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THE COLD HARDINESS AND FRUITFULNESS OF CONCORD GRAPEVINES AS RELATED TO CANE MORPHOLOGY AND LATE SEASON SOURCE-SINK RELATIONSHIPS IN THE VINE

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By

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ABSTRACT

THE COLD HARDINESS AND FRUITFULNESS
OF CONCORD GRAPEVINES
AS RELATED TO CANE MORPHOLOGY
AND LATE SEASON SOURCE-SINK RELATIONSHIPS
IN THE VINE

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Cane color and diameter were found to be useful criteria for judging the fruitfulness and hardiness of buds on Concord grapevines. Cane internode length and persistent lateral status could not be consistently related to bud hardiness. Dark, medium diameter canes are the best to retain at pruning.

Complete defoliation of Concord grapevines at veraison reduced cluster number, fruit maturation, bud hardiness, and fruit set, and delayed bud break in the spring. Fifty percent defoliation produced extremely adverse effects if leaves were removed from entire cordons of vines. Defoliation of alternate shoots or alternate leaves produced few or no adverse effects. The effects of defoliation are discussed in terms of photosynthesis, altered patterns of assimilate transport, and carbohydrate depletion, in the vine.

Shading or defruiting vines at veraison did not affect rates of sugar uptake by fruit, bud hardiness, or fruitfulness.

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INTRODUCTION

Given the marginal profitability of commercial production of Concord grapes in Michigan, the need for intelligent vineyard management is crucial to economic success. The cultural manipulations made by a grower during the year all affect the physiology of the grapevines and thus influence, to a greater or lesser degree, the ultimate productivity of the vineyard.

In Michigan, the most serious economic threats to commercial grape production are the losses of buds to extremely cold winter temperatures and late spring frosts. Once a vineyard is established at a given location, site selection, the most effective means of combatting these hazards, is no longer an available option to the grower. Short of expensive investments in elaborate frost protection equipment, which few growers can afford, only wise management, based on knowledge of the vines' physiology, remains as insurance against disastrously low yields.

Pruning strategy is one of the most important aspects of vineyard management. Unless the best available nodes are retained at pruning to bear the following year's crop, the survival of buds through the winter and the subsequent growth

and fruit production of the vines will be adversely affected.

In order to have well-matured, hardy canes from which to select at pruning time, conditions during the growing season must be optimal for growth and development of the vines. Barring extremely poor weather conditions, this requires the grower to supply adequate nutrients to the vines, and to afford them protection from insects, diseases, and weeds. Shoots must be properly trained so as to maximize the conversion of the sun's energy into photosynthetic products. Vines poorly trained or inadequately protected from pests cannot equal the productivity of properly managed vines. The end result of such negligence (or uninformed decision-making) is financial loss.

The research reported in this thesis deals with some of these cultural questions. One study investigates the relationship between the external morphology of grapevine canes and the hardiness and fruitfulness of buds on those canes. Knowledge of the nature of any such relationships would serve as an invaluable aid in the pruning of grapevines.

The second study reports on the effects of defoliation and shading on bud hardiness and fruitfulness. Since many environmental stresses, including nutrient deficiencies, severe insect or disease infestations, and careless use of herbicides can lead to premature loss of leaves, the consequences of late-season defoliation on the vine are necessary to understand. The causes of shading within vine canopies are several - suffice it to say that as a problem in Michigan

vineyards it is not uncommon.

The defoliation study was also undertaken to answer questions on the relationship of bud hardiness to other developmental processes in the grapevine. By altering the normal source-sink relationships of the vines in late summer through defoliation or fruit removal, and by monitoring their effects on subsequent fruitfulness and hardiness parameters of the vines, the degree of dependance of several physiological events, such as fruit maturation, cluster initiation, and cold acclimation, on late-season photosynthesis and transport of carbohydrate might be clarified.

LITERATURE REVIEW

Translocation patterns in the grapevine

During a grapevine's annual cycle of growth and development, the activation and deactivation of numerous meristematic and metabolic centers in various parts of the vine takes place (Pratt, 1971 and 1974). This growth and development is dependant on current photosynthesis and stored carbohydrate for a source of energy (Winkler et al., 1974; Kriedemann, 1975). Transport of assimilate from regions of production or storage (sources) to regions of utilization (sinks) takes place in the phloem (Zimmermann, 1960). In grapevines, the exclusive transit sugar is sucrose (Swanson, 1957; Swanson and El-Shishiny, 1958). Sequences of initiation, development, and growth of various tissues and organs of the grapevine are complex and overlapping (Pratt, 1971; Buttrose, 1974; Srinivason and Mullins, 1976; Scholefield and Ward, 1975). Changes in the relative sink activity or capacity in these different regions are thus common, and can influence the pattern of distribution of assimilate in the phloem system (Quinlan and Weaver, 1970; Zimmermann, 1960).

Source-sink relationships are subject to several other influences, such as light and disease (Crafts and Crisp, 1971). Thus, these relationships are complex and labile. In general,

sinks are supplied by the nearest sources (Canny, 1973), and transport in the phloem tends to be strictly longitudinal, with little movement laterally, except in cases of external disturbance (Zimmermann, 1960).

In grapevines, the earliest active major sinks are the growing tips and immature, expanding leaves of young shoots, and, to a lesser extent, flower clusters. This early growth depends on carbohydrate reserves from the bark (Hale and Weaver, 1962; Winkler and Williams, 1945), or the roots (Schrader, 1924). Leaves begin exporting photosynthate when they have attained one-third to one-half full size. At this time, transport is in an acropetal direction to the growing shoot apex (Hale and Weaver, 1962), with some photosynthate going to the flower clusters and differentiating buds in the axils of the exporting leaves (Leonard and Weaver, 1961).

As several leaves begin to export, the older, basal-most ones briefly become bi-directional (Shindy and Weaver, 1967), then strictly basipetal, transporters (Hale and Weaver, 1962). Apical leaves continue to feed the shoot tip (Quinlan and Weaver, 1970; Canny, 1973).

At bloom, or a few days thereafter, the flower clusters become strong sinks. They are fed primarily by basal leaves on the shoot (Quinlan and Weaver, 1970; Leonard and Weaver, 1961). Once berry set has occurred, the clusters become the dominant sinks on the vines (Hale and Weaver, 1962). By mid-summer, current photosynthate may go only to the fruit

clusters (Leonard and Weaver, 1961).

The berries, whose growth is described by a double-sigmoid curve and divided into two (Coombe, 1960), or three (Hale, 1968) distinct stages of development, continue as strong sinks until they are fully ripe. Maximum accumulation of sugar takes place after veraison, when the berries turn from green to their characteristic color at harvest (Coombe, 1960; Hale, 1968).

The parent vine is a strong sink from mid-summer on, once its' reserve carbohydrate supply is exhausted (Hale and Weaver, 1962). Storage of starch begins first in the stems, then the roots (Winkler and Williams, 1945). In California, carbohydrate increases in roots of Tokay grapes during August and September (Leonard and Weaver, 1961). If the situation is analogous to that in black locust trees, storage of photosynthetic product reaches its maximum in grapevines just before leaf drop (Siminovitch et al., 1953).

There is no evidence for transport of elaborated food substances throughout the vine during the dormant season (Winkler and Williams, 1945; Schrader, 1924 and 1926). The plugged condition of sieve areas in phloem tissue of Vitis during dormancy would seem to prohibit such transport (Esau, 1948 and 1957).

Starch-sugar interconversions do take place throughout the dormant season, however. In Concord grapevines, starch is converted to sugars until late January, when starch levels in canes, trunk, and roots reach their winter minimum levels.

Levels of free reducing sugars and sucrose are maximum at this time, which corresponds to the end of the rest period (Schrader, 1926; Richey and Bowers, 1924). This same pattern holds true for black locust (Siminovitch et al., 1953).

Renewed metabolic activity at the end of the rest period, and later the flush of new growth in the spring, cause a decline in the levels of free reducing substances, sucrose, and total sugars (Richey and Bowers, 1924; Winkler and Williams, 1945; Siminovitch et al., 1953).

Mechanism and control of translocation patterns in the phloem

Many theories have been propounded for the mechanism of carbohydrate transport in the phloem. One of the oldest, and most widely accepted, is the mass flow theory of Münch. It states that flow from sources to sinks occurs because of gradients of hydrostatic pressure set up due to differences in solute concentration at the places of synthesis and places of utilization or storage (Zimmermann, 1960). Other theories favored by some researchers raise several objections to the mass flow model (Canny, 1973).

Much research has focused on hormonal control of translocation patterns in the phloem. Tracer studies have implicated cytokinins (Crafts and Crisp, 1971; Shindy and Weaver, 1967), gibberellins (Shindy and Weaver, 1967; Quinlan and Weaver, 1970), auxins (Weaver, Shindy, and Kliewer, 1969), and other, uncharacterized carbon compounds (Kriedemann et al., 1976) as factors for the mobilization of photosynthate

in Vitis. Mass flow of carbohydrates may also be stimulated by increased transpiration of sink tissues (Swanson et al., 1976).

Artificial manipulation of patterns of translocation

Although sinks are normally fed by the nearest source leaves, there exists a "kind of homeostatic switching mechanism which redistributes assimilates from the remaining sources to compensate for the lost ones." (Canny,1973). Source-sink relationships within the plant are thus subject to alteration by several types of experimental manipulation.

Shifts in transport patterns have been reported in defoliation studies with Phaseolus vulgaris (Swanson et al., 1976) and Malus spp. (Quinlan, 1966). In Vitis vinifera, no movement of assimilate normally takes place between shoots on the same spur, prior to bloom. But if shoots adjacent to radioactively fed shoots are darkened or defoliated, they will import label from the fed shoots (Quinlan and Weaver, 1970). When defoliation on one-third of the shoots on entire canes of Sultana grapes was carried out at the end of the first rapid growth phase of the berries, transport from foliated shoots to clusters on defoliated shoots took place (May et al., 1969). Defoliation of newly expanding, importing leaves of several grape varieties resulted in improved flower cluster development (Nii, 1973 a and 1973 b).

Removal of sinks also alters the nature of translocation within the plant. Shoots of Vitis vinifera can be made

to export assimilate to other shoots by removal of their clusters and growing tips (Quinlan and Weaver, 1970). Varying source-sink ratios by leaf removal or by fruit removal do not necessarily produce the same effects, however (Buttrose, 1966 and 1968).

Following a year of heavy overcropping, the sink strength of the parent vine is increased (Hale and Weaver, 1962).

Normally, the efficiency of vine leaves for photosynthesis is approximately 25-30% of full sunlight (Kriedemann, 1968 and 1971). Mean efficiency of utilization of light energy in a vine canopy is only about 3.3% (Smart, 1974). Increases in photosynthetic efficiency of leaves remaining on vines under stress of partial defoliation have been reported (May et al., 1969; Kliewer and Fuller, 1973). This may be due to either an increased rate of photosynthesis (Hofäcker, 1978), or increased export of assimilate (Swanson et al., 1976), by the remaining leaves.

Conversely, removal of major sinks, or stem girdling, depresses the measured rate of net photosynthesis in the leaves (Kriedemann and Lenz, 1972; Hofäcker, 1978; Burt, 1964). Large source-sink ratios result in low utilization of photosynthate in source leaves, and may reduce their rate of photosynthesis (Humphries and Thorne, 1964; Christy and Swanson, 1976). Accumulation of starch in the leaves, such as is known to occur under temperature conditions that favor low net photosynthesis (Buttrose and Hale, 1971), may depress photosynthetic rate (Kriedemann and Lenz, 1972; Loveys and

Kriedemann, 1974). Photosynthetic rate may also be linked to abscisic acid levels and stomatal diffusive resistances of the leaves, both of which are known to vary with source-sink ratio (Hofäcker, 1978; Loveys and Kriedemann, 1974; Kriedemann et al., 1976). Rates of photosynthesis are also influenced by specific physiological events; notably new leaf emergence, flowering, and fruiting (Wolkowa et al., 1974), and can change with degree of fruit maturation or proximity to ripening fruit (Pandey and Farmahan, 1977).

Other effects of defoliation

Optimum yields and normal berry size and soluble solids content can be achieved on vines defoliated at fruit set. For different varieties of Vitis vinifera, it was found that a minimum of from 16-20 leaves per cluster of fruit on girdled shoots, and from 27-33 leaves per cluster of fruit on ungirdled shoots, was sufficient to achieve normal yields and maturity (Winkler, 1930 and 1932; Weaver, 1963). Movement of assimilate in these vines occurred over distances as great as three feet and through vine parts up to six years old (Winkler, 1932).

Severe or untimely defoliation does have marked deleterious effects on several aspects of growth and development. Among the factors affected by defoliation are berry weight, cluster weight, fruit soluble solids (Weaver, 1963), shoot maturity, fruitfulness, vegetative development (Howell and

Stackhouse, 1973), berry development, root dry weight (Buttrose, 1966), and bud hardiness (Stergios and Howell, 1977).

Pre-bloom defoliation of leaves below clusters on shoots of Ribier grapes reduced yields but improved berry weight and soluble solids (Jensen, Luvisi, and Levitt, 1976). Partial defoliation of lowbush blueberries at full bloom reduced fruit set, fruit maturity, and yield (Aalders et al., 1969). Dry weight of roots on non-fruiting, one-year-old Sultana grapevines was reduced by a 50% defoliation as late as harvest time, but cane and trunk dry weights were only affected by earlier defoliation (Kliewer and Fuller, 1973). Partial defoliation during early berry growth caused yield reductions of 27-40% in this variety (Kliewer and Ough, 1970). Defoliation of apical leaves of Sultana grapevines at anthesis + 1 month had a more severe effect on berry weight and soluble solids than removal of leaves from basal nodes, or alternate shoots (Kliewer and Antcliff, 1970). Foliated and defoliated shoots on the same cane of Sultana grapevines did not differ significantly in fruit soluble solids, when defoliation was carried out at the end of the first period of rapid berry growth. Berry weights and soluble solids for fruit from these shoots were lower than those from shoots where only basal leaves were removed, however. Clusters on shoots from entirely defoliated canes were lower in soluble solids and berry weights than fruit on adjacent, foliated canes. Shoots on foliated canes also matured more nodes, and had superior

fruitfulness the following year, than their defoliated counterparts (May et al., 1969). Defoliation at veraison of Shiraz grapevines, to two leaves above distal clusters on all shoots, negatively affected yields for three successive years (Peterson and Smart, 1975).

