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Is carbon starvation rather than excessive nitrogen supply the cause of inflorescence necrosis in *Vitis vinifera* L.?

by

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S u m m a r y : Five different levels of nitrogen (0, 1, 5, 10, 100 mM NH_4NO_3) were applied to potted *Vitis vinifera* L. plants grown in a controlled environment facility (phytotron) under 2 different levels of irradiance (30, 140 $\mu Em^{-2}s^{-1}$ PFD) during bloom. They were compared with potted plants in the field, exposed to differential leaf or inflorescence shading in combination with 2 levels of N supply (0, 10 mM NH_4NO_3). Net CO_2 assimilation rate, transpiration rate and stomatal conductance were reduced, and intercellular CO_2 partial pressure was increased under conditions of light limitation. The low-light treatments decreased net photosynthesis to zero in either experiment. Separate shading of the flower clusters failed to affect gas exchange of adjacent leaves, indicating low sink strength of the inflorescences. Nitrogen fertilization influenced only transpiration rate and stomatal conductance. In the phytotron, but not in the field, these parameters decreased with increasing N level. Severe symptoms of inflorescence necrosis appeared in the low-light treatment in the phytotron at the end of flowering. Necrotic symptoms also developed on shoot tips and tendrils, leading to abscission of these organs. Tissue necrosis was independent of N nutrition, and there were no necrotic manifestations in the field study. These results provide evidence that a stress-induced limitation of photoassimilate supply, along with competitive interactions among sinks, are involved in triggering senescence processes in grapevines.

K e y w o r d s : light, nitrogen, bloom, stress physiology, photosynthesis, transpiration, stomatal conductance, sink, inflorescence necrosis, senescence.

Introduction

The dependence of photosynthetic CO_2 assimilation upon irradiance has been known for a long time, and many studies have revealed strong correlations between photosynthesis and leaf nitrogen (N) content in various plant species (Evans 1989). However, the effects of N nutrition on grapevine gas exchange have usually been investigated at light saturation, although overcast situations occur rather frequently in temperate zone viticulture. In addition, grapevine leaves only transmit 6% of ambient sunlight (Smart and Robinson 1991). Depending on sun-leaf angle and leaf position within the canopy, light intensity on individual leaves may drop below the light compensation point of photosynthesis, particularly under dense cloud covers.

The severity and duration of stress situations may trigger acclimation processes in the whole plant (Björkman 1981), and partitioning of photosynthates to reproductive growth is decreased under resource-limiting conditions (Chiariello and Gulmon 1991). Rives (1961) related the "coulure" phenomenon in grapevines to competitive interactions among sinks, and Gysi (1983), Theiler and Müller (1986) and Jackson (1991) suggested that high soil N status and unfavorable meteorological conditions at bloom could be involved in the induction of physiological disorders, such as inflorescence necrosis (IN) and bunchstem necrosis (BSN, Stiellähme, rachis necrosis, shanking, waterberry, dessèchement de la rafle, palo negro), showing the same symptoms (Jackson and Coombe 1988). The initial necrotic indications associated with BSN become apparent around the stomata, and the first disintegrating tissues are guard cells and subsidiary cells (Theiler 1970). Nevertheless, we know of no studies connecting IN or BSN with photosynthesis. We therefore investigated the combined effects of N supply and limiting irradiance at bloom on gas exchange and the occurrence of IN under controlled environmental conditions. In addition, by differential shading of leaves or clusters in the field, we examined the sink priority of the inflorescences and the eventuality of inducing IN by restricting incident light on these organs only.

Materials and methods

G r o w t h a n d e x p e r i m e n t a l c o n d i t i o n s : Two-year-old grapevines *Vitis vinifera* L. (cv. Müller-Thurgau, grafted on SO4 rootstocks) were planted in 18-liter pots containing sandy loam soil and grown outdoors without fertilization during the 1990 season. After winter pruning to one 5-node cane in January 1991, plants were selected for uniform shoot growth and divided into 2 groups for either the phytotron or the field experiment.

