich mit fortschreitender Blattverfärhung
- Befallene Blätter zeigten mit zunehmender Blattverfärbung sowohl unter natürlichen wie konstanten Umweltbedingungen einen Rückgang der stomatären Leitfähigkeit, Photosynthese und Transpiration.

Signifikante negative Korrelationen zwischen dem Grad der Blattverfärbung und dem Chlorophyllgehalt sowie den oben genannten Parametern des Gaswechsels bestätigten die Brauchbarkeit eines auf visueller Bonitur beruhenden Klassifzierungssystems (Rilling 1989), das für die Selektion spinnmilbentoleranter Reben vorgeschlagen wurde.

Key words: mites, *Panonychus ulmi*, grapevine, leaf, damage, histology, necrosis, stomatal conductance, photosynthesis, transpiration, test method, analysis, selection, resistance, tolerance.

Introduction

In a previous paper, the population development of European red mite (*Panony-chus ulmi* Koch) on different grapevine cultivars was studied and a simple screening system for classification of mite damage to leaves, based on their discoloration, was proposed (RILLING 1989). In the present study, structural and functional aspects of mite feeding on grapevine leaves were analyzed, in order to check the validity of the visual test method versus objectively gained data.

Feeding damage on leaves caused by *P. ulmi* and other tetranychid species has been documented for a number of plant hosts (Tables 1 and 2). There may be considerable variation of the plant response to mite feeding, even by the same species (see 'Results and discussion'). To our knowledge besides data on chlorophyll losses given by SCHROPP *et al.* (1982), no investigations dealing with histological and physiological effects of *P. ulmi* on grapevine leaves have been published.

Materials and methods

Histological technique

Pieces of infested and undamaged Riesling leaves taken from field-grown plants were fixed in FAA (formalin: acetic acid: 70% ethanol = 5:5:90 v/v), dehydrated

and resin-embedded using 2-hydroxymethylacrylate (Technovit 7100; Kulzer GmbH, Friedrichsdorf 1, FRG) according to Grunewaldt-Stöcker (1985), and transversally sectioned at 5 µm thickness. Sections were stained with toluidine blue (Feder and O'Brien 1968), coated with immersion oil and examined with a light microscope.

Determination of chlorophyll contents

The same leaves were used to determine chlorophyll content and gas exchange (see below). Leaf discs of 12 mm Ø were extracted in dimethylsulfoxide (DMSO) at room temperature in the dark for about 16 h (method of HISCOX and ISRAELSTAM 1979, modified by STEIN et al. 1986). The absorption maxima and formula given by Ziegler and Egle (1965) for acetone extracts were used for photometric measurement and calculation (compare discussion of the modified method in STEIN et al. 1986).

Evaluation of frequency of feeding necroses

After DMSO extraction of chlorophyll, the feeding necroses were microscopically visible in the cleared leaf discs as brown spots. In a preliminary attempt, their frequency was roughly estimated at low magnification using a dissecting microscope. Besides an unaffected control, low medium and high density of necroses was distinguished as illustrated by Fig. 3.

Gas exchange measurements

a) Under natural ambient conditions

On August 7 and 8, 1986, the gas exchange of fully expanded but not senescent leaves of the field-grown V. vinifera selection Gm 6423-7 (6-year-old, grafted on 5C) was recorded, using a portable, non-climatized but ventilated cuvette for rapid comparative measurement of photosynthesis and transpiration under natural conditions (Porometer; H. Walz, Effeltrich, FRG) (for meteorological conditions see Fig. 4). The porometer cuvette is surrounded by a cylindrical radiation shield and air temperature is held close to ambient air temperature by circulating air along the walls of the chamber with a fan. The air within the cuvette is circulated by a small fan; the cuvette contains sensors for temperature (NTC thermistor and thermocouple), air humidity and light intensity (PAR). Even at high solar radiation and longer exposure time, the temperature in the cuvette does not rise more than 3-4 °C above ambient air temperature. From 9 a.m. to 4 p.m. (Central European summer time) the gas exchange of healthy looking (control) and infested leaves was measured alternatively using an IR analyser (Binos, Leybold-Heraeus, Hanau, FRG) which works in the differential mode. Both CO2 and H2O exchange of the enclosed part of the leaf was registered and stored by a DES 12 data logger (H. Walz). Gas exchange data were then evaluated according to equations given by von Caemmerer and Farquhar (1981).