Immaturity of shoots and susceptibility to winter injury were increased by hand defoliation of Cornus stolonifera bushes late in the growing season (Fuchigami et al., 1977), and by chemical defoliation of grapevines just prior to harvest (Larsen, 1961). Overcropping of grapevines also produces many of the harmful effects of defoliation (Weaver and McCune, 1960; Balasubrahmanyam et al., 1974; Kliewer and Weaver, 1971).

Physiological effects of shading

Sunlight interception and specific leaf exposure are important factors in determining crop yield (Smart, 1973; Kimball and Shaulis, 1958; Kriedemann, 1975). Reducing light available to the vine by 75% during the entire growing season severely reduced the mean daily increment in soluble solids of the fruit (Shaulis, Amberg, and Crowe, 1958). The same degree of shading at veraison also caused significant reductions in fruit soluble solids (Kliewer, Lider, and Schultz, 1967). Reducing available light by only 40%, if commenced at berry set, depressed the yield of vines the following year (Klenert, 1975). Second year effects of shade on grape soluble

solids have also been reported (Sparks and Larsen, 1966). Shade had similar effects on fruit yield and maturity in lowbush blueberry (Aalders et al., 1969).

Cluster and leaf primordia in developing grape buds increase in number until well after veraison in late summer (Buttrose, 1970), so light intensity during the latter half of the growing season may be very important in determining bud fruitfulness (Hopping, 1977). Differentiation of individual floral organs takes place in grape buds shortly before and after bud break in the spring following their initiation (Buttrose, 1974; Srinivason and Mullins, 1976; Scholefield and Ward, 1975). Decreased or delayed bud break caused by shading would thus have a negative effect on fruitfulness (Hopping, 1977). Other factors influenced by shading include fruit coloration (Kliewer, 1970), berry weight (Klenert,1974; Kliewer and Lider, 1968), and root starch storage (Kliewer, Lider, and Ferrari, 1972).

Effects of sugars and other translocatable substances on cold hardiness of plant tissues

Cold hardiness and freezing processes in plant tissues are very complex and only partially understood phenomena. The nature of freeze-induced injury to plant cells, and the general patterns of acclimation and deacclimation to cold temperatures exhibited by plants, are aptly reviewed in a number of recent publications (Burke et al., 1976; Levitt, 1972; Alden and Hermann, 1971; Parker, 1963).

Plants need foliage and light in order to mature and acclimate to winter conditions (Tumanov et al., 1976; Howell and Stackhouse, 1973). Storage of photosynthetic products in the fall, and conversion of starch to sugar in cells during cold acclimation, are well documented (Richey and Bowers, 1924; Schrader, 1924 and 1926; Winkler and Williams, 1945; Parker, 1963; Siminovitch et al., 1953). Correlations between increases in cell sap concentration and freezing tolerance are generally strongly positive (Levitt, 1972), but the exact role of sugars in the cold hardiness mechanism remains elusive.

Starch and sugars accumulated in the fall support the winter metabolism of the plant and provide the energy substrate for spring growth. They may also play a largely metabolic role in hardiness. Sugars may be required to activate enzymes that increase freezing tolerance through their action on cell membranes or other cellular components (Levitt, 1972; Alden and Hermann, 1971). Photosynthates formed during the cold acclimation period may be used preferentially to increase tolerance to low temperatures (Steponkus and Lanphear, 1968), possibly by stabilizing proteins that might otherwise be denatured by removal of structural water during freezing (Levitt, 1972; Alden and Hermann, 1971; Parker, 1963).

Solutions of sugars and sugar alcohols imbibed by cells can increase their freezing tolerance. Increased cell sap concentration may provide direct protection from intracellular ice formation when water migrates through the plasma membrane

and cell wall to ice masses forming in the intercellular spaces (Sakai, 1971). Protective polysaccharides, which interfere with the freezing process by altering the structure of ice masses, may also be formed in the plant cell walls (Olien, 1965).

Actively growing tissues are not capable of achieving much cold tolerance. An inverse relationship between freezing tolerance and development exists (Levitt, 1972). Conditions that favor growth and development, such as long photoperiod, result in the production in the leaves of hardiness inhibitors, which are translocated to other parts of the plant (Irving and Lanphear, 1967). Extracts from short-day (SD) induced, hardy plants increased the hardiness of plants under non-inductive, long-day (LD) conditions (Irving, 1969). Production of hardiness promoting substances under short days, and the dependance of at least an early stage of cold acclimation on promoter-inhibitor ratios, was suggested from translocation studies on Haralson apple (Howell and Weiser, 1970). Defoliation and cold temperatures counteract the effects of long-day produced, hardiness inhibiting substances (Irving and Lanphear, 1967), but cold temperatures may be essential for the attainment of maximum hardiness, either by triggering a second stage in cold acclimation (Howell and Weiser, 1970), or by affecting promoter-inhibitor levels independently of the SD-LD effect (Irving, 1969). There is some evidence that the hardiness promoting factor may be sucrose (Steponkus and Lanphear, 1967). Grafting studies with Cornus stolonifera

suggest that several inter-related endogenous ingredients are necessary for cold acclimation, including cessation of growth, substrate for synthetic processes, high ratio of promoters to inhibitors, and the proper metabolic machinery (Fuchigami, Evert, and Weiser, 1971).

The relationships between cane morphology and fruitfulness or hardiness

At the end of the growing season, grapevine shoots mature and enter a period of dormancy. As the shoots mature, a periderm layer begins to form at the base of the shoots, and develops acropetally (Esau, 1948 and 1965; Weaver, 1963). Factors which favor good fruit maturity and bud fruitfulness, namely exposure of leaves to sunlight (Smart, 1973; Buttrose, 1970) also favor good shoot maturity (Shaulis, Amberg, and Crowe, 1958). Defoliation (May et al., 1969), shading (Shaulis, Amberg, and Crowe, 1958), and overcropping (Kliewer and Weaver, 1971) adversely affect shoot maturity. Poor or delayed maturation of fruit and shoots has been linked to increased susceptibility to insects, diseases, and other environmental stresses (Weaver and McCune, 1960). Well-exposed, mature canes of Concord grape, as evidenced by dark periderm color, have superior cane and primary bud hardiness compared to poorly exposed, light colored canes (Howell, unpublished data).

Cane diameter, internode length, and lateral status (presence or absence of lateral shoots), have also been

correlated with fruitfulness (Partridge, 1925) and hardiness (Howell, unpublished data). Suggestions for selection of wood to be retained at pruning have been made on the basis of these criteria.

SECTION I

THE RELATIONSHIPS BETWEEN EXTERNAL CANE MORPHOLOGY AND BUD HARDINESS AND FRUITFULNESS

INTRODUCTION

The selection of pruning wood during the dormant season is one of the most important cultural decisions a grower must make in management of a vineyard. The number of buds retained will influence the balance between vegetative and reproductive development the following growing season, and thus have a direct bearing on potential yields. Research on the competitive aspects of vegetative and reproductive growth and development has led to recommendations for pruning levels and strategies for different varieties of grape grown under different environmental conditions.

Similarly, the location of retained nodes on a vine will affect growth patterns and yields. Certain buds are more fruitful than others by virtue of their more favorable position on a cane. Training systems have been developed which utilize the most favorably situated nodes to maximize the production of the vine.

In moderately vigorous to vigorous vineyards, a great deal of wood must be removed at pruning in order to ensure proper growth the following year. Many more well-situated canes may be available than can safely be retained. Although most or all might be incorporated into the particular training system in use, some basis for selection must be employed in choosing those to remove and those to keep.

The most obvious, and perhaps the only, criterion for selection available to the grower is the appearance of the canes. Variations in cane size, color, growth habit, and several other characteristics can be used as a basis for intelligent pruning strategy, if the relationships that exist between the external attributes of a cane and its potential for fruitful growth are known.

For this reason, a study was undertaken on Concord grapevines to determine the extent of the relationship between several parameters of cane morphology and the cold hardiness and fruitfulness of buds on these canes. While recommendations for the pruning of Concord grapevines have been made in the past on the basis of differential fruitfulness of buds on various cane types, the relationship of hardiness to cane morphology has not been as widely investigated. Since the ability of a bud to survive the winter is a necessary precedent to fruitful development, recommendations should be based not only on the potential fruitfulness of canes, but on their hardiness as well.

MATERIALS AND METHODS

Plant material

During the winters of 1976-77 and 1977-78, dormant, one-year-old canes were collected from moderately vigorous Concord grapevines at various locations around Lawton, Michigan, and at the MSU Horticultural Research Farm in East Lansing, Michigan. Single node sections of canes were segregated on the basis of different characteristics of external morphology, and subjected to artificial freezing stress under controlled conditions, in order to determine whether or not differential bud hardiness corresponded to variations in cane morphology. A total of eight freezing tests were conducted, in which categories of cane color, diameter, internode length, and persistent lateral status were evaluated for hardiness of primary, secondary, and tertiary buds. In all cases, vines were of full bearing age, and except for those at the MSU Hort. Farm, all were from commercially productive vineyards. Each of the training systems commonly employed in Michigan viticulture was represented in at least one evaluation. Cane color was included as a category in all eight of the hardiness trials. Dates and locations of cane collections, with descriptions of the various categories examined in each, are as follows:

1. MSU Hort. Farm (12-10-76). Cane color hardiness evaluation - Canes of medium diameter (6.0-7.5 mm.), with medium length internodes (12-14 cm.), and without persistent laterals (dormant lateral canes which developed as shoots from lateral buds in the axils of leaves on current season's growth) were separated into 'light' and 'dark' color categories.[1] Many more single node sections of cane were collected than were used in a test freeze; only those with the lightest and darkest overall bark color were used for 'light' and 'dark', respectively. An attempt was made to quantify cane color by use of the Munsell color charts (Munsell, 1916), but this was found to be impractical, as canes were seldom of uniform enough color to allow this kind of categorization. In this and all subsequent trials, only the fourth or fifth nodes on a cane were used as test material, to minimize any variation in bud hardiness due to node position.

2. Speich vineyard (1-7-77). Cane color hardiness evaluation - Canes were of medium diameter (5.5-6.4 mm.) and medium internode length (12-14 cm.), without persistent laterals.

3. Cronenwett vineyard (4-6-77). Cane color hardiness evaluation - Canes were of medium diameter (5.2-6.6 mm.) and medium internode length (12-14 cm.), without persistent laterals.

[1] The method described for segregation of canes by color was employed for all subsequent evaluations.

4. Rogers vineyard (1-14-77). Cane diameter hardiness evaluation - Canes of medium internode length (12-14 cm.) and without persistent laterals were collected and divided into three categories of cane diameter: small ($\leq$ 5.0 mm.), medium (5.2-6.4 mm.), and large ($\geq$ 6.6 mm.).

5. MSU Hort. Farm (4-1-77). Cane diameter hardiness evaluation - Canes of medium internode length (12-14 cm.) and without persistent laterals were collected and divided into small ($\leq$ 5.7 mm.), medium (6.0-7.5 mm.), and large ($\geq$ 7.8 mm.) diameter categories.

6. Rogers vineyard (1-14-77). Cane internode length hardiness evaluation - Canes of medium diameter (5.2-6.4 mm.) and without persistent laterals were separated into short ($<$ 12 cm.), medium (12-14 cm.), and long ($>$ 14 cm.) categories of internode length.

7. Cronenwett vineyard (3-26-77). Cane internode length hardiness evaluation - Canes of medium diameter (5.2-6.6 mm.) and without persistent laterals were divided into internode length categories as above.

8. Rogers vineyard (1-21-77). Cane persistent lateral status hardiness evaluation - Canes of medium diameter (5.2-6.4 mm.) and medium internode length (12-14 cm.) were collected and divided into three categories of persistent lateral status. These were: short persistent laterals ($\leq$ 5 nodes), long persistent laterals ($\geq$ 6 nodes), and no persistent laterals. Each cane segment contained four buds, which were

evaluated separately. The position of these buds on the cane

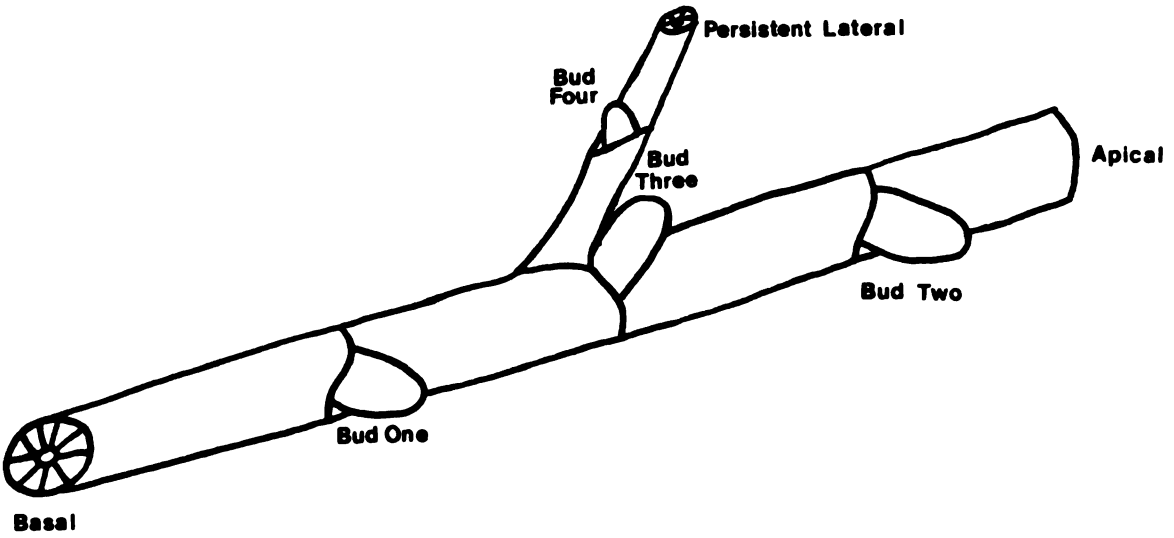


Figure 1. Diagrammatic representation of a segment of dormant grape cane containing a persistent lateral; showing positions of numbered buds.

segments is illustrated in Figure 1.

