Weather effects of stalk necrosis in *Vitis*

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Summary: A 5-step physiological explanation is offered for correlations found by THEILER and MÜLLER (1986) between aspects of the weather at flowering and the incidence of stalk necrosis in grape. Four of the steps are well supported in the literature and are discussed briefly.

The other step proposes that the development of xylem in the peduncle is stimulated by floral evapotranspiration. This postulate is tested with measurements of xylem cross-sectional area in clusters taken from vineyards located in diverse regions of New Zealand for which meteorological data were available. Statistical analysis indicates a clear distinction between material from the climatic extremes and a significant ($P = 0.05$) correlation between calculated values of evapotranspiration during flowering and peduncular xylem area.

The beginning of a physiological explanation for the seasonal effects on the incidence of stalk necrosis in grape has stimulated studies which may allow the selection of non-sensitive varieties.

Key words: stiellaehme, stalk necrosis, climate, flower, berry, peduncle, rachis, xylem, transpiration.

Introduction

In a recent publication THEILER and MÜLLER (1986) demonstrated strong correlations between the incidence of stalk necrosis (variously known as bunch stem necrosis, shanking, stiellähme, dessèchement de la rafle) in Müller-Thurgau grapes and a number of meteorological variables including daytime temperature, sunshine hours and precipitation. Moreover, they noted that these correlations existed only for weather conditions over the flowering period. They suggested that something happens at this stage of development, the effects of which are apparent only after veraison.

THEILER and MÜLLER s results are provocative in two ways. They raise commercial questions relating to the choice of variety, vineyard siting and canopy management, and they raise physiological questions relating to the nature of the causal link between weather and stalk necrosis. Our paper addresses the second of these aspects. A scheme is proposed which invokes a sequence of causes and effects to explain the correlation. The scheme starts with weather and ends with stalk necrosis (THEILER and MÜLLER's correlative statement) and contains five linking steps. Four of the hypothesised steps are examined by reference to the literature and one by an experiment.

The hypothesis

The hypothesis is presented in summary form in Fig. 1. We shall consider it one step at a time.

Step (i) - weather : flower evapotranspiration

Here we propose that flower evapotranspiration is affected by the prevailing weather. Although plants undoubtedly exert a strong control over evapotranspiration, this is only part of the story and few would seriously dispute that water losses from an exposed plant organ are strongly influenced by factors such as those identified by THEILER and MÜLLER (1986) viz. temperature, insolation and rainfall. Models which describe how meteorological variables drive evapotranspiration under a range of identified conditions are well established and their use is commonplace in scientific research and irrigation management systems.

Step (ii) - flower evapotranspiration : peduncle xylem area

In this step we propose that xylem area development in the peduncle is in proportion to the mean evapotranspiration rate of the inflorescence during the flowering period. We suggest that the xylem's carrying capacity (area) is stimulated in some way by demand during the tissue differentiation phase such that sap pressure gradient is stabilised. The flow : area link is consistent with the observation that in a very wide range of plants and organs xylem sap flow is related to the cross-sectional area of the xylem tissues (Siau 1971; Zimmermann and Brown 1971). We examine this relationship in the second part of our paper with an experiment.

Step (iii) - peduncle xylem area : xylem/phloem sap flow ratio

As with xylem areas and flows discussed above, translocation flow bears a close relation to the area of cross section of the phloem. Indeed the relationship, usually expressed as specific mass transfer or flux density (Evans and Dunstone 1970; Canny 1973), is most remarkably constant across a wide range of size scales, plant organs and genera. Now it is axiomatic that something which influences one variable will also influence the ratio which this variable bears to another. In the present situation, all else being equal, it follows that xylem area change may be assumed to result in a changed ratio of xylem to phloem tissues and this may fairly be taken to indicate a change in the ratio of their sap flows.