b) Under constant ambient conditions

In 1987 and 1988, the gas exchange of healthy and infested potted vines (varieties Bacchus, Gf. Koe-49-81, Gf. Koe-70-4, 3-year-old, own-rooted) was measured under constant climatic conditions using a climatized cuvette (Miniküvettensystem, H. Walz). Photosynthesis and transpiration of the vines which were grown in the open, were measured at near-optimum leaf temperature (25 °C) and at light saturation (850 μ mol quanta · m⁻² · s⁻¹, for details: DURING 1988). The leaf to air water vapour pressure difference (Δ_w) was maintained at 18—20 mbar · bar⁻¹.

For screening of leaf discoloration see RILLING (1989). In brief, degree of leaf discoloration 1 means normal green colour, 3, 5, 7, 9 increasing intensity of 'bronzing'.

Results and discussion

Histological changes

Corresponding with the preferred occurrence of P.ulmi on the lower leaf surface (RILLING 1989), feeding punctures penetrating from below prevailed (Fig. 1 A, D, F). Feeding injuries were generally confined to part of the leaf cell layers, due to a mean stylet length of 157 μ m (143—164 μ m) of female nymphs and adults (AVERY and BRIGGS 1968 a) and to a thickness of 170—180 μ m of the investigated grapevine leaves. The most frequent and heaviest destructions were found in the spongy mesophyll, though the injuries also extended to the palisade layer (Fig. 1 D, F, G). Damage to palisade cells by feeding from the upper leaf surface was less frequent (Fig. 1 E).

Considering the horizontal distribution of feeding injuries over the leaf blade, at slight infestation the feeding sites were associated with the thicker leaf veins (Fig. 2); a similar preference is mentioned by Andersen (1947), Avery and Briggs (1968 a) and Kielkiewicz and Van de Vrie (1983). However, penetration of conducting elements was never observed (Fig. 1 G) (cf. also Geliskes 1938; Blair 1951; Blair and Groves 1952; Avery and Briggs 1968 a; Tanigoshi and Davis 1978). In a more advanced stage of infestation, the area between veins was also punctured.

On the cellular level, the feeding injuries caused by *P. ulmi* to grapevine leaves showed the general features described by earlier authors for other host plants (Table 1). The stylets penetrated the periclinal walls of epidermal cells; pierced epider-

 ${\bf Table\ 1}$ Literature reports on structural changes caused by tetranychid mites on the leaves of different host plants 1)

Literaturübersicht über strukturelle Veränderungen an den Blättern verschiedener Wirtspflanzen durch Tetranychidenarten

Author/s	Mite species²)	Plant host
Geijskes (1938)	P. ulmi	Apple
BLAIR (1951)	P. ulmi	Apple
Gasser (1951)	P. urticae	Bean
Blair, Groves (1952)	P. ulmi	Apple
Liesering (1960)	T. urticae	Bean
Avery, Briggs (1968 a)	P. ulmi	Apple
SUMMERS, STOCKING (1972)	B. rubrioculus	Almond
Tanigoshi, Davis (1978)	T. mcdanieli	Apple
SANCES, WYMAN, TING (1979 a)	T. urticae	Strawberry
Albrigo, Childers, Syvertsen (1981)	P. citri, E. sexmaculatus	Grapefruit Orange
FRITSCHE, SCHMIDT, MÜLLER, THIELE (1982)	P. ulmi	Apple
Mothes, Seitz (1982)	T. urticae	Bean
Kielkiewicz, van de Vrie (1983)	T. urticae	Strawberry
Kielkiewicz (1985)	T. urticae	Strawberry

For further information see Tomczyk, Kropczyńska (1985).