The following method was used to set categories of cane diameter and internode length. In each vineyard, from 200-300 measurements of diameter and internode length were taken with vernier calipers on randomly selected canes at the middle of the 4th or 5th internodes. Diameter was recorded as the largest of two measurements taken at right angles to each other, and internode length was recorded as the distance from the middle of the 4th internode to the middle of the 5th internode.

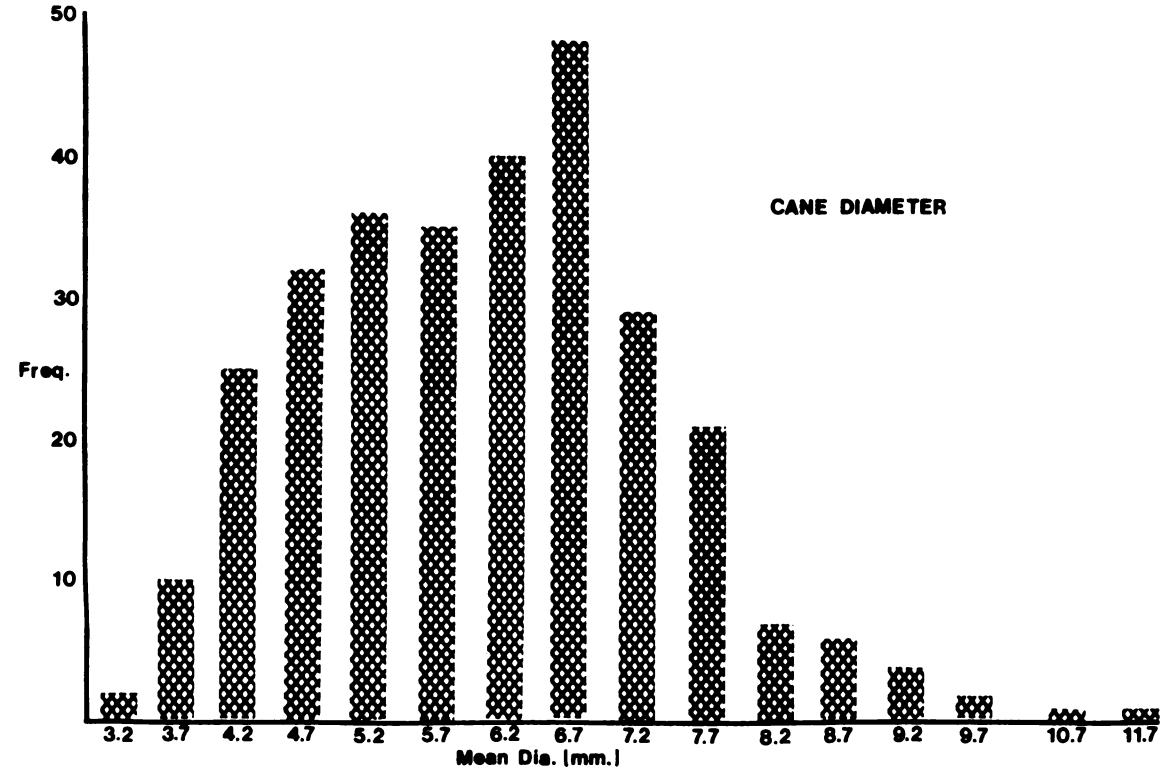
Means for each parameter were calculated every 10 or 20 measurements. Sampling was considered adequate when three consecutive mean determinations did not differ from each other by more than three-hundredths of a millimeter (0.03 mm.) for cane diameter or more than two-tenths of a centimeter (0.2 cm.) for internode length.

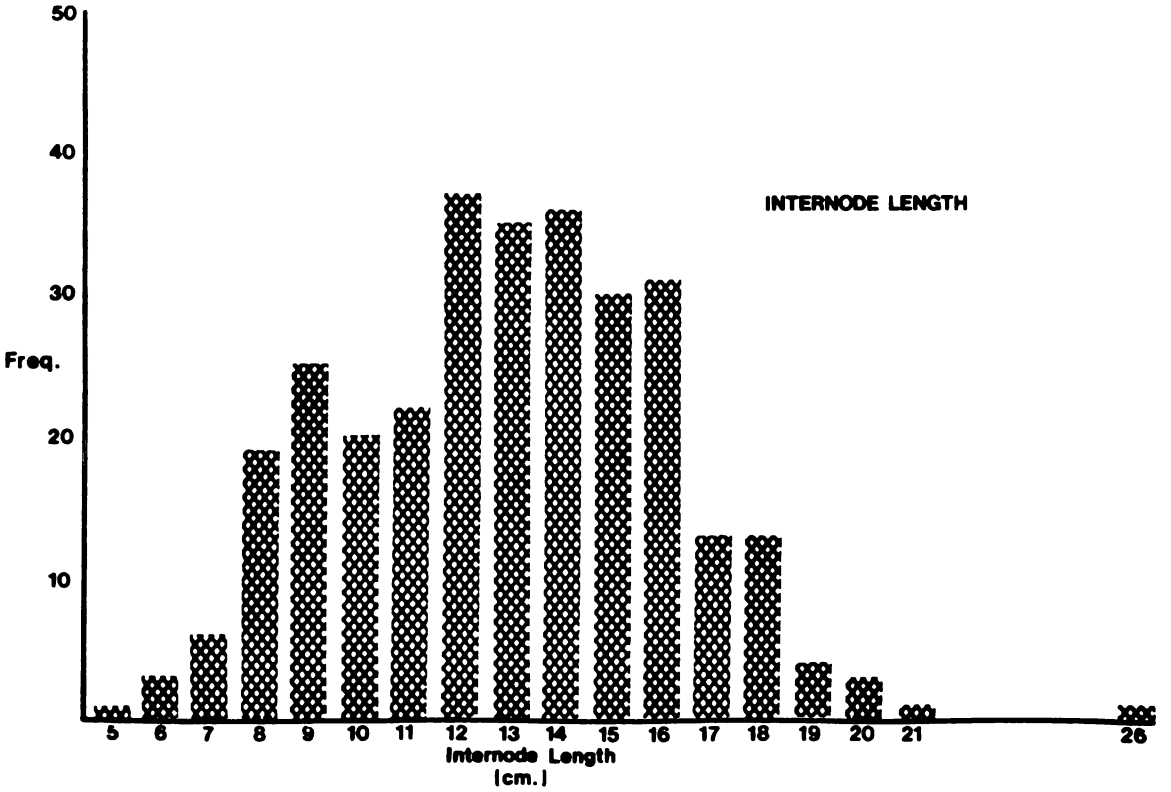
Since all vineyards sampled were of comparable vigor, the range and mean value of internode length was practically identical in all cases, and the same internode length categories were employed for each. Mean cane diameters varied a bit more from vineyard to vineyard, so separate diameter categories were derived for each. In the case of both internode length and diameter, categories were selected so that each contained approximately one-third of the total population of canes in the vineyards. Typical distributions for cane diameter and internode length for moderately vigorous Concord vineyards in SW Michigan during 1977 are presented graphically in Figures 2 and 3. These particular distributions are for the Speich vineyard in Lawton, Michigan.

In addition to materials collected for freezing tests, three field evaluations were conducted at the end of the dormant season, just before bud break, in the years 1977 and 1978. With the exception of persistent lateral status, the same categories were investigated as in the freezing trials. Percent bud mortality for the entire winter was determined for each category. Only primary buds were evaluated.

Figure 2. Distribution of cane diameters between nodes four and six for a moderately vigorous Concord vineyard.

Figure 3. Distribution of cane internode lengths between nodes four and six for a moderately vigorous Concord vineyard.


CANE DIAMETER
Freq.
50
40
30
20
10
3.2
3.7
4.2
4.7
5.2
5.7
6.2
6.7
7.2
7.7
8.2
8.7
9.2
9.7
10.7
11.7
Mean Dia. (mm.)


INTERNODE LENGTH
Freq.
50
40
30
20
10
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
26
Internode Length
(cm.)

General procedure for freezing and analyzing injury to plant material

Sections of dormant canes, when cut and collected in the vineyard, were immediately stored in sealable plastic bags to prevent dessication of the exposed tissues. These bags were kept in portable styrofoam chests on beds of ice to maintain a temperature near 0° C. in transport back to the laboratory. There they were stored at 0° C. until the freezing tests were conducted the following day.

Equal numbers of single node cane sections for each category being tested were wrapped in aluminum foil and placed in thermos-type jugs. The jugs used in any evaluation had previously been selected in a trial run from a larger number of jugs, on the basis of similarity of thermal characteristics. Only those that gave a temperature drop rate of 2-4° C./hr. under conditions identical to those employed in the actual experiments were used. Care was taken to package material so that buds were at the same level (top to bottom) in each jug, so as to minimize the effects of within-jug air stratification on the temperatures of the buds. In addition, four replicates (jugs) for each stress temperature were used, and cane position (inside to outside of jug interiors) was varied for each treatment in each replicate, in case the outside of the jug interiors cooled at a faster rate than the inside.

Freezing trials were conducted in a Revco freezer with

operating range of from above 0° C. to approximately -65° C. The freezer was set at 0° C. at the commencement of any run to correspond to the initial temperature of the material being tested. The temperature of the freezer was manually lowered so as to achieve a rate of temperature drop in the jugs of approximately 3° C./hr. Temperatures of the cane segments in the jugs were monitored with 26-gauge copper-constantan thermocouples attached to a Honeywell Electronik Potentiometer. Jugs were removed when appropriate test temperatures were attained, and placed in a 0° C. storage to thaw gradually.

The range of temperatures used in any test freeze depended upon the date at which the test was conducted. For any date, a range of temperatures was selected to insure that all of the test material would be killed at the lowest temperature, and all of it survive at the highest temperature. A list of test dates and temperature ranges is given in Table 1. In addition to the cane segments that were frozen, an equal number of nodes was held at 0° C. during the freezer runs and later evaluated along with the rest of the material.

The day after a test freeze, the thawed cane sections were placed in humid chambers at room temperature for 7-10 days, to allow time for browning of dead tissues to occur. Buds were then sectioned under a dissecting microscope and evaluated for injury according to the amount and location of brown tissue (Stergios and Howell, 1973). Data were recorded as either dead or alive for primary, secondary, and tertiary buds.

Table 1. Collection dates, categories tested, number of nodes evaluated, number of temperatures, and temperature ranges used for comparing relative hardiness of Concord grape buds on canes of different external morphology during the winter of 1976-77.

Collection date	Categories	Number of nodes	Number of temperatures	Temperature range Max.	Min.
12-10-76	Color	305	4	-20°C	-35°C
1-7-77	Color	72	5	-20°C	-32°C
1-14-77	Diameter Color	222	5	-20°C	-32°C
1-14-77	Internode length Color	234	5	-20°C	-32°C
1-21-77	P.l. status Color	726	5	-20°C	-32°C
3-26-77	Internode length Color	216	5	- 5°C	-21°C
4-1-77	Diameter Color	216	5	- 5°C	-21°C
4-6-77	Color	72	5	- 5°C	-21°C

Determination of critical temperatures and statistical analysis of the data

For each category in each hardiness trial, critical temperatures, calculated as T_{50} values, were computed. T_{50} is defined as the temperature at which 50% of the buds will be killed, and is calculated by means of the Spearman-Kärber equation (Howell and Bittenbender, 1974). Statistical analysis of the raw alive-dead data was accomplished using 2x2 Chi-square contingency tables to compute significant F values for comparison of mortality rates across test temperatures for all combinations of categories at each date (Steel and Torrie, 1960). Yates' correction for continuity was employed in all cases (Steel and Torrie, 1960). Analysis was identical for the three field evaluations except that no T_{50} values could be calculated.

Fruitfulness evaluations

Dormant canes were tagged in 1976-77 for fruitfulness analysis the following fall. Selection criteria for plant material were the same as those used in the cane diameter, internode length, and color, freezing tests. Shoots from tagged nodes were harvested in September 1977. Clusters were counted and weighed, and samples of fruit from each were analyzed for soluble solids content with a hand refractometer. Fruitfulness was determined by dividing the total weight of

the harvested fruit by the total number of tagged nodes bearing shoots. No statistical analysis was performed on this data.

RESULTS

Bud hardiness vs. cane color

Bud hardiness of light and dark canes did not differ significantly in any of the hardiness evaluations. This was true for primary, secondary, and tertiary buds (Tables 2-5). Except for those of small diameter, dark canes did tend to have hardier buds than light canes, at least during midwinter. In the spring, when some deacclimation had occurred, light canes tended to be as hardy or hardier than dark canes. Despite these trends, there was no statistical difference in mortality of buds on light and dark canes pooled across dates, locations, and stress temperatures.

No significant differences in field kill of primary buds on light and dark canes were found in one vineyard on 3-25-77 (Table 6). For the same vineyard the following spring (4-4-78), light canes had significantly less primary bud mortality than dark canes on large diameter canes. For small or medium diameter canes, there was no difference in primary bud kill on light and dark canes.

Table 2. Critical temperatures[a] for canes of different periderm color.

Location/date	Bud	Color	
		Light	Dark
Hort. Farm 12-10-76	1'	-21.4	-23.1 n.s.
	2'	-23.5	-23.7 n.s.
	3'	-23.4	-24.0 n.s.
Speich 1-7-77	1'	-24.5	-26.5 n.s.
	2'	-25.0	-26.5 n.s.
	3'	-26.5	-27.0 n.s.
Cronenwett 4-6-77	1'	-12.3	-13.0 n.s.
	2'	-13.0	-14.3 n.s.
	3'	-14.3	-15.0 n.s.

[a] T_{50}(°C)

Bud hardiness vs. cane diameter

In midwinter, there was no significant difference in hardiness of primary buds on canes of different diameters. On dark canes, secondary buds were significantly hardier on large diameter canes than on small diameter canes. There were no differences in hardiness of tertiary buds (Table 3).