Step (iv) - xylem/phloem sap flow ratio : Ca/K content of cluster

Potassium has for a long time been known to be strongly phloem mobile forming the dominant cationic species in extracted sieve tube sap (Ziegler 1975). Calcium on the other hand is traditionally thought of as phloem immobile (Marschner 1983). Both ions are of course freely mobile in the xylem sap. The generally low levels of Ca and high levels of K in fruits are thought to arise through a common pattern of growth in which the xylem, while making a significant early contribution to growth, is largely replaced by a dominant phloem contribution later on (Simon 1978). This state of affairs has led to the idea that some classes of mineral imbalance disorders may result from imbalance between phloem and xylem supplies (Ferguson and Watkins 1989).

weather
↓ (i)
flower evapotranspiration
↓ (ii)
peduncle xylem area
↓ (iii)
xylem/phloem sap flow ratio
↓ (iv)
Ca and K content of cluster
↓ (v)
stalk necrosis

Fig. 1: A sequence of five steps by which it is proposed the weather at flowering affects the incidence of stalk necrosis. Each step is in the form of a subsidiary hypothesis, viz. weather effects flower evapotranspiration, which affects peduncle xylem area, and so on.

Step (v) - Ca and K in cluster : stalk necrosis

Stalk necrosis in grape is thought to be a mineral imbalance disorder, although agreement on which minerals are involved does not seem to have been reached. This confusion is not unexpected if we allow that a non pathogenic or physiological necrosis could well have a number of different causes. One possibility is that stalk necrosis occurs as a result of an imbalance between K and Ca. For example, FEUCHT *et al.* (1975) showed that stalk necrosis in grape can be associated with high K/Ca ratios in the peduncles (but compare CHRISTENSEN and BOGGERO (1985) who found otherwise).

The experiment

An experiment was performed to examine the postulate of step (ii) that development of peduncular xylem is stimulated by evapotranspiration rate.

Materials and methods

Material

Riesling was chosen for the experiment because it was widely available and because it is known to be susceptible to stalk necrosis. THEILER and COOMBE (1985) noted that development of xylem tissues in grape peduncles occurs exclusively over a brief early period of about 2 weeks duration, from just before to just after first bloom (this finding agrees with our own observations). In the present study therefore, clusters were collected in January and February 1986, 4-6 weeks after flowering, to allow ample time for xylem development to have been completed.

Collections were made from four different vineyards in New Zealand chosen to represent as wide a range of climate types as possible and for which detailed meteorological records would be

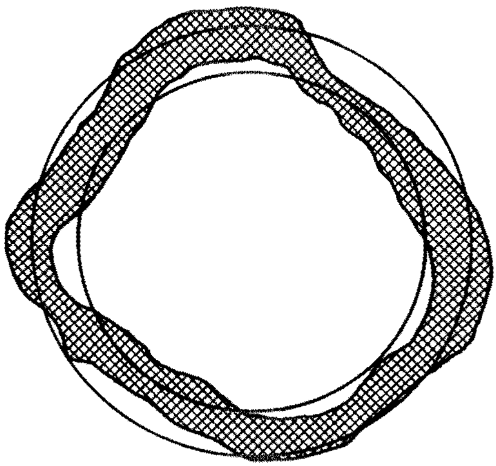

Fig. 2: A diagram to illustrate the 'circles' method used to measure xylem cross-sectional area in the grape peduncle. The irregular xylem image is shown hatched and circles which best match the inner and outer limits are superimposed. Circles were selected by eye from a set of standards.

available. In the North Island the vineyards were in Martinborough (Wairarapa), Mangere (Auckland), Te Kauwhata (North Waikato), and in the South Island, Queenstown (Central Otago).

Measurement of xylem areas

Transverse sections of peduncle tissue were cut by hand from regions just proximal to each of the first three nodes within each cluster. A thin and complete section was chosen to represent each region and placed on a marked slide. This gave three sections per cluster for area measurement. The number of berries downstream of each region was recorded. The sections were stained in phloroglucinol and HCl (PURVIS *et al.* 1964) to colour the lignified xylem tissues a distinct red.