²⁾ B. = Bryobia, E. = Eotetranychus, P. = Panonychus, T. = Tetranychus.

mal cells were flattened, their contents coagulated and stained intensively (Fig. 1 D, F). In the underlying mesophyll cells, the cell organelles, especially the chloroplasts, had disappeared and the cytoplasm was shrunk back to the cell walls, or cells were totally emptied. The cell walls were deformed or even ruptured. In a final stage, especially in the spongy mesophyll and possibly favoured by its natural intercellular spaces, large necrotic holes appeared, some of which contained cellular debris (Fig. 1 D, F). Necroses

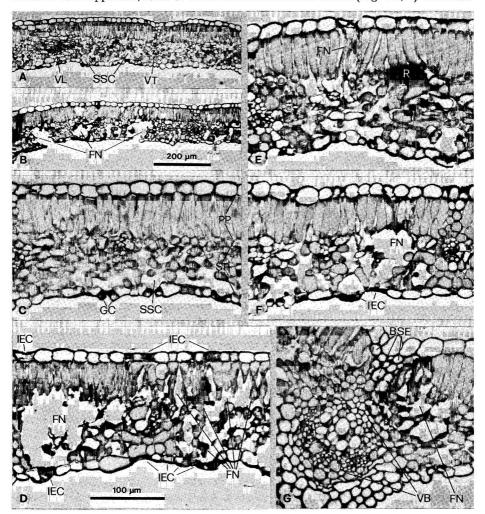


Fig. 1: Cross sections through Riesling leaves showing injuries caused by *P. ulmi.* — A) General view of uninfested leaf, B) of injured leaf; same magnification. The reduced thickness of the infested leaf is obvious. — C—G) More detailed views, all at same magnification: C) Unaffected leaf. D) Severely damaged spongy mesophyll and parts of the palisade layer. Mites have fed from both epidermal layers. E) Feeding necrosis penetrating from above. Epidermal and palisade cells are damaged. F) Feeding necrosis penetrating from below and extending over the whole thickness of leaf. G) Feeding necrosis adjacent to a major leaf vein, which is not affected. — BSE = bundle sheath extension (cf. ESAU 1953), FN = feeding necrosis, GC = guard cells of stoma, IEC = unjured epidermal cell, PP = palisade parenchyma, R = idioblast including intensively staining bundle of raphides, SP = spongy parenchyma, SSC = substomatal chamber, VB = vascular bundle, VL = minor vein cut longitudinally, VT = minor vein cut transversally.

originated from above in the palisade layer and adjacent mesophyll were generally less extended (Fig. 1 E).

Tanigoshi and Davis (1978), Mothes and Seitz (1982) and Kielkiewicz (1985) found ultrastructural alterations of the chloroplasts in mesophyll cells adjacent to the feeding lesions, which could be triggered by degradation substances of the immediately injured plant cells or by saliva constituents produced by the mites. Indeed, Liesering (1960), Avery and Briggs (1968 b) and Storms (1971) detected secretion of isotopes by the mites into the leaves or even their translocation to remote parts of the host plants. There is some evidence, which must however be corroborated by further investigation, that in case of *P. ulmi* and grapevine such extension of damage from punctured to adjacent cells also exists. In the examined mature grapevine leaves no signs of regeneration processes, as observed by Avery and Briggs (1968 a) for apple and by Alerigo *et al.* (1981) for citrus species, were detected.

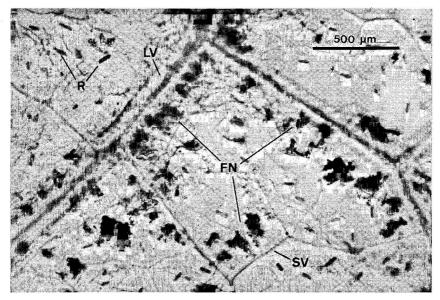


Fig. 2: Feeding injury caused by *P. ulmi* on a grapevine leaf disc clarified by dimethylsulfoxide. The brown feeding necroses (FN) are accompanying the leaf veins (LV = large, SV = smaller leaf vein).

Bundles of raphides (R) are also visible as rectangular inclusions.

Saugschäden durch *P. ulmi* an einer Blattscheibe, die durch Dimethylsulfoxid aufgehellt wurde. Die braunen Nekrosen (FN) begleiten die Blattadern (LV = große, SV = kleinere Ader). Raphidenbündel (R) sind als rechteckige Einschlüsse ebenfalls sichtbar.