Phytotron: On February 1, 1991, 90 vines were distributed in two identical rooms of our controlled environment facility (phytotron). Light was provided by a combination of high-pressure sodium vapor lamps and metal halide lamps. At first, both rooms were operated with a

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winter climate program (2/2 °C day/night temperature; 98/98% day/night relative humidity; 8 h photoperiod; 100 $\mu Em^{-2}s^{-1}$ photon flux density (PFD)). After 10 days, they were switched to spring program (12/4 °C; 54/85 %; 12 h; 320 $\mu Em^{-2}s^{-1}$) for 24 days. Then, the summer program (20/11°C; 58/75 %; 16 h; 750 $\mu Em^{-2}s^{-1}$) was started, 4 days before bud break. The vines were thinned to 2 shoots with 2 clusters each and trained vertically on 1.5 m stakes. The expanding leaf area gradually decreased incident irradiance in the cluster zone to about 140 $\mu Em^{-2}s^{-1}$ during the course of the experiment.

Five N nutrition levels, covering a range from deficiency to excess, were implemented on 9 vines in each of 2 light environments during the bloom period. They were 0 (N0), 1 (N1), 5 (N5), 10 (N10) and 100 (N100) mM NH_4NO_3 in 2 l of distilled H_2O, applied on April 15, 23, 29 and May 6. The light regimes were chosen to simulate overcast conditions, representing heavy and moderate densities of cloud covers, respectively. They were imposed in the 2 separate phytotron chambers, lasting from April 26 (first flowers open) till May 13. In the low-light chamber, we reduced PFD in the cluster zone to 30 $\mu Em^{-2}s^{-1}$ (LL), and in the moderate-light chamber, PFD was maintained at 140 $\mu Em^{-2}s^{-1}$ (ML).

Field: This study was established on June 29, (first flowers open) with 36 vines trained like the phytotron plants, but thinned to 1 shoot with 1 cluster per plant. Using 6 single-plant replications, 2 N levels were combined with 3 shade regimes. The N levels were 0 (N0) and 10 (N10) mM NH_4NO_3 in 2 l of tap water (containing 0.15 mM NO_3^-, no NH_4^+), applied on June 29, July 4 and July 9. The shade treatments were imposed from June 29 until July 15 (end of bloom). They consisted of: inflorescences shaded with conical hats of white paper (treatment IS: 100 $\mu Em^{-2}s^{-1}$ PFD) with leaves exposed to full sunlight, leaves shaded with white shade cloth (treatment LS: 30 $\mu Em^{-2}s^{-1}$ PFD) with inflorescences exposed to full sunlight and unshaded control (US: 1100-1400 $\mu Em^{-2}s^{-1}$ PFD).

Gas exchange: We measured CO_2 and H_2O concentration differences, temperature and PFD on the leaf adjacent to the first cluster from the base of the shoot between 10 and 12 a.m., using a portable LCA-2 infra-red gas analyzer system (Analytical Development Co. Ltd., Hoddesdon, England). Net CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance to H_2O vapor transfer (g_s) and sub-stomatal cavity CO_2 partial pressure (C_i) were calculated in the data logger according to VON CAEMMERER and FARQUHAR (1981). In the phytotron, the measurements were taken twice a week on 3 plants per treatment from prior to the first N application until the vines were sampled (total of 9 measurements). In the field, gas exchange was measured only once at full bloom (July 5) on all vines.

The data were subjected to a two-way analysis of variance. Homogeneity of variance was tested using Bartlett's test and differences between means were tested using Duncan's multiple range test. Correlation coefficients were calculated for selected parameters. All statistical tests were performed on WIDAS (Wissenschaftlich Integriertes Daten-Auswertungs-System, MSI Dr. Wälti AG, Switzerland).