Because of the large number of sections to be examined (more than 250) a quick method for estimating xylem cross-sectional area was required. Using a projection microscope in a darkened room, the magnified images were focused onto a sheet of paper on which circles of known radii had been inscribed. The pair of circles which best matched the inside and outside boundaries of the xylem were chosen by eye making allowance for irregularities in circularity (see Fig. 2). Xylem area was then computed as the difference between the areas of the two circles divided by the enlargement factor. The 'circles' method had been previously checked against a tedious but more certain one. This involved tracing around the irregular inner and outer boundaries of the xylem image when projected onto a sheet of plain paper, cutting this out with scissors and weighing. Measurements obtained using the 'circles' method bore a close linear relation to measurements obtained from the same slides using the 'scissors' method showing no significant systematic divergence from a 1 : 1 line. Moreover, no 'circles' estimate of area departed by more than 12 % from the 1 : 1 line. With variability between specimens rather larger than this, the method was judged satisfactory.

Evapotranspiration estimates

Mean daily evapotranspiration (mm d^{-1}) was calculated for each vineyard from local meteorological data. In each case means cover a 9-d period spanning the date of first flower. Estimates of potential evapotranspiration based upon meteorological variables were adjusted to allow for precipitation on the basis that actual evapotranspiration was depressed below potential evapotranspiration when soil water content was less than half field capacity (PRIESTLEY and TAYLOR 1972).

Results

Not unexpectedly, measurements of xylem area at different points in the same cluster were found to vary considerably. It was thought that the area at a point might depend on the number of berries downstream. In order to remove this source of variability in the main experiment, a separate study was made of the relationship between xylem area and the number of berries downstream. Clusters used for this came from a single vineyard. A close linear relation ($r = 0.86$, $n = 54$) was found between the cross-sectional area of xylem at any point in the peduncle and the number of berries downstream (see Fig. 3). So that xylem area measurements from different sized clusters and different nodes were comparable, area data were therefore normalised by dividing by the number of berries downstream to give the variable 'xylem cross-sectional area per berry'. This allowed an assessment of the extent of xylem area development in clusters collected from the four different vineyards.

Statistical analyses were carried out on log transformed values to correct a slightly asymmetrical distribution. Mean xylem areas per berry for each vineyard are plotted against evapotranspiration estimates in Fig. 4. Error bars represent the sample estimate of the population mean ($P = 0.05$). The vineyards fall into three distinct groupings ($P = 0.001$ or better). Linear regression gives a regression coefficient $r = 0.978$ which for $n = 4$ indicates a significant ($P = 0.05$) correlation.

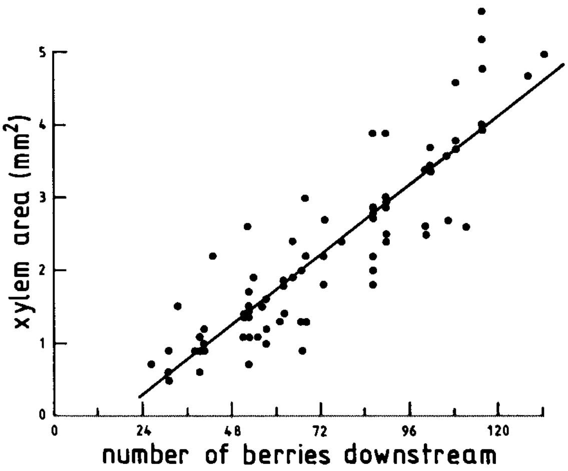

Fig. 3: The plot of xylem cross-sectional area vs the number of berries downstream. Linear regression ($r = 0.86$, $n = 54$) indicates that the two variables are strongly correlated. The remaining variability does not appear to be systematic and is attributed to the natural variability of material and to measurement error.