Medium diameter canes, regardless of color, had significantly greater primary bud hardiness than large diameter canes on 4-1-77. For dark canes, primary buds on medium diameter canes were also significantly hardier than on small diameter canes. There were no differences in secondary or tertiary bud hardiness on this date (Table 3).

Large diameter canes had a higher mortality of primary buds than small or medium diameter canes at the end of the winter of 1976-77 (Table 6). Cumulative mortality of primary buds in the same vineyard the following winter was significantly higher for large diameter canes, regardless of periderm color, than for either small or medium diameter canes (Table 6). Large diameter canes also suffered significantly greater primary bud mortality at another location during the winter of 1977-78 (Table 6).

Table 3. Critical temperatures[w] for canes of different diameter.

Location/date[x,y]	Bud	Diameter[z]	Color Light	Color Dark
Rogers 1-14-77	1'	Small	-25.0	-23.5 n.s.
		Medium	-24.0	-26.5 n.s.
		Large	-25.5 n.s.	-27.1 n.s.
	2'	Small	-27.0	-25.0 n.s. b
		Medium	-24.5	-27.5 n.s. ab
		Large	-27.1 n.s.	-30.3 n.s. a
	3'	Small	-27.0	-27.5 n.s.
		Medium	-27.0	-28.5 n.s.
		Large	-27.6 n.s.	-30.3 n.s.
Hort. Farm 4-1-77	1'	Small	-19.0 ab	-13.7 n.s. b
		Medium	-20.3 a	-17.7 n.s. a
		Large	-13.7 b	-10.3 n.s. b
	2'	Small	-19.0	-15.7 n.s.
		Medium	-19.7	-19.0 n.s.
		Large	-18.3 n.s.	-17.7 n.s.
	3'	Small	-19.0	-17.0 n.s.
		Medium	-20.3	-17.7 n.s.
		Large	-19.0 n.s.	-20.3 n.s.

[w] T_{50} (°C)

[z] See 'Materials and Methods' for dimensions

[x] Within rows, means followed by same letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means with same letter not significantly different by Chi-square analysis at F=.05

Bud hardiness vs. cane internode length

There were no significant differences in hardiness of primary, secondary, or tertiary buds among canes of different internode lengths on either date (Table 4).

Bud hardiness vs. persistent lateral status

For dark canes, primary buds in node one (Figure 1) were less hardy on canes with long persistent laterals than on canes with short persistent laterals (Table 5). Otherwise, hardiness of primary, secondary, and tertiary buds was statistically identical regardless of persistent lateral status or node position on the cane.

Fruitfulness of various cane types

Fruitfulness (yield/node) tended to increase with cane diameter and was considerably higher for dark canes than for light canes (Table 7).

Table 4. Critical temperatures[a] for canes of different internode lengths.

Location/date	Bud	Internode length[b]	Color Light	Color Dark
Rogers 1-14-77	1'	Short	-26.5	-27.0 n.s.
		Medium	-24.0	-26.5 n.s.
		Long	-26.0	-26.5 n.s.
			n.s.	n.s.
	2'	Short	-28.5	-27.5 n.s.
		Medium	-24.5	-27.5 n.s.
		Long	-28.0	-27.5 n.s.
			n.s.	n.s.
	3'	Short	-29.0	-29.0 n.s.
		Medium	-29.5	-29.5 n.s.
		Long	-29.5	-29.5 n.s.
			n.s.	n.s.
Cronenwett 3-26-77	1'	Short	-17.0	-18.0 n.s.
		Medium	-19.5	-19.5 n.s.
		Long	-20.0	-19.0 n.s.
			n.s.	n.s.
	2'	Short	-18.5	-19.0 n.s.
		Medium	-19.5	-19.0 n.s.
		Long	-19.0	-18.0 n.s.
			n.s.	n.s.
	3'	Short	-21.0	-19.5 n.s.
		Medium	-20.0	-19.5 n.s.
		Long	-20.0	-19.0 n.s.
			n.s.	n.s.

[a] T_{50}(°C)

[b] See 'Materials and Methods' for dimensions

Table 5. Critical temperatures[x] for canes of different persistent lateral status.

Bud	Bud No.[y]	Color	Persistent lateral status[z,w] Short	Long	Absent	
1'	One	Light	-23.5	-25.3	-23.8	n.s.
		Dark	-25.5a	-20.8b	-25.0	ab
	Two	Light	-23.0	-22.3	-23.8	n.s.
		Dark	-22.5	-25.3	-24.5	n.s.
	Three	Light	-25.5	-22.3	-23.7	n.s.
		Dark	-24.0	-22.3	-23.5	n.s.
	Four	Light	-22.5	-23.0	-	n.s.
		Dark	-24.5	-22.3	-	n.s.
			n.s.	n.s.		
2'	One	Light	-25.5	-26.0	-25.8	n.s.
		Dark	-26.5	-23.8	-25.0	n.s.
	Two	Light	-23.5	-24.5	-23.3	n.s.
		Dark	-24.0	-27.5	-24.5	n.s.
	Three	Light	-26.0	-24.5	-25.3	n.s.
		Dark	-24.0	-24.5	-26.0	n.s.
	Four	Light	-23.5	-25.3	-	n.s.
		Dark	-27.5	-23.0	-	n.s.
			n.s.	n.s.		
3'	One	Light	-25.5	-26.8	-26.2	n.s.
		Dark	-27.5	-24.5	-25.0	n.s.
	Two	Light	-25.5	-24.5	-25.3	n.s.
		Dark	-25.5	-29.0	-26.5	n.s.
	Three	Light	-26.5	-25.3	-26.2	n.s.
		Dark	-27.5	-26.8	-27.0	n.s.
	Four	Light	-23.5	-23.8	-	n.s.
		Dark	-24.5	-24.5	-	n.s.
			n.s.	n.s.		

[w] In rows, means followed by same letter not significantly different by Chi-square analysis at P=.05

[x] T_{50}(°C) [y] See Figure 1 for explanation, p.23

[z] See 'Materials and Methods' for dimensions

Table 6. Percent primary bud mortality of different cane types.

Internode length[u]	MSU Hort. Farm 3-25-77 Color	Diameter[u] Small	Medium	Large
Short	Light	11.1	17.1	33.3 n.s.
	Dark	10.3	4.6	50.0[v] n.s.
		n.s.	n.s.	n.s.
Medium	Light	6.3	12.3	25.0[v] n.s.
	Dark	17.7	14.3	22.2 n.s.
		n.s.	n.s.	n.s.
Long	Light	0.0[v]	3.5	37.5 n.s.
	Dark	0.0[v]	8.6	18.2 n.s.
		n.s.	n.s.	n.s.

Color	MSU Hort. Farm 4-4-78 Diameter[w] Small	Medium	Large[x,y]
Light	5.9a	6.1a	22.9b A
Dark	1.9a	7.8a	54.5b B
	n.s.	n.s.	

Cronenwett vineyard 4-4-78 Diameter[w,z,x] Small	Medium	Large
5.1a	4.5a	30.7b

[u]See 'Materials and Methods' for dimensions

[v]Based on very small sample sizes due to relative scarcity of these categories

[x]Within rows, means followed by same letter not significantly different by Chi-square analysis at F=.05

[y]Within columns, means with same letter not significantly different by Chi-square analysis at F=.05

[z]Cane colors not segregated for this evaluation

[w]1977 dimensions used. See 'Materials and Methods'

Table 7. Fruitfulness of different cane types (9-12-77).[a]

Diameter[b]	Internode length[b]	Color	Yield[c]
Small	Medium	Light	90.0
		Dark	133.0
Medium	Short	Light	138.8
		Dark	215.8
Medium	Medium	Light	83.8
		Dark	53.4
Medium	Long	Light	170.3
		Dark	292.0
Large	Medium	Light	176.3
		Dark	219.7

[a]Cronenwett vineyard - Lawton, Michigan
[b]See 'Materials and Methods' for dimensions
[c]Grams/node

DISCUSSION

Partridge (1925) found that medium diameter canes (6.7 mm.) with long internodes (18 cm.) were the most fruitful on Concord grapevines. Cane morphology-fruitfulness data obtained in this study are in general agreement with these findings (Table 7), if the different ranges of values for diameter and internode length employed in the two studies are taken into account. The one puzzling thing in my study is that medium diameter, medium internode canes had the lowest fruitfulness of all categories (Table 7). Because this category was the most common one on the vines, it was probably undersampled. The accuracy of fruitfulness values for these canes is thus suspect.

It appears that dark periderm color is indicative of superior fruitfulness of the primary buds. Partridge did not measure fruitfulness as related to cane color. If dark color reflects good exposure to sunlight, then the greater fruitfulness of dark canes could be the result of improved cluster initiation and fruit set, both of which benefit from good leaf exposure and high rates of photosynthesis (Buttrose, 1974; Hopping, 1977).

Relationships between cane morphology and bud hardiness were not very clear. The decided advantage in hardiness of dark canes reported by Howell (unpublished data) for Concord grapevines in New York did not exist among the vines sampled

for this study. However, the extremes of periderm color present on the more vigorous vines used in his study were not present on my vines (Howell, personal communication). This could explain the trend toward greater hardiness in dark canes, but the lack of any significant differences (Tables 2-5).

The superior hardiness of light canes in the spring (Table 3) might reflect a tendency toward delayed deacclimation in these canes. This could be the result of lower levels of carbohydrate reserves due to poorer exposure and depressed rates of photosynthesis and storage at these nodes.

The degree to which optimum exposure, as evidenced by dark cane color, plays a role in determining ultimate bud fruitfulness or hardiness could explain the stronger relationship between fruitfulness and cane color than between hardiness and cane color. Adequate sunlight is certainly necessary for both fruitfulness and hardiness. The determination of bud fruitfulness, however, would be influenced by exposure for longer periods of time than the acclimation of buds to cold temperatures. Exposure during the entire growing season in which clusters are initiated is important to fruitfulness, as is exposure during the following spring, when floral organs are being differentiated and the ultimate viability of pollen and ovules is being influenced (Pratt, 1971). The entire process of acclimation to cold, on the other hand, can be achieved in a period of weeks in late fall (Levitt, 1972). Furthermore, the hardiness of buds is but one determinant of the overall fruitfulness of a cane.

Large diameter canes were less hardy than medium diameter canes (Tables 3,6). Johnson (1978) found the same relationship between bud hardiness and cane diameter for susceptibility to spring frosts. Very large canes are often produced on vines which have been overpruned. Overpruning favors rank vegetative development, late-season shoot growth, and poor cane maturity. This leads to poor survival of the buds on these canes. The relationship between large diameter and poor hardiness may thus reflect the inverse relationship between freezing tolerance and development known to exist for plant tissues (Levitt, 1972).

Hardiness could not be related to internode length or persistent lateral status of the canes. Partridge (1925) found no clear relation between internode length and fruitfulness, due to the great variability in internode lengths within individual canes. He did find that laterals on large diameter canes were more fruitful than nodes of the parent cane, and hinted at the greater frost hazard of these nodes due to their tendency to break bud earlier in the spring.

SUMMARY AND CONCLUSIONS

The relationship between external cane morphology and bud fruitfulness and hardiness was investigated on Concord grapevines. The most fruitful buds tended to be on medium or large diameter canes with dark periderm. Primary bud survival was best on medium or small diameter canes.

Since yields are determined by bud fruitfulness and survivability, cultural practices must be employed that produce both the optimum type of shoot growth, and select the best type of canes to bear future crops. Knowledge of relationships between cane morphology and bud fruitfulness and hardiness are thus crucial to wise vineyard management. Improper pruning or training could translate into large reductions in yields, and consequently profits.

Based on the results of this study, selection of medium diameter canes of dark color at pruning would result in the highest yields. During the growing season, practices which favor good canopy exposure, such as shoot positioning, would be advisable.

SECTION II

THE EFFECTS OF CONTROLLED DEFOLIATION AND SHADING IN CONCORD GRAPEVINES

INTRODUCTION

All aspects of grapevine growth and development depend on energy derived from the products of photosynthesis. During the latter part of the growing season, several events take place within the vine which require carbohydrate supplies to proceed normally. Fruit, buds, shoots, trunks, and roots all compete for the limited amounts of photosynthate available from the leaves.

If environmental conditions are favorable, the leaves have little trouble meeting the needs of all these carbohydrate sinks. Often, however, the vines are under some degree of stress, either as a result of unusual weather conditions or because of the effects of careless vineyard management. As mentioned earlier, premature defoliation or a reduction in effective photosynthetic area within the vine canopies can be results of such stress.

This study investigates the effects of defoliation and light reduction at veraison on certain key developmental aspects of vine growth. Knowledge of such stress effects not only helps in planning sound viticultural programs, but contributes to an overall understanding of the nature of specific physiological events in grapevines.

MATERIALS AND METHODS

Plant material and experimental design

Vines used in this experiment were mature, fully bearing Concord grapevines growing at the MSU Horticultural Research Farm in East Lansing, Michigan. Individual vines were selected on the basis of comparable vine size (determined by the weight of one-year-old prunings removed the previous winter). A total of 64 vines were divided among four replicates (blocks) in a randomized complete block design. Two vines, adjacent to each other in each block, were assigned to each treatment. Treatments were assigned to vine pairs randomly within blocks. At least one non-treatment vine intervened between treatment vine pairs in all cases. Vines had been balance-pruned since their original planting, and were trained on a Hudson River Umbrella system of trellising. The eight treatments applied to the vines were as follows:

1. 100% defoliation - all leaves were removed from the vines.

2. 50% defoliation; alternate cordons - all leaves were removed from entire trunks of the vines. Vines were generally trained on two trunks, one extending in either direction from the vine's center along the top wire as 'arms', or cordons. Where a vine had only a single trunk, this had been trained

such that the trunk divided at, or slightly below, the top wire, and the two divisions continued in opposite directions on the top trellis wire as the two 'arms', or cordons, of the vine. In this case one of the two cordons was completely defoliated.

3. 50% defoliation; alternate shoots - all leaves on alternate shoots of the entire vines were removed. Thus, starting at the end of one cordon, working toward the center of the vine, and then out to the end of the other cordon, leaves were removed from entire shoots in an "on-off-on-off..." fashion.