Inflorescence necrosis: On May 13, 3 plants from each phytotron treatment were sampled. The inflorescences were separated into rachis and flowers, and fresh as well as dry weights were determined. Four days later (end of bloom), symptoms of IN were registered as % necrotic flowers per cluster on the 6 remaining plants per treatment combination. In the field experiment, IN was registered when the shade regimes were removed. Because the symptoms resembled those originating from early *Botrytis cinerea* Pers. infestation, samples of necrotic tissue were taken at random. They were surface sterilized by dipping in either 70 % ethanol or 1% NaOCl in 70 % ethanol for 30 s. After rinsing five times for 30 s with distilled H_2O, the samples were sectioned with a razor blade. The sections were distributed either on potato dextrose agar for detection of mycelial growth or in sterile humid chambers for sporulation. The samples were incubated at 20 °C in the dark for 7 days and then examined for fungal growth under a binocular microscope.

Results

Gas exchange: In the phytotron, mean net CO_2 assimilation rate per unit leaf area was 7 $\mu mol\ CO_2 m^{-2}s^{-1}$ at the start of the experiment (first N application) and gradually declined parallel to the decreasing irradiance due to the growing shoots. No treatment effects on leaf gas exchange were detectable before the light regimes were imposed, 11 days after the first N application. Therefore, the results presented here are pooled values from 3 consecutive measurements within one week after imposition of the light treatments. In moderate light (ML), A was 3.3 $\mu mol\ CO_2 m^{-2}s^{-1}$ on average (Fig. 1: A), while under severe

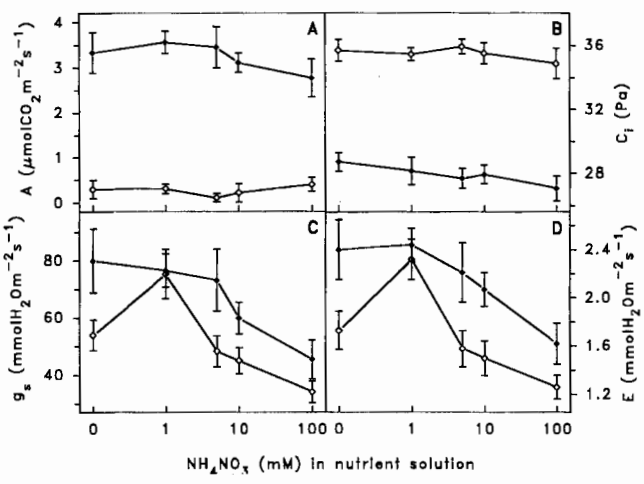

Fig. 1: Effect of irradiance and N application during bloom on gas exchange of potted grapevines in the phytotron. Net CO_2 assimilation rate A (**A**), sub-stomatal cavity CO_2 partial pressure C_i (**B**), stomatal conductance g_s (**C**) and transpiration rate E (**D**) of the leaf opposite to the first inflorescence from the base. Open symbols: treatment LL, 30 $\mu Em^{-2}s^{-1}$ PFD; full symbols: treatment ML, 140 $\mu Em^{-2}s^{-1}$ PFD. Values are means ± SE (n=9).

light restriction (LL), net photosynthesis was close to zero. In the LL environment, C_i nearly increased to the level of ambient CO_2 concentration (C_a = 38.6 Pa), which was a rise of 27% relative to ML (Fig. 1: B). No significant N-induced alteration of A and C_i could be detected in either light regime, despite the vast range of N levels applied. In either light treatment, A correlated negatively with C_i (LL: r = -0.84, P < 1%; ML: r = -0.47, P < 1%) and positively with g_s (LL: r = 0.31, P < 5%; ML: r = 0.79, P < 1%), regardless of N supply.

Even in LL, no complete closure of the stomata could be observed (Fig. 1: C). This is interesting, since g_s directly affected E (r = 0.97, P < 1%). These leaves transpired on average still 78 % of those in ML (Fig. 1: D). Light restriction obviously altered E less dramatically than A, and this may have permitted the N effect to become apparent. In LL, there were maxima in g_s and E at N1, and in either light treatment, elevated N supply reduced g_s and E. Although the reductions were only significant at N100, the fluctuations were essentially parallel in the two light environments. For calculation of correlations, the light regimes were therefore combined (n = 90). The relationship of N level to both g_s (r = -0.42, P < 1%) and E (r = -0.43, P < 1%) was negative.