Querschnitte durch Rieslingblätter mit durch *P. ulmi* verursachten Schädigungen. — A) Übersichtsbild eines nichtbefallenen Blattes, B) eines geschädigten Blattes; gleiche Vergrößerung. Die Dicke des befallenen Blattes ist deutlich verringert. — C—G) Detailansichten bei gleicher Vergrößerung: C) Nicht geschädigtes Blatt. D) Schwammparenchyma und Teile des Palisadenparenchyms stark geschädigt. Die Milben durchbohrten sowohl die untere wie die obere Epidermis. E) Von der Blattoberseite ausgehende Nekrose. Geschädigte Epidermis- und Palisadenzellen. F) Von der Blattunterseite ausgehende Nekrose, die sich über die ganze Blattdicke erstreckt. G) Nekrose neben einer stärkeren Blattader, die selbst nicht angestochen ist. — BSE = Leiste der Leitbündelscheide (vgl. Esau 1953), FN = Nekrose, GC = Schließzellen des Spaltöffnungsapparates. IEC = geschädigte Epidermiszelle, PP = Palisadenparenchym, R = Idioplast mit intensiv angefärbtem Raphidenbündel, SP = Schwammparenchym, SSC = Atemhöhle, VB = Gefäßbündel, VL = längsgeschnittene kleine Blattader, VT = quergeschnittene kleine Blattader.

Frequency and extension of the feeding necroses

In a coarse evaluation of cleared leaf discs, the rate of leaf area covered by brown necrotic spots was estimated (cf. also BLAIR 1951). Preliminary results showed an accumulation of feeding necroses together with the increase of leaf discoloration (Fig. 3). It appears promising to refine visual screening of leaf damage by measurement of the injured leaf area, which could take use of an image analysis system developed in this institute by R. BLAICH (unpublished).

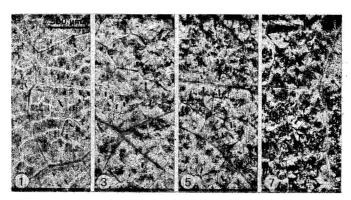


Fig. 3: Density of feeding necroses due to *P. ulmi* (FN) in clarified grapevine leaf discs differing in their degree of discoloration (numbers). Degree 1: control; 3: low, 5: medium, 7: high frequency, corresponding to ca. 10, 25, 50 % of leaf area covered by necroses.

Häufigkeit der durch *P. ulmi* verursachten Nekrosen (FN) in aufgehellten Rebenblattscheiben unterschiedlichen Verfärbungsgrades (Zahlen). Grad 1: Kontrolle; 3: niedrige, 5: mittlere, 7: hohe Nekrosendichte, wobei ca. 10, 25 und 50 % der Blattfläche von den Nekrosen eingenommen werden.

Changes of chlorophyll contents

On average of cultivars — cv. Bacchus (Fig. 5) is presented here — the chlorophyll contents were reduced at degrees 3 to 7 from 85 % to 50 % of the amount measured in degree 1 leaves. Leaves of degree 9 contained 20 % or less of control leaves. For this reason, leaves of degree 9 were excluded from physiological measurements. The chlorophyll a:b ratio was consistently by 3:1, irrespective of the class of damage. No change of the a:b ratio was also mentioned by Poskuta et al. (1975). A reduction of the chlorophyll contents correlated with the level of feeding injury has been frequently reported (Table 2); for grapevine, loss of chlorophyll due to P. ulmi and T. urticae infestation has been shown by Schropp et al. (1982). Some authors, however, found only minor changes, even in severely damaged leaves (Poskuta et al. 1975; Kolodziej et al. 1979; Sances et al. 1979 b).

Gas exchange

In August 1986, CO_2 assimilation and transpiration of field-grown, healthy and infested leaves of the selection Gm 6423-7 were measured during the day. As is shown in Fig. 4, the weather turned out to be very hot and dry and light intensity increased to more than 2 mmol quanta \cdot m⁻² \cdot s⁻¹ in the afternoon. Injured leaves (degree 5 of discoloration) generally exerted lower rates of CO_2 assimilation and transpiration compared to control leaves (degree 1). Note that CO_2 assimilation, transpiration and stomatal conductance (the latter not shown) were lowest in control leaves from about 12 to 13 h. In infested leaves, gas exchange parameters also declined in late morning but

somewhat earlier and to a greater extent. A similar midday stomatal closure of grapevine leaves has been reported by LANGE and MEYER (1979) and DOWNTON et al. (1987). Under semiarid conditions, LOVEYS and DURING (1984) observed an increase in abscisic acid content of vine leaves during the morning and a maximum content at midday. It is speculated that in our experiments, due to a more intensive stress, the ABA content of injured leaves might have increased earlier in the morning compared to control leaves. This may have caused the earlier transient stomatal closure and the reduction of the rate of photosynthesis and transpiration.