4. 50% defoliation; alternate leaves - every other leaf on all shoots of the entire vines was removed. The first leaf occurring at the base of any shoot was retained (a few basal nodes had naturally abscised their leaves), and the others were removed in an "off-on-off-on..." fashion.

5. 50% shade - vines were covered with a tent made of green saran material that freely admitted air and transmitted 50% of photosynthetically active radiation. The tents were placed over the vines on wooden frames attached to the line posts in the rows and secured to the ground by rope and stakes. No foliage was removed.

6. 100% defruited - vines had all fruit clusters removed. No foliage was removed.

7. Control - no foliage or fruit was removed, nor was shade applied. Lateral shoots were removed from this and all of the above treatments to ensure a greater degree of homogeneity among shoots on treatment vines.

8. Laterals - no foliage or fruit was removed, nor was shade applied. Lateral shoots were retained. This treatment was included for purposes of comparison with control only.

All treatments were applied on 8-17-77, when approximately 10-15% of the fruit on all vines had undergone veraison (color change from green to bluish-purple, associated with the onset of the final stage of grape berry development). New leaves that appeared on shoots of defoliated vines were not subsequently removed, but these were very few and never attained more than one-fourth to one-third mature size.

Measurement of data

Intensity of incident solar energy was measured at several points, both inside and outside the saran tent, on shaded vines, for both cloudless and overcast days, with a Lambda Instruments Corp. Li-Cor light meter with quantum sensor and digital integrator. Temperature records were kept for both control and shaded vine canopy interiors during the course of the experiment with 7-day recording thermographs and maximum-minimum thermometers.

Soluble solids content of the fruit was measured with a hand refractometer on 8-17-77 and 9-3-77. Samples were collected from the two apical-most berries from each of four randomly selected basal clusters. A method very similar to this is recommended for sampling grapes by researchers in New York (Shaulis, 1956).

The entire crops of all vines were harvested on 9-20-77. Clusters were counted and weighed, and fruit soluble solids were measured. Berry weights were calculated by weighing samples of 50 berries collected from the 10 apical-most berries on 5 randomly selected basal clusters, and dividing by 50. By using only apical berries from basal clusters for soluble solids and berry weight determinations, sampling error among the various treatments was kept to a minimum. Vines split by one of the three 50% defoliation treatments were harvested separately for foliated and defoliated nodes.

Counts were made of total number of foliated nodes (those with fully expanded leaves) and total number of count nodes (nodes retained on dormant one-year-old canes at the previous winter's pruning, from which the bulk of the crop is produced) for each vine. In the case of vines split by one of the 50% defoliation treatments, the tallies for count nodes retained were made separately for the foliated and defoliated portions of the vines.

One-year-old dormant canes were sampled from each vine on three dates during the winter of 1977-78 for bud hardiness evaluations. Vines split by 50% defoliation treatments were sampled separately for foliated and defoliated nodes. Nodes from all sampled canes were segregated on the basis of position on the cane. Basal nodes (1-4), middle nodes (5-8), and apical nodes (9-12) were analyzed separately. After sampling for the final hardiness evaluation, vines were balance-pruned and total number of retained nodes was recorded for each.

Handling of cane segments and freezing technique was identical to that employed in the cane morphology hardiness evaluations of 1976-77, with minor exceptions. Instead of freezing test materials in thermos-type jugs, modified styrofoam chests were utilized, into which the foil wrapped bundles of cane sections were placed. This change was necessitated by the larger number of treatments involved in this experiment. Additionally, a Part-Low cam driven temperature programming unit was installed on the Revco freezer to allow automatic operation of the freezer during hardiness runs. A newer model Honeywell Electronik Recording Potentiometer replaced that used in the earlier experiments. This instrument kept a continuous printout of cane temperatures by monitoring up to 24 thermocouples embedded in the canes inside the styrofoam boxes. Post-freezing handling of test materials did not differ from 1976-77. Tissue browning was again used as the basis for assessing freeze-induced injury. A list of dates and temperature ranges for these hardiness evaluations is given in Table 1.

Cumulative winter kill of primary buds was assessed in May 1978, by counting all primary buds on treatment vines that failed to develop, and dividing by the total number of retained buds. Separate totals were obtained for each portion of split-defoliated vines. During bud development ratings were made of the stage of development of all primary buds. Buds were rated as dormant (no visible signs of activity), scale-crack (bud scales beginning to separate), swell-one (scales separated

Table 1. Collection dates, number of nodes evaluated, number of temperatures and temperature ranges used for determining Concord grape bud hardiness during the winter of 1977-78.

Collection date	Number of nodes	Number of temperatures	Temperature range Max.	Min.
1-9-78	264	5	-16°C	-32°C
2-18-78	264	5	-18°C	-34°C
4-3-78	264	5	- 4°C	-20°C

and bud exposed and swollen to a small, greenish-brown globe), swell-two (bud markedly elongated and green or pink with a pink tip), or burst (first leaves beginning to separate from the bud). Comparisons among treatments were then made to ascertain if any differences in rate of bud development existed, as manifested in the percentages of buds remaining dormant at the time of evaluation. All buds ranked dormant at the initial assessment were later re-checked to make sure that none of them were actually dead. Those that proved to be dead were subtracted from the total for dormant buds obtained at the first count.

Estimates of onset of full bloom were made by counting the numbers of open and total flowers on several flower clusters from non-treatment vines, until reasonable estimates could be obtained by visual approximation of the percent bloom of a given cluster. Estimated percent bloom was then recorded for three days during the bloom period.

Soluble solids of developing fruit was measured during the 1978 growing season. Five samples were obtained at roughly equal intervals of time beginning $3\frac{1}{2}$ weeks before veraison and ending at harvest. Sampling technique was identical to that employed in 1977. The 1978 crop was harvested on 9-29-78, and the same measurements were taken as in the previous fall. Techniques of measurement were also the same, except that berry weights were calculated from samples of 25 berries, instead of 50. In addition, fruitfulness measurements were taken, by dividing the total yield of each vine by the number of retained

nodes, and by the number of shoots, on the vine.

Analysis of data

Data analysis for all hardiness evaluations was conducted exactly as for the cane morphology experiments of 1976-77. Critical temperatures were calculated, and statistical analysis was by Chi-square using the discrete injury data. Comparisons among treatments for cumulative percent primary bud mortality and bud development in the spring were also made by Chi-square. Yates' correction for continuity was again employed. All other data was analyzed by Analysis of Variance (AOV) for a randomized complete block design with 10 treatments (all except laterals, with the foliated and defoliated sides of 'split' vines treated separately) and 4 replicates (blocks). Comparisons between control and laterals were not analyzed statistically. Mean comparisons among all treatments analyzed by AOV were made by Duncan's New Multiple Range Test, at the 5% level of significance.

RESULTS

Conditions within shaded vine canopies

Measurements of incident light energy outside and inside saran tents of shaded vines confirmed that approximately 50% light reduction was provided by the shading material used. The actual (mean) figure was 48.4%. Air temperatures within canopies of shaded vines never varied by more than a few degrees from temperatures within control vine canopies (Appendix A). Differences in yield, fruit maturity, or bud hardiness found for shaded vines were thus taken to be primary effects of light reduction.

Soluble Solids 1977

No significant differences in fruit soluble solids existed among treatments at the initiation of the experiment (Table 2).

After 16 days, effects of severe defoliation on fruit soluble solids and evidence for altered translocation of photosynthate within stressed vines had already appeared. The increment in soluble solids over this period for fruit from defoliated cordons was significantly higher than that for fruit from completely defoliated vines, but was significantly lower

than all other treatments, except shade and defoliated shoots. No other differences among treatments existed on this date (Table 2).

At harvest, several significant differences existed among the treatments for fruit soluble solids (Table 2). The four lowest values (in increasing order) were for completely defoliated, defoliated cordon, shaded, and defoliated shoot vines. Thus, on defoliated vines, severity of stress was directly related to both the amount of defoliation and (for partly defoliated vines) the distance between foliated and defoliated portions of the vines.

Evidence for transport of photosynthate from foliated to defoliated nodes within stressed vines is best seen in the total change in soluble solids of the fruit from veraison to harvest (Table 2). Defoliated cordons had a total increment significantly greater than completely defoliated vines (more than twice as great), yet significantly lower than all other treatments. For the 17 days just prior to harvest (9-3 to 9-20) the only significant difference was for completely defoliated vines, which had a lower increase than all other treatments. The presence of lateral shoots did not seem to have any effect on post-veraison increase in soluble solids. Laterals and control showed practically identical increases (Table 2).

Table 2. Fruit soluble solids 1977.[v]

Treatment	Soluble solids[w] 8-17	9-3	Inc.[x]	9-20	Inc.[y]	Inc.[z]
Defruited	8.63	-	-	-	-	-
100% defol.	8.68	9.44	0.76c	11.20e	1.76b	2.52c
50% shade	8.82	12.16	3.34ab	15.26c	3.10a	6.44a
Alt. shoot (Fol.)	8.86	12.66	3.80a	16.07bc	3.41a	7.21a
Alt. shoot (Defol.)	8.86	12.18	3.32ab	15.49c	3.31a	6.63a
Alt. leaf (Fol.)	9.03	12.51	3.48a	15.77c	3.26a	6.74a
Alt. leaf (Defol.)	9.03	12.51	3.48a	15.91bc	3.40a	6.88a
Alt. cordon (Fol.)	9.05	13.21	4.16a	16.69ab	3.48a	7.64a
Alt. cordon (Defol.)	9.05	11.15	2.10b	14.19d	3.04a	5.14b
Control	9.64 n.s.	13.81	4.17a	16.98a	3.17a	7.34a
Laterals	10.20	14.73	4.53	17.56	2.83	7.36

[v]Grams/100 grams fruit

[w]Within columns, means followed by same letter not significantly different at p=.05 by Duncan's multiple range test

[x]Change in soluble solids from 1st to 2nd sampling dates

[y]Change in soluble solids from 2nd to 3rd sampling dates

[z]Change in soluble solids from 1st to 3rd sampling dates

1977 yield

All treatments were statistically the same in yield of fruit per node, except for the defoliated portion of alternate leaf vines, which yielded significantly higher than completely defoliated vines (Table 3). However, alternate leaf vines carried a heavier crop load than other treatment vines during the 1977 growing season (Appendix D), and at least some of the higher yield of these vines probably reflects this. Therefore, it appears that increases in fruit soluble solids (primarily sugars), and increases in fruit non-solids (primarily water) are not that closely related. The correlation coefficient for 1977 yield and post-veraison increase in soluble solids was r=0.52, which is non-significant (Appendix C).

Berry weight and sugar/berry 1977

Berry weight was significantly reduced in completely defoliated vines only (Table 4). All other treatments had heavier berries.

The data for sugar per berry emphasizes the importance of post-veraison ripening in the cycle of berry development. All treatments were significantly greater than 100% defoliation. Control, foliated shoots, and foliated cordons had significantly higher sugar per berry than defoliated cordons, but foliated and defoliated sides of alternate shoot and alternate leaf vines did not differ significantly from each other (Table 5).

Table 3. 1977 and 1978 fruit yield[y]

Treatment	1977 yield[z]	1978 yield[z]	% change
Defruited	-	258.88a	-
100% defol.	124.80b	25.68c	-79.4
50% shade	135.60ab	240.48a	+77.3
Alt. shoot (Fol.)	144.35ab	253.28a	+75.5
Alt. shoot (Defol.)	155.38ab	239.03a	+53.8
Alt. cordon (Fol.)	190.28ab	236.18a	+24.1
Alt. cordon (Defol.)	149.23ab	152.53b	+ 2.2
Alt. leaf (Fol.)	183.23ab	237.70a	+29.7
Alt. leaf (Defol.)	196.88a	233.25a	+18.5
Control	136.40ab	269.68a	+97.7
Laterals	127.26	257.18	+102.1

[y]Grams fresh weight/node retained

[z]Within columns, means with the same letter not significantly different at p=.05 by Duncan's multiple range test

Table 4. 1977 and 1978 berry weight.[y]

Treatment	1977 berry weight[z]	1978 berry weight[z]
Defruited	-	3.09ab
50% shade	3.24a	3.01ab
100% defol.	2.80b	2.68c
Alt. cordon (Defol.)	3.46a	3.14a
Alt. cordon (Fol.)	3.37a	3.01ab
Alt. shoot (Defol.)	3.48a	3.03ab
Alt. shoot (Fol.)	3.38a	2.95ab
Alt. leaf (Defol.)	3.27a	2.99ab
Alt. leaf (Fol.)	3.23a	2.92b
Control	3.43a	3.00ab
Laterals	3.25	2.91

[y]Grams

[z]Within columns, means followed by the same letter not significantly different at p=.05 by Duncan's multiple range test

Table 5. 1977 and 1978 sugar per berry.[y]

Treatment	1977 sugar/berry[z]	1978 sugar/berry[z]
Defruited	-	0.4595ab
50% shade	0.4930cd	0.4608ab
100% defol.	0.3133e	0.4723ab
Alt. cordon (Defol.)	0.4905d	0.4943a
Alt. cordon (Fol.)	0.5633ab	0.4665ab
Alt. shoot (Defol.)	0.5383abcd	0.4710ab
Alt. shoot (Fol.)	0.5430abc	0.4443ab
Alt. leaf (Defol.)	0.5193bcd	0.4683ab
Alt. leaf (Fol.)	0.5095cd	0.4415ab
Control	0.5818a	0.4370b
Laterals	0.5698	0.4433

[y]Grams

[z]Within columns, means followed by the same letter not significantly different at p=.05 by Duncan's multiple range test

Photosynthetic activity and transport in defoliated vines

The fact that defoliation of parts of vines did not prevent accumulation of sugars in the fruit proves that import of assimilate into the clusters continued in the absence of the leaves that would normally feed them. That some of the increase can be attributed to sources other than photosynthate from the leaves is demonstrated by the slight degree of sugar accumulation that occurred even in completely defoliated vines after their leaves had been removed. Normal maturation of fruit on partly defoliated vines (with the exception of a small but significant reduction in the increase of sugars in fruit from defoliated cordons) shows that the bulk of the increase was due to photosynthesis in the remaining leaves. From Table 6, which gives the per leaf contribution of soluble solids to the fruit after veraison, it is suggested that, in the presence of stress (defoliation and the accompanying decrease in source-sink ratio), these leaves responded either by increasing their rate of photosynthesis or the rate at which they shipped assimilate to the ripening fruit (possibly at the expense of storage in other parts of the vines). Even when the possible utilization of vine storage carbohydrate for fruit ripening (taken as the per node contribution to soluble solids of fruit on completely defoliated vines) is discounted, the increased activity of remaining leaves on partly defoliated vines is evident.