In the field, leaf shading reduced A to zero or even below, while cluster shading failed to affect leaf gas exchange (Fig. 2: A). The sun-exposed leaves of the US and IS regimes assimilated 12.6 µmol $CO_2 m^{-2} s^{-1}$, on average. In LS, C_i was 61% higher (Fig. 2: B) and g_s 85% lower (Fig. 2: C) than in US/IS. None of these parameters significantly responded to N nutrition, although the measurements in US and IS were taken at light saturation. Merging the values of the US and IS regimes, the correlation of A and C_i resulted in r = -0.86 (P < 1%) and that of A and g_s in r = 0.65 (P < 1%). In the LS treatment, A correlated negatively with C_i (r = -0.70, P < 1%) but did not correlate with g_s (r = -0.03, n.s.). In LS, E was reduced to 44% of US/IS (Fig. 2: D), and the N effect was reversed compared with the phytotron data: the N-deficient vines (N0) transpired at a significantly lower rate than the N10 plants in either shade treatment.

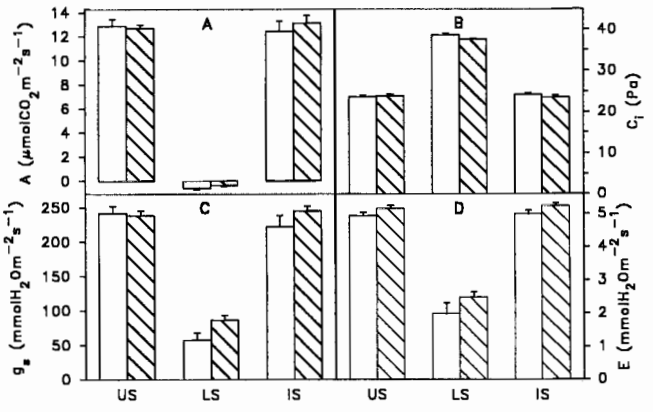

Fig. 2: Effect of either leaf or cluster shading and N application during bloom on gas exchange of potted grapevines in the field. Abbreviations as in Fig. 1. Shade treatments: unshaded control (**US**); leaves shaded (**LS**); inflorescences shaded (**IS**). Left bar of each pair: H_2O; right bar: 10 mM NH_4NO_3. Values are means ± SE (n=6).

Inflorescence necrosis: Neither light intensity nor N status affected inflorescence fresh weight in the phytotron (data not shown). Light restriction, however, significantly reduced the dry weight of both rachis and flowers (Fig. 3: A), without consistently altering the flowers to rachis ratio, indicating decreased carbon partitioning to the flower clusters. The dry matter content of the inflorescences was 25% higher in ML compared to LL and increased with increasing N level in either light regime (LL: r = 0.60, P < 1%; ML: r = 0.73, P < 1%). Nevertheless, there was no consistent N effect on dry weight. Consequently, irradiance but not N level altered flowering behavior. In ML, flowering was normal and berry set very regular, whereas in LL, many flowers, pedicels and rachides became necrotic (Fig. 3: B). Abscission layers were often formed in branches or peduncles, leading to abortion of whole or parts of inflorescences. Hardly any necrotic manifestations were visible at the sampling date. Just after sampling, however, severe symptoms became apparent on the remaining vines within 2 to 3 days. The lower cluster was often more severely affected than the upper cluster, and similar symptoms were observed on shoot tips and tendrils in LL. The necrotic characteristics were not caused by *B. cinerea*, since neither mycelial growth nor sporulation occurred after incubation in the dark. It is therefore likely that IN had been induced by light restriction. Yet, the severity of IN could not be assigned to N application, due to large variation within treatments. In contrast to these results, there was no evidence of necrotic or senescing tissue in the field study.