Measurements of gas exchange under constant ambient conditions revealed decreasing rates of stomatal conductance, photosynthesis and transpiration with increasing discoloration of infested leaves (Fig. 5). On average of cultivars, photosynthesis of severely damaged leaves (degree 7) was reduced by 61 %, stomatal conductance by 59 %, transpiration by 51 % compared to control leaves (degree 1).

Our results coincide with most reports in literature (Table 2) showing a decrease in CO_2 assimilation due to mite infestation, which was proportional to loss of chlorophyll, population density and duration of feeding, respectively. Some authors, however, observed reduction of photosynthesis only in case of strong bronzing (Boulanger 1958; Avery 1964), while others reported a strong depression of photosynthesis which was not accompanied by marked leaf discoloration or reduction of chlorophyll contents (Hall and Ferree 1975; Poskuta *et al.* 1975; Sances *et al.* 1979 b).

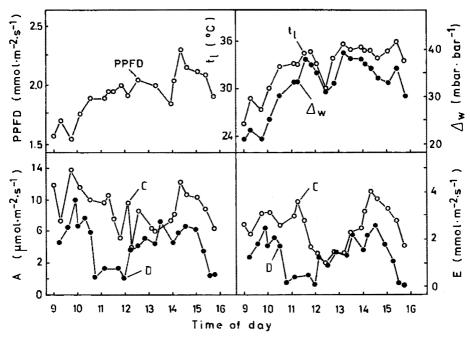


Fig. 4: Diurnal changes of photosynthesis (A) and transpiration (E) of control (C = degree of discoloration 1) and damaged leaves (D = degree 5) of field-grown selection Gm 6423-7 on August 7 and 8, 1986 (Central European summer time). PPFD = photosynthetic photon flux density, t_l = leaf temperature, Δ_w = leaf to air water vapour pressure difference.

Tagesgang der Photosynthese (A) und Transpiration (E) von Kontrollblättern (C = Verfärbungsgrad 1) und durch Spinnmilben geschädigten Blättern (D = Verfärbungsgrad 5). Neuzüchtung Gm 6423-7 aus dem Freiland, 7./8. August 1986 (mitteleuropäische Sommerzeit). PPFD = Lichtintensität, t_1 = Blattemperatur, Δ_w = Blatt-Luft-Wasserdampfdruckdifferenz.

Table 2

Literature reports on chemical and physiological changes caused by tetranychid mites on the leaves of different host plants¹)

Literaturübersicht über chemische und physiologische Veränderungen in den Blättern verschiedener Wirtspflanzen durch Tetranychidenarten

Author/s	Mite species ²)	Plant host	Chemical constituent	Metabolic process
Andersen (1947)	P. ulmi	Apple	Chlorophyll, Carbohydrates	Transpiration
Chapman, Lienck, Curtis (1952)	P. ulmi, T. urticae	Apple	Chlorophyll	
Lienck, Chapman, Curtis (1956)	P. ulmi, T. urticae	Apple	Chlorophyll	
Boulanger (1958)	P. ulmi	Apple	Chlorophyll	Photosynthesis, Transpiration
Wedding, Riehl, Jeppson (1958)	P. citri	Lemon, Orange		Photosynthesis, Transpiration
Liesering (1960)	T. ųrticae	Bean	Chlorophyll, Xanthophyll, Carotine	Photosynthesis, Respiration, Transpiration
AVERY (1964)	P. ulmi	Plum, Apple		Photosynthesis
Avery, Briggs (1968 a)	P. ulmi	Plum, Apple	Chlorophyll, Sugars, Amino acids, Phenols	
Avery, Briggs (1968 b)	P. ulmi	Plum		Translocation (14C from saliva)