Table 6. Per leaf contribution to fruit soluble solids accumulated after veraison in 1977.

Treatment	Increase in soluble solids per leaf[w,x]	
50% shade	0.01141bc	
100% defol.	0.00561c	
Alt. cordon (Defol.)	0.01708b	0.01147[y]
Alt. cordon (Fol.)	0.02533a	
Alt. shoot (Defol.)	0.02447a	0.01886[y]
Alt. shoot (Fol.)	0.02668a	
Alt. leaf (Defol.)	0.02563a	
Alt. leaf (Fol.)	0.02511a	0.01950[y]
Control	0.01405b	
Laterals	0.01097	
Alt. Cordon (whole vine)	0.01840[z]	
Alt. shoot (whole vine)	0.02277[z]	
Alt. leaf (whole vine)	0.02257[z]	

[w]Total change in soluble solids from veraison to harvest divided by the number of foliated nodes on the vine. For partly defoliated vines, denominator for either value (fol. or defol.) is the number of foliated nodes on the whole vine, since these leaves are the sources of the fruit sugars.

[x]Within columns, means followed by the same letter not significantly different at p=.05 by Duncan's multiple range test

[y]The minimum contribution of each leaf, derived by subtracting the value for 100% defoliated vines from the treatment value

[z]Mean of foliated and minimum defoliated values

Bud hardiness during the winter of 1977-78

On all dates, completely defoliated vines were significantly less hardy than all other treatments for primary buds (Table 7). Defoliated cordons also had poorer primary bud hardiness in general, but only on 2-18 was this significantly lower than control. Any differences in primary bud hardiness during January or February, with the exception of 100% defoliation, which continued to be less hardy, had disappeared by early April, when considerable dehardening had taken place in all treatments. Defruited vines, while showing consistently good primary bud hardiness, did not benefit significantly from removal of fruit sinks the previous summer. The presence of lateral shoots did not affect bud hardiness, nor did shade have a significant effect.

Differences among basal, middle, and apical nodes of individual canes for primary buds were non-significant for all treatments on all dates, with the exception of apical nodes on completely defoliated vines, which were significantly less hardy than basal nodes on 1-9-78. An overall trend toward reduced hardiness of apical nodes in stressed vines (100% defoliation, defoliated cordons, and to a lesser extent defoliated shoots) is apparent at all dates (Tables 8-10). This is further borne out in the differences among treatments in hardiness of primary buds at apical nodes on 2-18-78 (Table 9). Differences in primary bud hardiness for this date seem to be largely the reflection of differences in hardiness among apical buds.

Table 7. Critical temperatures[y] of primary buds during the winter of 1977-78.

Treatment	Critical temperature[z] 1-9-78	2-18-78	4-3-78
Defruited	-26.7a	-25.5ab	- 9.8a
50% shade	-25.0ab	-23.8abc	- 8.8a
100% defol.	-15.8c	-16.8d	- 5.5b
Alt. cordon (Defol.)	-23.7b	-22.5c	- 9.0a
Alt. cordon (Fol.)	-24.2ab	-25.4ab	- 9.2a
Alt. shoot (Defol.)	-24.3ab	-23.2bc	- 9.5a
Alt. shoot (Fol.)	-25.0ab	-25.3ab	- 9.9a
Alt. leaf (Defol.)	-23.5b	-25.5ab	- 9.0a
Alt. leaf (Fol.)	-24.8ab	-25.5ab	- 9.5a
Control	-26.0ab	-26.2a	-11.3a
Laterals	-25.3ab	-24.9abc	-10.9a

[y] T_{50} (°C)

[z] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

Table 8. Effects of treatment and node position on hardiness[t] of primary buds on 1-9-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-27.0a A	-26.0a A	-27.0a A
50% shade	-24.5ab A	-25.0a A	-25.5a A
100% defol.	-18.0c A	-15.5b AB	-14.0b B
Alt. cordon (Defol.)	-24.0ab A	-24.5a A	-22.5a A
Alt. cordon (Fol.)	-24.0ab A	-24.0a A	-24.5a A
Alt. shoot (Defol.)	-25.0ab A	-23.0a A	-25.0a A
Alt. shoot (Fol.)	-23.0ab A	-25.5a A	-26.5a A
Alt. leaf (Defol.)	-22.5b A	-24.0a A	-24.0a A
Alt. leaf (Fol.)	-25.0ab A	-25.0a A	-24.5a A
Control	-26.0ab A	-26.0a A	-26.0a A
Laterals[z]	-24.0ab A	-25.5a A	-26.5a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main cane on vines in which lateral shoots were retained and allowed to mature

Table 9. Effects of treatment and node position on hardiness[t] of primary buds on 2-18-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-25.0a A	-25.0a A	-26.5ab A
50% shade	-23.5a A	-23.0a A	-25.0abc A
100% defol.	-17.5b A	-16.0b A	-17.0d A
Alt. cordon (Defol.)	-24.0a A	-22.5a A	-21.0c A
Alt. cordon (Fol.)	-24.5a A	-25.5a A	-26.0ab A
Alt. shoot (Defol.)	-23.0a A	-24.0a A	-22.5bc A
Alt. shoot (Fol.)	-24.5a A	-26.0a A	-25.5ab A
Alt. leaf (Defol.)	-24.5a A	-26.5a A	-25.5ab A
Alt. leaf (Fol.)	-25.0a A	-25.0a A	-26.5ab A
Control	-24.0a A	-24.0a A	-26.5ab A
Laterals[z]	-24.0a A	-24.0a A	-26.5ab A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main cane on vines in which lateral shoots were retained and allowed to mature

Table 10. Effects of treatment and node position on hardiness[t] of primary buds on 4-3-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	- 9.0ab A	-10.3a A	-10.0a A
50% shade	- 9.0ab A	- 8.0a A	- 9.5a A
100% defol.	- 6.0b A	- 6.0b A	- 4.5b A
Alt. cordon (Defol.)	- 9.5ab A	-10.5a A	- 7.0ab A
Alt. cordon (Fol.)	- 7.0ab A	- 9.0a A	-11.5a A
Alt. shoot (Defol.)	-10.0ab A	- 8.5a A	-10.0a A
Alt. shoot (Fol.)	- 8.0ab A	-10.5a A	-11.0a A
Alt. leaf (Defol.)	- 9.5ab A	- 9.0a A	- 8.5ab A
Control	-10.0ab A	-11.0a A	-10.5a A
Laterals[z]	-11.0a A	-10.5a A	-11.0a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main cane on vines in which lateral shoots were retained and allowed to mature

Overall trends and significant differences among treatments for secondary and tertiary bud hardiness were quite similar to those for primary buds (Appendix B). Differences among basal, middle, and apical buds were few but again apical nodes of severely stressed vines seemed to suffer more than basal or middle nodes. Despite the lack of patterns as clear as those for the yield data, it is interesting to note that on all dates, the only treatments with significantly poorer bud hardiness were treatments without leaves. In no instance did a defoliated treatment have significantly better bud hardiness than a foliated treatment.

Within individual compound buds, the same relative hardiness relationship existed on all dates. Tertiary buds were as hardy or hardier than secondary buds, which were as hardy or hardier than primary buds (Appendix B).

Cumulative field kill of primary buds during the winter of 1977-78

The effects of defoliation stress on primary bud hardiness can be seen dramatically in the percentages of primary buds killed during the winter of 1977-78 (Table 11). Nearly 90% of the primary buds on completely defoliated vines were either killed or failed to develop by May 1978, a significantly greater amount than on all other treatments. Defoliated cordons had less than half this mortality rate (41.4%), but this was significantly greater than all remaining treatments. Defoliated shoots and foliated cordons had significantly

greater primary bud kill than control or shaded vines. The pattern for cumulative primary kill is similar to that for accumulation of sugars in the fruit except that foliated cordons, which were able to supply photosynthate to ripen fruit on defoliated cordons with no adverse effects on their own fruit, suffered somewhat in supplying substrate or factors that improved the cold tolerance of defoliated cordons, relative to completely defoliated vines.

Delay of vegetative development in the spring of 1978

Data for percentages of primary buds remaining in the dormant condition on 5-16-78 suggest a delay in spring bud growth with increased defoliation stress (Table 12). Interestingly, while completely defoliated vines had a significantly greater percentage of dormant buds than all other treatments, and seemed to be delayed the most, both sides of alternate cordon and alternate shoot vines were delayed to about the same extent. There was a trend toward slightly greater delay on defoliated portions of these vines, and all four treatments showed significantly greater percentages of dormant buds than control vines. Shaded vines apparently experienced some delay relative to control, but alternate leaf and defruited vines did not.

Observations on the extent of flowering on three successive days in June of 1978 suggested no treatment effect on date of anthesis, which was the same in all cases.

Table 11. Percent primary bud mortality during the winter of 1977-78.

Treatment	Percent primaries killed[y]
Defruited	9.9ab
50% shade	7.3a
100% defol.	88.4d
Alt. cordon (Defol.)	41.4c
Alt. cordon (Fol.)	13.3b
Alt. shoot (Defol.)	14.8b
Alt. shoot (Fol.)	11.6ab
Alt. leaf (Defol.)	8.1ab
Alt. leaf (Fol.)	7.8ab
Control	6.6a
Laterals	12.4b

[y]Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

Table 12. Percent dormant buds on 5-16-78.

Treatment	Percent dormant buds[y]
Defruited	23.8ab
50% shade	29.4bc
100% defol.	68.7e
Alt. cordon (Defol.)	45.2d
Alt. cordon (Fol.)	34.6cd
Alt. shoot (Defol.)	38.0cd
Alt. shoot (Fol.)	31.8bc
Alt. leaf (Defol.)	19.1a
Alt. leaf (Fol.)	20.6a
Control	22.0a
Laterals	26.0ab

[y]Within columns, means with the same letter not significantly different by Chi-square analysis at F=.05

1978 fruit maturation and yield

No significant differences in fruit soluble solids existed prior to veraison in 1978. Time of veraison was not affected by the previous year's treatments. After veraison (Aug. 30), fruit on vines that had been completely defoliated accumulated more sugar, and had significantly higher soluble solids than all other treatments at harvest, probably due to the small amount of fruit and the improved exposure of leaves on these vines (Table 13).

As expected, completely defoliated vines showed a sharp decline in yield in 1978 (Table 3), despite the fact there were no serious frosts in the spring, and that yields in general were considerably higher than in 1977. Defoliated cordons yielded significantly more than completely defoliated vines, but significantly less than all other treatments. Yields for all other treatments were statistically identical.

Much of the reduction in yield for 1978 can be attributed to poor survival of primary buds on severely stressed vines, but a look at the data for yield components reveals other contributing factors. The number of clusters per node of buds that did survive the winter and produce shoots in 1978 was significantly less on completely defoliated vines than on all treatments except defoliated cordons, shade, and foliated shoots. Clusters per node were statistically the same on all other treatments. Control and defruited vines had the greatest numbers of clusters per node (Table 14). The number

of berries per cluster was also significantly reduced on completely defoliated vines (Table 14). Thus, fruitfulness of these vines was affected by reduced number of clusters/shoot, and by poorer berry set in the spring of 1978, as well as by a low bud survival rate. In the case of defoliated cordons, though they tended to have lower clusters per shoot and berries per cluster, relative to control, poor yields in 1978 were apparently due primarily to reduced bud hardiness the previous winter.

In light of the poor yields of severely stressed vines, it is not surprising that completely defoliated vines and defoliated cordons had the highest sugar per berry values in 1978 (Table 5). Only defoliated cordons were significantly higher than control, however, due to significantly lower berry weights on completely defoliated vines (Table 4). This possibly reflects reduced water absorbing capacity of these vines due to poor carbohydrate storage and root growth resulting from complete defoliation the previous summer.

The figures for percent change in yield from 1977 to 1978 show the extent of second year effects of defoliation on yield (Table 3). An increase in yield of nearly 100% for control vines reflects the generally superior growing season in 1978. Completely defoliated vines, which suffered a nearly 80% yield reduction and were nearly killed outright during the winter, attest to the importance of foliage in the latter part of the growing season for normal maturity of shoots. For other treatments, the extent of reduction in yield relative to gains made

Table 13. Fruit soluble solids 1978.[y]

Treatment	Soluble solids[z] 8-3	8-15	8-27		9-7	9-29
Defruited	4.05	4.56	6.53		10.30a	14.88a
50% shade	3.95	4.67	6.33	V	11.22ab	15.30a
100% defol.	4.17	4.75	6.10	E	11.97b	17.50b
Alt. cordon (Defol.)	4.05	4.43	6.19	R A I S	10.74a	15.70a
Alt. cordon (Fol.)	3.90	4.44	6.22	O N	10.79a	15.54a
Alt. shoot (Defol.)	3.93	4.51	6.27	A U	10.68a	15.53a
Alt. shoot (Fol.)	3.98	4.37	6.35	G U	10.64a	15.10a
Alt. leaf (Defol.)	3.87	4.48	6.41	S T	10.68a	15.64a
Alt. leaf (Fol.)	3.91	4.63	6.80	3 0	10.69a	15.12a
Control	3.93	4.54	6.01		10.14a	14.57a
	n.s.	n.s.	n.s.			
Laterals	4.00	4.62	6.47		10.55	15.27

[y]Grams/100 grams fruit

[z]Within columns, means followed by the same letter not significantly different at p=.05 by Duncan's multiple range test

Table 14. 1978 fruitfulness parameters

Treatment	Clusters/node[y, z]	Berries/cluster[z]
Defruited	2.67a	33.63ab
50% shade	2.16ab	32.85ab
100% defol.	1.62b	27.80c
Alt. cordon (Defol.)	2.14ab	30.05bc
Alt. cordon (Fol.)	2.41a	33.73ab
Alt. shoot (Defol.)	2.41a	32.85ab
Alt. shoot (Fol.)	2.24ab	34.63a
Alt. leaf (Defol.)	2.43a	31.40abc
Alt. leaf (Fol.)	2.43a	31.80ab
Control	2.68a	33.00ab
Laterals	2.53	36.18

[y]Number of clusters per shoot that developed from retained buds

[z]Within columns, means with the same letter not significantly different at p=.05 by Duncan's multiple range test

by control vines in 1978 is proportional to the stress (distance between foliated and defoliated portions, or sources and sinks, of the vine). Defoliated cordons showed a very slight improvement over 1977 but certainly fared much better than completely defoliated vines. Foliated cordons, however, showed only a 24.1% increase over 1977, much less than control. Defoliated shoots gained nearly 54% in yield over 1977, while foliated shoots improved by better than 75%, nearly as much as control. Low percent increases for alternate leaf vines probably reflect their heavier crop loads in 1977. Thus, the entire vines, and not just the defoliated portions, suffered second year effects from loss of leaves in 1977. This is further evidence for altered patterns of translocation in these vines as a result of defoliation.