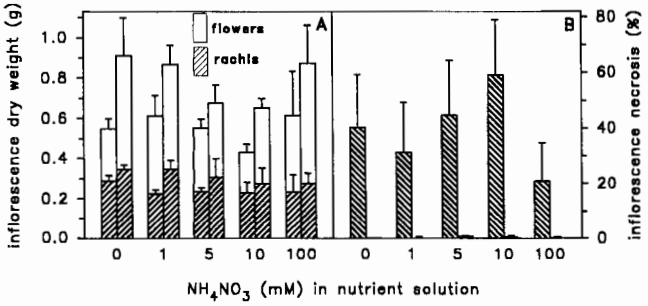

Fig. 3: Effect of irradiance and N application on inflorescence dry mass accumulation (**A**) and inflorescence necrosis (**B**) of potted grapevines in the phytotron.
Left bar of each pair: treatment LL, 30 µEm^{-2}s^{-1} PFD; right bar: treatment ML, 140 µEm^{-2}s^{-1} PFD. Values are means ± SE (n=6).

Discussion

The results from the low-light treatments in both the phytotron and the field indicate that irradiance was near the light compensation point of photosynthesis, and CO_2 fixation was just enough to balance the demand of respiratory processes. They further suggest that the N effect on A was masked by light limitation, since the photochemical reactions, which are independent of N nutrition, become the limiting factor at low irradiance. The low photosynthetic rates were thus caused by the shortage in ATP and NADPH for regeneration of the substrate ribulose 1,5-bisphosphate (VON CAEMMERER and FARQUHAR 1981,

SEEMANN 1989). Light-saturated rates of photosynthesis typically are linearly related to the amount of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), which is reported to increase linearly with leaf N content. Chlorophyll content (Chl), too, closely correlates with total leaf N and therefore with Rubisco (reviewed by EVANS 1989). The failure of A to respond to N supply at light saturation in the field may reflect difficulties in interpreting single-leaf gas exchange measurements. These vines were on a low N status, since they had been grown without fertilization in the previous season, and N was supplied only at the onset of flowering, 10 days later than in the phytotron. If N is supplied to plants after prolonged N stress, it is first translocated to the shoot tip for developing new leaves. This was confirmed by non-destructive Chl measurements. Neither leaf shading nor N nutrition altered Chl in the leaves used for gas exchange measurements 6 days after the first N application. Only 10 days later, Chl decreased in these leaves in the LS/N10 vines and in the N0 vines of all light regimes and increased in the N10 vines of the US and IS regimes, while both leaf shading and N supply markedly increased Chl in the youngest developed leaf compared to the control (data not shown).

The high C_i values under light limitation in both our experiments fit the results of DÜRING (1988) and may be associated with remobilization of carbohydrates, connected with increased rates of maintenance respiration (AMTHOR 1989) and with a large rise in glycolytic enzyme activity (LANCE and GUY 1992), leading to non-photorespiratory CO_2 evolution. According to GEIGER and SERVAITES (1991), the ability of perennial plants to survive when the supply of photoassimilated carbon becomes limited, is related to remobilization of buffer reserves from older, sequentially senescing leaves and permanent parts of the plant and translocation to organs with high sink priority to provide a temporary supply of carbon for maintenance and/or growth processes. Leaf senescence was accelerated by light restriction, particularly in combination with N deficiency, in our study. Although the accuracy of the C_i estimation was verified for a range of irradiances from dark to saturation by SHARKEY *et al.* (1982), it has recently been debated for (detached) leaves under stress conditions (DOWNTON *et al.* 1988, DÜRING 1992). However, the water stress imposed by these authors provided a limitation of both photosynthetic substrate and reducing power, while in our study, light only restricted the reducing power. With regard to the above mentioned authors, we assume that acclimation responses of source leaves to these two kinds of restriction are different. No correction of the values obtained from the data logger was therefore effected. The reduced g_s at low irradiance did not limit A, since stomatal control can only be assumed, if the relationships of both C_i and g_s to A are positive (FARQUHAR and SHARKEY 1982). According to SHARKEY and RASCHKE (1981), C_i can become the major controlling factor of the stomatal response to light. The low g_s in the low-light treatments was thus a reaction to elevated C_i, indicating partial stomatal closure due to light-limited photosynthesis.