Avery, Lacey (1968)	P. ulmi	Plum	Auxin-like activity	
STORMS (1971)	T. urticae	Bean	Gibberellins	Translocation (32P from saliva)
SUMMERS, STOCKING (1972)	$\it B.~rubrioculus$	Almond	Chlorophyll	
Atanasov (1973)	T. atlanticus	Bean	Chlorophyll	Photosynthesis, Transpiration
HERBERT, BUTLER (1973)	$P.\ ulmi$	Apple	N, P, K	
Hall, Ferree (1975)	T. urticae	Apple		Photosynthesis
Poskuta, Kołodziej-Tomczyk, Kropczyńska (1975)	T. urticae	Strawberry	Chlorophyll	Photosynthesis, Respiration
Zwick, Fields, Mellenthin (1976)	P. ulmi, T. urticae, T. mcdanieli	Apple	Chlorophyll	
Andrews, LaPré (1979)	T. pacificus	Almond	Chlorophyll	Photosynthesis, Transpiration
Kołodziej, Kropczyńska, Poskuta (1979)	T. urticae	Strawberry, Chrysanthemum	Chlorophyll	Photosynthesis, Respiration
SANCES, WYMAN, TING (1979 b)	T. urticae	Strawberry	Chlorophyll	Photosynthesis, Transpiration, Stomatal conductance, Mesophyll conductance
FERREE, HALL (1980)	T. urticae	Apple	N, Carbohydrates	Photosynthesis, Transpiration, Leaf water status

Table 2 (continued)

Author/s	Mite species²)	Plant host	Chemical constituent	Metabolic process
Sances, Wyman, Ting, van Steenwyk, Oatman (1981)	T. urticae	Strawberry		Photosynthesis, Transpiration
DEAngelis, Larson, Berry, Krantz (1982)	T. urticae	Peppermint		Transpiration, Leaf water status
Borichenko, Manolov (1982)	P. ulmi	Apple	Sorbitol, Amino acids, Organic acids, High-molecular compounds	Photosynthesis
Sances, Toscano, Hoffmann, LaPré, Johnson, Bailey (1982 a)	О. рипісае	Avocado	Chlorophyll	Photosynthesis Transpiration, Stomatal conductance, Mesophyll conductance
Sances, Toscano, Oatman, LaPré, Johnson, Voth (1982 b)	T. urticae	Strawberry		Photosynthesis, Transpiration
Schropp, Eichhorn, Ipach (1982)	P. ulmi, T. urticae	Grapevine	Chlorophyll, Fe	
Tomczyk, van de Vrie (1982)	T. urticae	Chrysanthemum	Chlorophyll, Sugars	Photosynthesis
DeAngelis, Berry, Krantz (1983 a)	T. urticae	Peppermint	Sugars, Starch	Leaf water status, Osmotic adjustment

DeAngelis, Berry, Krantz (1983 b)	T. urticae	Peppermint	Chlorophyll	Photosynthesis, Stomatal conductance
DeAngelis, Marin, Berry, Krantz (1983 c)	T. urticae	Peppermint	Essentiel oils	
Plourde, Goonewardene, Kwolek, Nielsen (1983)	P. ulmi	Apple	Chlorophyll	
BRITO, STERN, SANCES (1986)	T. turkestani, T. urticae, T. pacificus	Cotton		Photosynthesis, Stomatal conductance, Mesophyll conductance
Hildebrand, Rodriguez, Brown, Volden (1986)	T. urticae	Soybean	N, P, Chlorophyll, Carotinoids, Sugars, Starch, Proteins, Oil	
Youngman, Jones, Welter, Barnes (1986)	P. citri, P. ulmi, T. urticae, T. pacificus	Almond		Photosynthesis, Stomatal conductance, Mesophyll conductance
Hare, Youngman (1987)	P. citri	Orange		Photosynthesis, Stomatal conductance
HILDEBRANDT, RODRIGUEZ, BROWN, LUU, VOLDEN (1987)	T. urticae	Soybean	Peroxydases	

For further information see van de Vrie, McMurtry, Huffacker (1972) and Tomczyk, Kropczyńska (1985).
 B. = Bryobia, O. = Oligonychus, P. = Panonychus, T. = Tetranychus.

Decrease of stomatal (and mesophyll) conductance — the limiting factors of CO_2 assimilation — depending on the level of feeding injury has also been demonstrated repeatedly (Sances *et al.* 1982 a; Deangelis *et al.* 1983 b; Youngman *et al.* 1986), whereas according to Hare and Youngman (1987) these parameters were not influenced by the presence of spider mites.