Relationships between hardiness and fruiting parameters

Significant correlations existed between 1977 fruit maturation (post-veraison increase in soluble solids) and susceptibility of primary buds to winter injury in 1977-78 (cumulative percent primary bud mortality). Significant correlations existed between 1977 fruit maturation and 1978 fruitfulness parameters (clusters/node, yield/node retained, yield/shoot, berries/cluster). Significant correlations also existed between 1977-78 primary bud mortality and 1978 fruitfulness parameters (Appendix C).

DISCUSSION

Complete defoliation of Concord grapevines at veraison had an immediate and significant effect on fruit growth and maturity. The 34% reduction in soluble solids (Table 2) and 18% reduction in berry weight (Table 4) are very similar in magnitude to the effects on Sultana vines reported by Kliewer and Antcliff (1970).

Even in the total absence of leaves, fruit on these vines continued to increase in soluble solids content. At harvest, fruit from completely defoliated vines had increased 29% in soluble solids since veraison, accounting for 22.5% of the total sugar in the fruit (Table 2). Fruit on these vines was obviously a powerful enough sink to mobilize sources of carbohydrate in parts of the vine other than the leaves. The magnitude of this mobilization also increased after an initial lag. By harvest time, fruit on defoliated vines was importing sugar at twice the rate that it had been during the first sixteen days after defoliation (Table 2).

There are two possible sources for the sugars accumulated by this fruit. Berries and green shoots are known to photosynthesize, but research by Koch and Alleweldt (1978), and Kriedemann and Buttrose (1971) has shown that photosynthesis is normally less than respiration in these tissues. Unless defoliation stimulated dramatically increased rates of

photosynthesis in shoots and berries, the sugars in the fruit could not have originated in this way. Most likely their origin was in reserve polysaccharides of the vascular parenchyma or roots (Crafts and Crisp, 1971).

The extent of the effects of partial (50%) defoliation depended on the resultant distance between foliated and defoliated portions of the vine, demonstrating the sink power of ripening fruit on Concord grapevines. Clusters on defoliated cordons, removed from sources of photosynthate in remaining leaves by distances as great as 10-12 feet, were able to draw on these sources soon after defoliation had occurred, though at a rate significantly less than that on control vines. The origin of at least some of this assimilate must have been the leaves on the foliated cordons, since the rate of increase was significantly greater than that on completely defoliated vines. During this initial sixteen day post-defoliation period, clusters on defoliated shoots and clusters at foliated nodes of alternate leaf vines (because of the phyllotaxy of the grapevine, clusters at foliated nodes of these vines were those deprived of their normal sources of sugar) imported photosynthate at the same rate as fruit on control vines. Mobilization over these shorter distances was thus very quick and effective, but during the following seventeen day period, clusters on defoliated cordons had increased their rate of importation to that on control vines (Table 2).

Thus, the ripening grape cluster is not only a very powerful sink for photosynthate, but continuous pathways for

transport of assimilate must traverse the entire grapevine, encompassing even greater distances than those reported in earlier work (Winkler, 1932; May et al., 1969). Furthermore, transport must occur in all directions - acropetal, basipetal, and lateral.

Fruit ripened to nearly the same extent on both sides of partly defoliated vines, despite having only half the number of leaves available to supply photosynthate, suggesting that the amount of sugar contributed to the fruit by each leaf on these vines was greater than the per leaf contribution on control vines (Table 6). Either shipment of photosynthate to the fruit was increased at the expense of shipment to other sinks within the vines (trunks, roots, etc.), or the actual rate of photosynthesis in remaining leaves was increased by defoliation stress. Buttrose (1966) has shown that both of these phenomena can occur, and Hofäcker (1978) has reported increases of 20% in the rate of photosynthesis of leaves on vines under stress of partial defoliation. In this study, the per leaf contribution to fruit soluble solids after veraison increased by as much as 62% (for alternate shoot vines), even after discounting the probable contribution of mobilization of reserve carbohydrate by fruit on defoliated portions of the vines (Table 6). Since no measurements of photosynthetic rate or storage carbohydrate were undertaken in this study, the exact nature of this increase cannot be determined.

In two cases out of three (alternate shoots and alternate leaf), the power of the fruit sinks on defoliated portions was

so great that the fruit on the foliated portions suffered somewhat in total soluble solids, relative to control. On alternate cordon vines, fruit on defoliated cordons did not exert a strong enough sink effect to hurt the ripening of the fruit on the foliated cordons (Table 2). It appears that, over short and intermediate distances on the vine, the ability of the ripening clusters to mobilize photosynthate from remaining leaves is greater than the ability of the leaves to accomodate the increased demand, at least within the relatively short period of time allowed by this study.

Shade, applied at veraison, significantly reduced total fruit soluble solids at harvest (Table 2). While a 50% attenuation in light intensity would probably not affect the photosynthesis of well-exposed leaves, those in the interior of the canopy, which barely maintain a net positive CO_2 balance under the best conditions (Kriedemann, 1975), could have been affected. This would be especially true on cloudy or overcast days. Under these conditions, exterior leaves might have to contribute photosynthate to meet the respiratory needs of interior leaves. At the very least, the interior leaves would be eliminated as sources of sugar for the ripening fruit. Interestingly, the per leaf contribution of soluble solids to the fruit after veraison on shaded vines was the lowest of all treatments (Table 6).

Despite the effects of severe defoliation stress on fruit maturity, no treatment differed significantly from control in yield in 1977 (Table 3). Although completely defoliated vines

yielded the least, and had the lightest berries, all of the difference in yield between them and control can be attributed to the greater number of berries per cluster on completely defoliated vines (Appendix D). In other words, while defoliation altered the translocation patterns of photosynthate within vines, it apparently had little or no effect on translocation patterns of water in the vines. This agrees with findings of Kliewer and Antcliff (1970), that berry growth, one aspect of which is cell expansion due in part to water uptake, is not significantly affected unless defoliation is done very early in the developmental cycle of the fruit.

Correlations between critical temperatures and cumulative mortality for primary buds were very high for all three test dates (Appendix C), indicating that the methods employed in artificially stressing plant materials yielded accurate assessments of relative hardiness. The degree to which calculated T_{50} values correspond to actual field hardiness of the buds cannot be determined, but comparison of these values to actual temperatures recorded at the vineyard site for the months of January, February, and April, 1978 (Appendix E), would lead one to estimate mortality rates in fairly close agreement with those that occurred on the vines over the entire winter. This assumes, of course, that the calculated T_{50} values are the actual field T_{50} values, and ignores such factors as relative hardiness during periods not investigated in this study (most notably during acclimation and early winter), possible differences between air and bud temperatures in the field, and the

nature of the temperature-response curves around the theoretical T_{50} values.

The adverse effect of severe defoliation on bud hardiness is in close agreement with the findings of Stergios and Howell (1977) for Concord grapevines and Fuchigami et al. (1977) for Cornus stolonifera. The patterns that emerged, particularly for cumulative primary bud mortality (Table 11), and the high negative correlation between mortality and 1977 fruit maturity (Appendix C), indicate that leaves play a vital role in both ripening the fruit and allowing the vine to acclimate to cold temperatures. In the case of the fruit, the role of the leaves is to provide sugars. This might be the case for hardiness as well, at least in part, depending upon the extent to which sugars, as either indirect, metabolic contributors to cold hardiness, or as direct cryoprotectants, play a role in the hardiness mechanism. Hormonal, or other, factors produced by the leaves might also contribute to hardiness. Whatever their composition, the translocatable nature of these substances is similar to that found for hardiness promoting factors by Fuchigami et al. (1971), Steponkus and Lanphear (1967), and Howell and Weiser (1970).

Defoliation stress appeared to have a greater adverse effect on apical bud hardiness than on hardiness of buds from the basal or middle portions of a cane, particularly on completely defoliated vines and defoliated cordons. It is known that shoot maturation in the fall proceeds acropetally from the base of the shoots (Esau, 1948), so it is conceivable that a limited supply of hardiness promoting factors would reach

apical nodes only after the needs of the rest of the cane had been met.

Differences in bud hardiness were minimal in the early spring, when considerable deacclimation had occurred and metabolic activity in the buds had commenced. This does not suggest the early loss of hardiness by defoliated vines in the spring mentioned by Stergios and Howell (1977), but a slower rate of deacclimation relative to unstressed vines, possibly due to reduced availability of substrate for renewed metabolic activities.

The removal of fruit did not affect the hardiness of buds. Fruit removal resulted in a dramatically increased source-sink ratio, a condition that can cause a decline in the rate of photosynthesis of the leaves (Kriedemann and Lenz, 1972; Hofacker, 1978). Any anticipated improvement in hardiness due to the elimination of strongly competitive sinks for photosynthate could be offset by a reduced activity in the leaves. Since no measurements of hardiness were taken in late fall or early winter, it cannot be stated categorically that defruiting did not have a beneficial effect on hardiness, but such an effect, if it existed, was short-lived.

The cumulative primary bud kill of vines with lateral shoots was significantly greater than control (Table 11), but at no date was the calculated T_{50} different between these two treatments. I believe that the seemingly higher mortality of primary buds on vines with laterals is due to the fact that buds in the axils of lateral canes often do not develop into

shoots, even though they survived the winter, due to the dominance of buds on the lateral canes.

Late-season reduction in light intensity also had no effect on bud hardiness. Enough activity evidently continued in the leaves of shaded vines to provide the necessary substrate and/or factors to adequately harden buds.

The apparent delay in vegetative development in the spring of 1978 associated with defoliation the previous season might reflect a limited amount of storage carbohydrate in stressed vines, on which early growth and development depend. The magnitude of this effect was greater than that for either 1977 fruit maturation or bud hardiness, in that bud development on each side of alternate shoot and alternate cordon vines was delayed to an equal extent (Table 12).

Severe reductions in the 1978 yields of completely defoliated vines and defoliated cordons (Table 3) can be attributed to three factors. Essentially all of the reduction on defoliated cordons was due to winter kill of primary buds. In the case of complete defoliation, this was the primary factor, but defoliation also reduced the number of clusters on shoots that developed from surviving buds, as well as the number of berries in each cluster (Table 14). Cluster primordia develop during the season of bud initiation, so that reduced clusters/shoot in 1978 could be the result of effects in the period between leaf removal and onset of rest in 1977. Alternatively, reduced clusters/shoot could be due to a larger percentage of shoots developing from secondary buds on severely stressed vines. These shoots tend to be less fruitful than primary shoots.

Reduced berries/cluster reflects poor fruit set in completely defoliated vines, which could have resulted from poor differentiation of floral organs. Differentiation of individual floral parts takes place during the spring following cluster initiation, so that low storage carbohydrate levels in completely defoliated vines could be the cause of poor fruit set.

Flowering was not affected by defoliation, but this is not a contradiction of the suggested explanation for poor berry set. Anthesis is strictly a temperature related phenomenon (Pratt, 1971), and reduced carbohydrate reserves would not affect date of full bloom.

It is tempting, in light of the overall effects of defoliation on hardiness and fruitfulness, the significance of correlations among hardiness and fruitfulness parameters, and known facts about the sequence of growth and development in the grapevine, to interpret the findings of this study in terms of the depletion of carbohydrate supplies necessary for the attainment of maximum fruit maturity, bud hardiness, and fruitfulness.

Within the time span encompassed by this experiment, several events took place, in the following sequence: 1) the vines were defoliated; 2) differentiation of cluster primordia in previously initiated buds was completed; 3) the fruit of the 1977 crop underwent its final stage of development; 4) the vines acclimated to cold temperatures and entered a period of rest; 5) deacclimation and renewed metabolic activity leading to spring bud push took place; 6) new shoot growth and differentiation of individual floral organs occurred, leading to

anthesis and fruit set; 7) the 1978 crop completed its development and ripened. The effects of the first event, defoliation, on the subsequent events, are summarized in Figure 1.

A manifestation of severity of defoliation stress was the time of appearance of the first negative effects. For completely defoliated vines, the effects were seen immediately. For partly defoliated vines, the effects were delayed or nonexistant, depending on the extent of the stress. Level of defoliation on these vines was the same (50%), and severity of stress was determined solely by the distance between sources and sinks. If sinks were not close enough to remaining leaves to stimulate adequate increases in production or shipment of carbohydrate to meet all their needs, then stress effects occurred. While factors other than carbohydrate depletion may have accounted for some of the responses, particularly that of bud hardiness, I believe it to be the best explanation of the observed effects, and worthy of further investigation.

Figure 1. 1977-78 calendar of Concord grape development and effects of defoliation.[1]

[1]Bars of different height represent significantly different values, but no other statement about the magnitude of the responses is implied

Clusters/node 1978
Post-veraison SS 1977
Primary bud hardiness '78
Bud push 1978
veraison defol.
harvest
June 1977
July
Aug.
September
Oct.
Nov.
Dec. - March
April
May
1978
control
all leaf defol.
all leaf fol.
all shoot fol.
all shoot defol.
all cordon defol.
all cordon fol.
100 % defol.