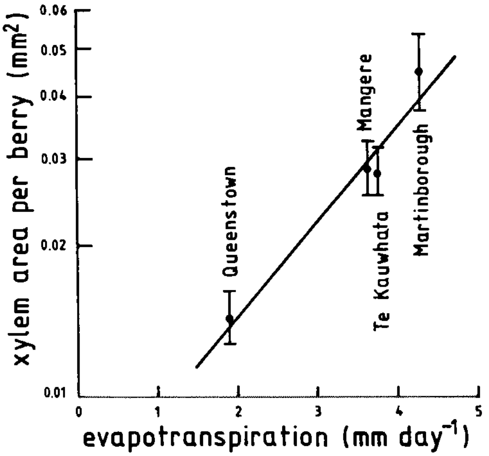

Fig. 4: The plot of xylem cross-sectional area per berry vs a calculated mean daily evapotranspiration at the time of flowering. Error bars represent the sample estimate of the population mean ($P = 0.05$).

Discussion

The results show a clear distinction between vineyards in the cross-sectional area of peduncular xylem in Riesling grapes and this distinction correlates significantly with meteorological factors in line with step (ii) our our hypothesis. That is, the experiment supports the postulate that xylem area development in grape peduncles is in proportion to the mean evapotranspiration rate during the flowering period.

The remaining steps of the hypothesis (i, iii, iv, v) find good support in the literature as has been shown. We therefore conclude that the hypothesis offers a satisfactory explanation of the effects of weather upon stalk necrosis in grape. This opens the way for breeding screens and management practices to be evolved which minimise or eliminate the problem.

In view of the importance of stalk necrosis to the grape industry, further research along the lines of that reported here would be worthwile. A number of aspects could be looked at in greater detail. Step (ii) of the hypothesis should be examined in an experiment involving more vineyards and which made comparisons with measured rather than with calculated values of floral evapotranspiration. The encouraging results presented here would also justify a more extensive study of the whole hypothesis. This study might include varieties which covered a range of susceptibilities to stalk necrosis and with an attempt made to assess the incidence of stalk necrosis. The intermediate variables are also amenable to measurement. These include the Ca/K composition of the fruit and the xylem : phloem sap flow ratio (LANG 1989).

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Reaction norms of the new grape varieties with complex resistance to environmental conditions

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Abstract: Agrobiological, some physiological and uvological properties of the new varieties bred by the Institute have been evaluated (Podarok Magaracha, Antei Magarachski and Yubileiny Magaracha). These varieties with complex resistance to pests and diseases are grown in commercial vineyards under different soil and climatic conditions in Crimea, both in the zones of open and protected viticulture. Agricultural and biological properties of the varieties have been studied, and their high fruitfulness has been shown. The proportion of fruiting shoots reaches 85 %, and the coefficient of fruitage (K_1) is 1.3. The fruiting shoot percentage, the coefficient of fruitage, the coefficient of fruitfulness (K_2) and the average cluster weight have been shown to be substantially affected by soil and climatic conditions along with agricultural methods.

The norms of reaction to the alterations of soil and climatic conditions and to agricultural methods have been established for individual indicators characterizing certain properties of the varieties. The coefficients of sensitivity of the varieties to the alterations of soil and climatic conditions and to agricultural methods have also been established. The most dramatic changes in these indicators are due to the different training systems and, to a slighter extent, to the total number of shoots per vine. The sensitivity of the varieties to the alterations of the conditions of culture have been shown to be different. Antei Magarachski has a weak degree of reaction with the coefficient of sensitivity 0.28-0.31, while Podarok Magaracha is highly sensitive to the same alterations with the coefficient of sensitivity 0.74-0.88.

In commercial culture, these cultivars can be used to establish own-rooted vineyards in phylloxera-infected zones, which makes their culture less labor consuming and reduces pesticide load on the environment.