A decrease of transpiration in injured leaves, which reflects the reduction of stomatal conductance, is also reported by Andrews and LaPré (1979), Sances *et al.* (1979 b, 1982 a and b). On the other hand, an increase of transpiration due to tetranychid infestation is described by Andersen (1947), Liesering (1960), Atanasov (1973) and Ferree

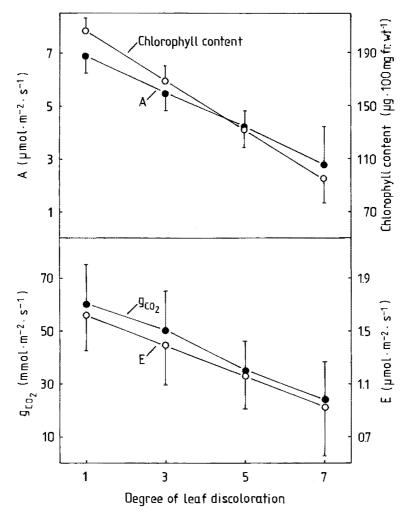


Fig. 5: Rate of photosynthesis (A), chlorophyll content, stomatal conductance for CO₂ (g_{CO2}) and transpiration (E) of control and damaged leaves at constant environmental conditions. Variety Bacchus, 1987. Vertical bars indicate least significant differences at the 5 % level.

Photosyntheserate (A), Chlorophyllgehalt, stomatäre Leitfähigkeit für CO_2 (g_{CO_2}) und Transpiration (E) von Kontrollblättern und durch Spinnmilben geschädigten Blättern. Sorte Bacchus, 1987. Senkrechte Balken: Grenzdifferenzen bei $P=5\,\%$.

and Hall (1980). There was, furthermore, changing intensity of transpiration, depending on mite density or duration of feeding, respectively (Boulanger 1958; Wedding et al. 1958; Sances et al. 1981). An investigation by Deangelis et al. (1982) revealed different influence of spider mite on stomatal (daytime) and cuticular (nighttime) transpiration. Leaves of Mentha piperita infested by T. urticae transpired less than control leaves during the day, whereas transpiration of injured leaves was considerably higher than normal during darkness, thus resulting in water stress of the attacked plants. A similar phenomenon could not be detected, due to the methods used in the present experiments, but cannot be excluded for P. ulmi infested grapevines, when considering the perforation of the protective epidermal layers by the mites' stylets.

Concluding remarks

According to the effects of *P. ulmi* on the cellular structure and gas exchange of grapevine leaves, the damage by this pest involves at least the following components, all of which decrease the level of photosynthesis:

- Mechanical injury, caused by stylet penetration, reduces the number of photosynthetically active cells.
- Reduced stomatal conductance limits the amount of CO₂ which is available for photosynthesis.
- Furthermore, there is evidence that the structure (and function) of the cells adjacent to the feeding sites is also negatively affected.

Possible water loss through feeding punctures of the epidermal layers must also be taken into account. From this, water stress and further metabolic changes in grapevine leaves fed by *P. ulmi* may result.

The results presented confirm significant correlations between the degree of leaf discoloration and a number of elementary physiological parameters which are essential for the productivity of grapevines. Thus, the previously proposed visual indexing system (RILLING 1989) is valid for quick estimation of the feeding damage caused by *P. ulmi* to grapevine leaves, provided the test is performed under standardized conditions. As the lowest class of leaf damage (degree 3) represents already a decrease of photosynthesis by about 20 %, there could be a need to subdivide the beginning of the screening scale. Here, recording of the density of feeding necroses could be a valuable tool.

Summary

The damage caused by feeding of *Panonychus ulmi* on leaves of *Vitis vinifera* cvs was investigated:

- (1) Histological changes due to feeding activity of P. ulmi occurred in lower and upper epidermal cells, spongy mesophyll and palisade layer of leaves. The injuries varied from decomposition of cell organelles to total destruction of cells, resulting in necrotic holes within the mesophyll tissue.
- (2) The frequency and extension of feeding necroses increased with the increase of leaf discoloration due to spider mites ('bronzing').
- (3) The chlorophyll content of infested leaves declined when the degree of leaf discoloration increased.
- (4) Under constant and natural ambient conditions, stomatal conductance, photosynthesis and transpiration of infested leaves decreased with increasing degree of discoloration.

Significant negative correlations between the degree of leaf discoloration and chlorophyll content as well as the above parameters of gas exchange confirm the validity of a visual screening system (RILLING 1989) which has been proposed for selection of grape-vines tolerant to spider mite infestation.

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Dr. G. RILLING Priv. Doz. Dr. H. DURING BFA für Rebenzüchtung Geilweilerhof D 6741 Siebeldingen