The conflicting effects of N supply on g_s and E in the two experiments suggest that, besides C_i, there was another controlling factor involved in stomatal regulation, which acted independent of irradiance. Abscisic acid (ABA) raises stomatal sensitivity to CO_2 in response to leaf water deficits (HARTUNG and SLOVIK 1991), and N deficiency typically increases ABA in leaves (CHAPIN 1991). This is consistent with the field data, but is in contrast to the results from the phytotron. However, even though all phytotron vines received the same quantity of water, the soil surface desiccated between two N application dates in the low-N pots, while it always remained wet in the high-N pots, which indicates lower water uptake by the roots or even water-logging due to excessive ionic concentration in the rhizosphere, reducing the leaf mesophyll water potential. This may have accounted for the declines in g_s and E, reflecting partial stomatal closure, irrespective of photosynthetic potential. SCIENZA and DÜRING (1980), too, found that N deficiency simultaneously increased g_s and leaf ABA content in different grapevine varieties.

Grape clusters are net importers of assimilates, affecting photosynthesis of adjacent leaves (KOBLET 1969, SCHULTZ 1989). Decreasing the sink strength, e.g. by shading or removal of sink tissue, typically results in product inhibition of A in source leaves within about one day (see VON DER CRONE KOPP 1992, for review). The missing response to inflorescence shading in our field study and the reduced dry matter partitioning to the clusters in the phytotron LL regime suggest that their relative sink priority is low. As noted by HALE and WEAVER (1962), photosynthates are partitioned preferentially to vegetative growth early in the season. GLAD *et al.* (1992), analyzing phloem sap exudates, showed that sink strength of grape inflorescences only increases after 70 % flowering. The rapid increase in respiratory CO_2 evolution of inflorescences at anthesis, reported by BLANKE and LEYHE (1989), may be related to high metabolic activities, despite low sink priority. The number and size of sinks competing for carbon during stress periods and their relative priority are involved in activating senescence mechanisms of tissues requiring high energy and carbon inputs in order to guarantee survival of perennial plants (GEIGER and SERVAITES 1991). Since long-term survival and therefore allocation to vegetative growth has priority over reproductive growth in grapevines (especially before pollination is completed), inflorescences may be treated like old leaves. We assume that, by the time the light stresses were imposed, the vines' reserve status was lower in the phytotron than in the field, because of different numbers of shoots and clusters per vine. For the same reason, the competition for photo-synthates and reserves between rapidly growing organs was higher in the phytotron during the stress period. The results from both our experiments suggest that the amount of carbon deriving from photosynthetic CO_2 acquisition and reserve mobilization may have been sufficient to sustain both vegetative and reproductive growth in all treatments except the LL regime in the phytotron.

Inflorescence necrosis is thought to be induced by NH_3 toxicity (SILVA *et al.* 1986, JACKSON and COOMBE 1988). JORDAN (1989) found increased NH_3 concentrations in rachis

and berries of shaded vines and a positive relationship of NH_3 content to the severity of IN. However, since N supply had no impact on IN in our investigation, substantial quantities of NH_3 cannot have been derived from excessive N uptake and reduction, which is consistent with the results of LÖHNERTZ (1991). Because photorespiration is reduced in proportion to photosynthesis at low irradiance (SHARKEY 1988), the contribution of NH_3 released during photorespiratory processes, too, can only have been minor in the present study, even though it may be up to 10 times the production of NH_4^+ during primary N assimilation (WALLSGROVE *et al.* 1983). On the other hand, remobilization of carbohydrates during periods of carbon starvation involves simultaneous protein breakdown releasing glutamate, that is catabolized by glutamate dehydrogenase (GDH) to 2-oxoglutarate, which enters the tricarboxylic acid cycle to provide carbon skeletons for essential maintenance processes (ROBINSON *et al.* 1992). Increased GDH activity is associated with senescence and NH_3 release. The remobilization of substrates during stress periods may thus provide a considerable source for NH_3. Accumulation of NH_3 can be prevented by reassimilation into glutamine by glutamine synthetase (GS) in the cytoplasm and transport from the tissue (KAMACHI *et al.* 1991), provided that GS is active, i.e. in the light. In addition, NH_3 may be emitted from the sub-stomatal cavity to the atmosphere (SCHJOERRING *et al.* 1991), but this would require open stomata. Thus, even though the symptoms of IN may be caused by toxic NH_3 accumulation, this might be a secondary phenomenon related to senescence and simultaneous withdrawal of carbon and nutrients, triggered by (light) restricted gas exchange in combination with low relative sink priority.

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Literature cited

AMTHOR, J.S.; 1989: Respiration and crop productivity. Springer-Verlag, New York.

BJÖRKMAN, O.; 1981: Responses to different quantum flux densities. In: LANGE, O.L.; NOBEL, P.S.; OSMOND, C.B.; ZIEGLER, H.(Eds.): Encyclopedia of Plant Physiology, Vol. **12A**, 57-107. Springer-Verlag, Berlin.

BLANKE, M.M.; LEYHE, A. 1989: Carbon economy of the grape inflorescence. 1. Carbon economy in flower buds of grape. Wein-Wiss. **44**, 33-36.

CAEMMERER, S. VON; FARQUHAR, G. D.; 1981: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**, 376-387.

CHAPIN, F. S. III; 1991: Integrated response of plants to stress. A centralized system of physiological responses. BioScience **41**, 29-36.

CHIARIELLO, N. R.; GULMON, S. L.; 1991: Stress effects on plant reproduction. In: MOONEY, H. A.; WINNER, W. E.; PELL, E. J. (Eds.): Response of Plants to Multiple Stresses, 161-188. Academic Press, San Diego.

CRONE KOPP, A. B. VON DER; 1992: Einfluss der Sinkaktivität auf den Metabolismus der Photosynthese. Diss. ETH Zürich, Schweiz.

DOWNTON, W. J. S.; LOVEYS B. R.; GRANT, W. J. R.; 1988: Stomatal closure fully accounts for the inhibition of photosynthesis by abscisic acid. New Phytol. **108**, 263-266.

DÜRING, H.; 1988: CO_2 assimilation and photorespiration of grapevine leaves: Responses to light and drought. Vitis **27**, 199-208.

- -; 1992: Low air humidity causes non-uniform stomatal closure in heterobaric leaves of *Vitis* species. Vitis **31**, 1-7.

EVANS, J. R.; 1989: Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia **78**, 9-19.

FARQUHAR, G. D.; SHARKEY, T. D.; 1982: Stomatal conductance and photosynthesis. Ann. Rev. Plant Physiol. **33**, 317-345.

GEIGER, D. R.; SERVAITES, J. C.; 1991: Carbon allocation and responses to stress. In: MOONEY, H. A.; WINNER, W. E.; PELL, E. J. (Eds.): Response of Plants to Multiple Stresses, 103-127. Academic Press, San Diego.

GLAD, C.; REGNARD, J. L.; QUEROU, Y.; BRUN, O.; MOROT-GAUDRY, J. F.; 1992: Phloem sap exudates as a criterion for sink strength appreciation in *Vitis vinifera* cv. Pinot noir grapevines. Vitis. **31**, 131-138.

GYSI, C.; 1983: Einfluss der Stickstoffmenge und -form auf das Auftreten der Stiellähme an Riesling x Sylvaner. Mitt. Klosterneuburg **33**, 122-126.

HALE, C. R.; WEAVER, R. J.; 1962: The effect of developmental stage on direction of translocation of photosynthate in *Vitis vinifera*. Hilgardia. **33**, 89-131.

HARTUNG, W.; SLOVIK, S.; 1991: Physicochemical properties of plant growth regulators and plant tissues determine their distribution and redistribution: Stomatal regulation by abscisic acid in leaves. Transley Review No. 35. New Phytol. **119**, 361-382.

JACKSON, D. I.; 1991: Environmental and hormonal effects on development of early bunch stem necrosis. Amer. J. Enol. Viticult. **42**, 290-294.

- -; COOMBE, B. G.; 1988: Early bunchstem necrosis in grapes - a cause of poor fruit set. Vitis **27**, 57-61.

JORDAN, D. T.; 1989: Ammonium in grapevines: Seasonal levels in tissue and xylem extracts, and a tendril model system. PhD Thesis Oregon State Univ., USA.

KAMACHI, K.; YAMAYA, T.; MAE, T.; OJIMA, K.; 1991: A role for glutamine synthetase in the remobilization of leaf nitrogen during natural senescence in rice leaves. Plant Physiol. **96**, 411-417.

KOBLET, W.; 1969: Wanderung von Assimilaten in Rebtrieben und Einfluss der Blattfläche auf Ertrag und Qualität der Trauben. Wein-Wiss. **24**, 277-319.

LANCE, C. J.; GUY, C. L.; 1992: Changes in pigment levels, Rubisco and respiratory enzyme activity of *Ficus benjamina* during acclimation to low irradiance. Physiol. Plant. **86**, 630-638.

LÖHNERTZ, O.; 1991: Soil nitrogen and the uptake of nitrogen in grapevines. In: RANTZ, J. M. (Ed.): Proc. Int. Sympos. Nitrogen in Grapes and Wine, Seattle Washington, USA. June 1991, 1-11. Cal Central Press, Sacramento.

RIVES, M.; 1961: La coulure de la vigne. Bull. Techn. Inform. **164**, 957-959.

ROBINSON, S. A.; STEWART, G. R.; PHILLIPS, R.; 1992: Regulation of glutamate dehydrogenase activity in relation to carbon limitation and protein catabolism in carrot cell suspension cultures. Plant Physiol. **98**, 1190-1195.

SCHJOERRING, J. K.; KYLLINGSBÆK, A.; MORTENSEN, J. V.; 1991: Ammonia exchange and nitrogen dynamics of barley crops at different levels of N supply. In: ANGELETTI, G.; BEILKE, S.; SLANINA, J. (Eds.): Air pollution research report **39**, 383-393. Joint Workshop COST 611/Working Party 3 and EUROTRAC. TNO, Delft, The Netherlands. October 28-30, 1991. Commission Europ. Communities.

SCHULTZ, H. R.; 1989: CO_2-Gaswechsel und Wassertransport von Stark- und Schwachlichttrieben bei *Vitis vinifera* L. (cv. Riesling) in Abhängigkeit von Klima- und Pflanzenfaktoren. Ansatz eines empirischen Assimilationsmodells. Diss. Justus-Liebig-Univ. Giessen. Geisenheimer Ber. **5**, BR Deutschland.

SCIENZA, A.; DÜRING, H.: 1980: Stickstoffernährung und Wasserhaushalt bei Reben. Vitis **19**, 301-307.

SEEMANN, J. R.; 1989: Light adaptation/acclimation of photosynthesis and the regulation of ribulose-1,5-bisphosphate carboxylase activity in sun and shade plants. Plant Physiol. **91**, 379-386.

SHARKEY, T. D.; 1988: Estimating the rate of photorespiration in leaves. Physiol. Plant. **73**, 147-152.

- -; IMAI, K.; FARQUHAR, G. D.; COWAN, I. R.; 1982: A direct confirmation of the standard method of estimating intercellular partial pressure of CO_2. Plant Physiol. **69**, 657-659.

- -; RASCHKE, K.; 1981: Separation and measurement of direct and indirect effects of light on stomata. Plant Physiol. **68**, 33-40.

SILVA, H.; GIL, G.; RODRIGUEZ, J.; 1986: Desecación del escobajo de la vid (palo negro): ¿Un exceso de nitrógeno amoniacal? Aconex **14**, 9-10.

SMART, R. E.; ROBINSON, M.; 1991: Sunlight into Wine. A Handbook for Winegrape Canopy Management. Winetitles, Adelaide.

THEILER, R.; 1970: Anatomische Untersuchungen an Traubenstielen im Zusammenhang mit der Stiellähme. Wein-Wiss. **25**, 381-417.

- -; MÜLLER, H.; 1986: Beziehungen zwischen Klimafaktoren und dem Stiellähmebefall bei Riesling x Sylvaner. Vitis **25**, 8-20.

WALLSGROVE, R. M.; KEYS, A. J.; LEA, P. J.; MIFLIN, B. J.; 1983: Photosynthesis, photorespiration and nitrogen metabolism. Plant Cell. Environ. **6**, 301-309.

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