SUMMARY AND CONCLUSIONS

The effects of altered source-sink ratios and reduced insolation, achieved by defoliation, defruiting, and shading of Concord grapevines at veraison, were investigated.

Removal of fruit had no effects on vine development. Shading produced minimal adverse effects on bud fruitfulness and fruit maturation. The effects of complete defoliation were devastating to all aspects of vine growth and development into the second year of the study. Partial defoliation reduced fruit maturity, bud hardiness, and bud fruitfulness depending on the severity of defoliation stress, which increased directly with increased distance between foliated and defoliated portions of the vines.

Based on these results, the importance of sound cultural management of vineyards cannot be overemphasized. Diseases, insects, careless use of herbicides, and severe overcropping can all lead to premature leaf-fall. Poorly pruned or trained vines cannot provide optimum exposure for the leaves. To maximize yields of commercially acceptable fruit, practices must be employed which minimize the stresses placed on the growing vines.

APPENDICES

APPENDIX A

Table 1. Light attenuation in shaded vine canopies.[a]

Outside canopy	Inside canopy
27	14
24	14
21	12
45	15
61	29
66	32
40	19
34	19

[a]Values are integrator units and give the relative incident light energy per unit time

Table 2. Temperatures in control and shaded vine canopies.[a]

Date	Temperature Max.	Min.		Date	Temperature Max.	Min.
8-16	84	66		8-16	82	64
-17	80	57		-17	80	56
-18	79	44		-18	79	46
-19	78	42	CONTROL	-19	78	44
-20	79	44		-20	79	45
-21	67	59		-21	67	59
-22	84	55		-22	84	54
-23	74	54		-23	74	56
-24	78	48		-24	79	50
-25	78	47		-25	78	47
-26	86	50		-26	86	52
-27	92	71		-27	93	70
-28	93	70		-28	93	70
-29	81	63		-29	82	62
-30	84	58		-30	85	58
-31	86	60		-31	86	60

[a] F

Table 2 (cont'd.).

9-1	79	70			9-1	79	68
-2	79	66			-2	77	66
-3	79	59	C		-3	79	60
-4	80	60	O	S	-4	79	60
-5	83	56	N	H	-5	82	56
-6	75	62	T	A	-6	76	60
-7	80	52	R	D	-7	80	51
-8	81	58	O	E	-8	82	58
-9	79	61	L		-9	82	61
-10	80	58			-10	82	57
-11	72	51			-11	71	49
-12	77	46			-12	76	46
-13	70	50			-13	71	49
-14	61	56			-14	60	55
-15	72	48			-15	72	48

[a] ^{o}F

APPENDIX B

Table 1. Effects of treatment and node position on hardiness[t] of secondary buds on 1-9-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-29.5a A	-26.5a A	-28.0ab A
50% shade	-28.5ab A	-27.0a A	-28.0ab A
100% defol.	-18.0c A	-17.0b AB	-14.5c B
Alt. cordon (Defol.)	-26.0b A	-28.0a A	-24.0b A
Alt. cordon (Fol.)	-27.5ab A	-27.5a A	-27.5ab A
Alt. shoot (Defol.)	-27.5ab A	-26.0a A	-27.0b A
Alt. shoot (Fol.)	-27.0ab A	-29.0a A	-29.0a A
Alt. leaf (Defol.)	-25.5b B	-29.0a A	-28.5ab AB
Alt. leaf (Fol.)	-28.5ab A	-28.0a A	-28.5ab A
Control	-28.0ab A	-28.5a A	-27.5ab A
Laterals[z]	-28.0ab A	-28.0a A	-29.0a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main cane on vines in which lateral shoots were retained and allowed to mature

Table 2. Effects of treatment and node position on hardiness[t] of secondary buds on 2-18-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-28.0a A	-27.5a A	-27.5a A
50% shade	-27.0a A	-27.0a A	-28.0a A
100% defol.	-18.5b A	-16.0b A	-18.0b A
Alt. cordon (Defol.)	-26.0a A	-27.0a A	-26.0a A
Alt. cordon (Fol.)	-26.5a A	-27.0a A	-28.5a A
Alt. shoot (Defol.)	-25.5a A	-26.0a A	-24.5a A
Alt. shoot (Fol.)	-28.0a A	-27.0a A	-27.0a A
Alt. leaf (Defol.)	-25.5a A	-27.5a A	-27.5a A
Alt. leaf (Fol.)	-26.0a A	-27.0a A	-28.0a A
Control	-26.0a A	-27.0a A	-28.0a A
Laterals[z]	-26.0a A	-26.5a A	-28.0a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main cane on vines in which lateral shoots were retained and allowed to mature

Table 3. Effects of treatment and node position on hardiness[t] of secondary buds on 4-3-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-12.5a A	-11.5a A	-10.0a A
50% shade	-11.0ab A	-10.5ab A	-11.0a A
100% defol.	- 7.0b A	- 6.5b A	- 4.5b A
Alt. cordon (Defol.)	-11.0ab A	-12.5a A	- 9.0a A
Alt. cordon (Fol.)	-10.0ab A	-13.0a A	-12.0a A
Alt. shoot (Defol.)	-13.5a A	-11.0a A	-12.0a A
Alt. shoot (Fol.)	-12.0a A	-13.5a A	-11.5a A
Alt. leaf (Defol.)	-12.0a A	-12.5a A	-11.5a A
Alt. leaf (Fol.)	-10.5ab A	-10.5ab A	-12.0a A
Control	-11.5ab A	-12.0a A	-10.0a A
Laterals[z]	-11.5ab A	-11.0a A	-11.0a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main cane on vines in which lateral shoots were retained and allowed to mature

Table 4. Effects of treatment and node position on hardiness[t] of tertiary buds on 1-9-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-29.5a A	-29.0a A	-28.5ab A
50% shade	-28.5ab A	-27.5a A	-28.5ab A
100% defol.	-19.5c A	-17.0b AB	-15.5c B
Alt. cordon (Defol.)	-28.0ab A	-27.0a A	-25.5b A
Alt. cordon (Fol.)	-26.5ab A	-27.0a A	-28.5ab A
Alt. shoot (Defol.)	-27.5ab A	-27.5a A	-27.0ab A
Alt. shoot (Fol.)	-27.5ab A	-29.0a A	-28.0ab A
Alt. leaf (Defol.)	-26.0b A	-28.0a A	-28.5ab A
Alt. leaf (Fol.)	-28.0ab A	-28.5a A	-29.0ab A
Control	-29.0ab A	-28.5a A	-28.5ab A
Laterals[z]	-28.5ab A	-28.0a A	-30.5a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main canes on vines in which lateral shoots were retained and allowed to mature

Table 5. Effects of treatment and node position on hardiness[t] of tertiary buds on 2-18-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-28.5a A	-27.5a A	-28.5a A
50% shade	-25.5a A	-28.0a A	-28.5a A
100% defol.	-18.0b A	-16.5b A	-18.0b A
Alt. cordon (Defol.)	-26.5a A	-27.5a A	-26.5a A
Alt. cordon (Fol.)	-26.5a A	-27.5a A	-29.0a A
Alt. shoot (Defol.)	-26.5a A	-25.0a A	-26.5a A
Alt. shoot (Fol.)	-28.0a A	-28.5a A	-27.0a A
Alt. leaf (Defol.)	-26.0a A	-27.5a A	-29.0a A
Alt. leaf (Fol.)	-27.0a A	-27.0a A	-28.5a A
Control	-25.5a A	-28.0a A	-28.5a A
Laterals[z]	-26.0a A	-27.5a A	-28.0a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main canes on vines in which lateral shoots were retained and allowed to mature

Table 6. Effects of treatment and node position on hardiness[t] of tertiary buds on 4-3-78.

Treatment	Critical temperature[t,x,y] Basal nodes[u]	Middle nodes[v]	Apical nodes[w]
Defruited	-13.0a A	-11.8ab A	-12.5a A
50% shade	-11.5a A	-10.5ab A	-11.0a A
100% defol.	- 7.0b A	- 8.0b A	- 6.0b A
Alt. cordon (Defol.)	-12.5a AB	-13.0a A	- 8.5ab B
Alt. cordon (Fol.)	-11.0ab A	-13.0a A	-13.0a A
Alt. shoot (Defol.)	-13.5a A	-12.0ab A	-12.5a A
Alt. shoot (Fol.)	-12.5a A	-13.0a A	-11.5a A
Alt. leaf (Defol.)	-13.0a A	-12.0ab A	-12.5a A
Alt. leaf (Fol.)	-11.0ab A	-11.5ab A	-12.0a A
Control	-11.0ab A	-11.5ab A	-10.5a A
Laterals[z]	-13.0a A	-12.0ab A	-11.5a A

[t] T_{50} (°C) [u] Nodes 1-4 [v] Nodes 5-8 [w] Nodes 9-12

[x] Within rows, means with the same capital letter not significantly different by Chi-square analysis at F=.05

[y] Within columns, means followed by the same letter not significantly different by Chi-square analysis at F=.05

[z] Values are for buds on the main canes of vines in which lateral shoots were retained and allowed to mature

Table 7. Comparisons of hardiness[y] within compound buds.

Treatment	1-9-78[z] 1'	2'	3'	2-18-78[z] 1'	2'	3'	4-3-78[z] 1'	2'	3'
Defruited	-26.7b	-28.0ab	-29.0a	-25.5b	-27.7ab	-28.8a	- 9.8a	-11.3a	-12.4a
50% shade	-25.0b	-27.8a	-28.2a	-23.8b	-27.3a	-27.3a	- 8.8a	-10.8a	-11.0a
100% defol.	-15.8a	-16.5a	-17.4a	-16.8a	-17.5a	-17.5a	- 5.5a	- 6.0a	- 7.0a
Alt. cordon (Defol.)	-23.7b	-26.0ab	-26.8a	-22.5b	-26.3a	-26.9a	- 9.0a	-10.8a	-11.3a
Alt. cordon (Fol.)	-24.2b	-27.5a	-27.5a	-25.4b	-27.4ab	-27.7a	- 9.2b	-11.7ab	-12.3a
Alt. shoot (Defol.)	-24.3b	-26.7ab	-27.2a	-23.2b	-25.3ab	-26.0a	- 9.5b	-12.2ab	-12.7a
Alt. shoot (Fol.)	-25.0b	-28.2a	-28.2a	-25.3b	-27.4ab	-27.8a	- 9.9a	-12.3a	-12.3a
Alt. leaf (Defol.)	-23.5b	-27.5a	-27.7a	-25.5a	-26.8a	-27.5a	- 9.0b	-12.0a	-12.5a
Alt. leaf (Fol.)	-24.8b	-28.3a	-28.5a	-25.5a	-27.0a	-27.5a	- 9.5a	-11.0a	-11.5a
Control	-26.0b	-28.0ab	-28.7a	-26.2a	-27.0a	-27.4a	-11.3a	-11.2a	-11.0a
Laterals	-25.3b	-28.3a	-29.0a	-24.9a	-26.9a	-27.2a	-10.9a	-11.2a	-12.2a

[y] T_{50} (°C)

[z] Within rows, means followed by the same letter not significantly different by Chi-square analysis at F=.05

APPENDIX C

Table 1. Correlations among parameters of fruit maturity, fruitfulness, and hardiness.

Treatment	1	2	3	4	5	6	7
Defruited	-	-	2.67	33.63	9.9	258.88	287.33
50% shade	6.44	135.60	2.16	32.85	7.3	240.48	259.42
100% defol.	2.52	124.80	1.62	27.80	88.4	25.68	221.38
Alt. cordon(d)	5.14	149.23	2.14	30.05	41.4	152.53	260.29
Alt. cordon(f)	7.64	190.28	2.41	33.73	13.3	236.18	272.41
Alt. shoot(d)	6.63	155.38	2.41	32.85	14.8	239.03	280.55
Alt. shoot(f)	7.21	144.35	2.24	34.63	11.6	253.28	286.52
Alt. leaf(d)	6.88	196.88	2.43	31.40	8.1	233.25	253.81
Alt. leaf(f)	6.74	183.23	2.43	31.80	7.8	237.70	257.81
Control	7.34	136.40	2.68	33.00	6.6	269.68	288.74
Laterals	7.36	127.26	2.53	36.18	12.4	257.18	293.58

	1	2	3	4	5	6	7

1: change in soluble solids from veraison to harvest, 1977 (g./100 g.)
2: 1977 yield (grams/node retained)
3: clusters/node, 1978
4: berries/cluster, 1978
5: percent primary bud mortality, 1977-78
6: 1978 yield (grams/node retained)
7: 1978 yield (grams/shoot pushed)

Correlation Coefficients

1x2; r=+0.52 n.s.
1x3; r=+0.87 **
1x4; r=+0.91 **
1x5; r=-0.93 **
1x6; r=+0.97 **
1x7; r=+0.83 **

3x4; r=+0.72 *
3x5; r=-0.86 **
3x6; r=+0.89 **
3x7; r=+0.81 **

4x5; r=-0.85 **
4x6; r=+0.91 **
4x7; r=+0.89 **

5x6; r=-0.99 **
5x7; r=-0.76 **

6x7; r=+0.87 **

* significant at the 5% level
** significant at the 1% level

Table 2. Correlations between critical temperatures[a] and cumulative primary bud mortality, 1977-78.

Treatment	Critical temperature 1-9-78	2-18-78	4-3-78	Percent primary bud mortality
	1	2	3	4
Defruited	-26.7	-25.5	- 9.8	9.9
50% shade	-25.0	-23.8	- 8.8	7.3
100% defol.	-15.8	-16.8	- 5.5	88.4
Alt. cordon (Defol.)	-23.7	-22.5	- 9.0	41.4
Alt. cordon (Fol.)	-24.2	-25.4	- 9.2	13.3
Alt. shoot (Defol.)	-24.3	-23.2	- 9.5	14.8
Alt. shoot (Fol.)	-25.0	-25.3	- 9.9	11.6
Alt. leaf (Defol.)	-23.5	-25.5	- 9.0	8.1
Alt. leaf (Fol.)	-24.8	-25.5	- 9.5	7.8
Control	-26.0	-26.2	-11.3	6.6
Laterals	-25.3	-24.9	-10.9	12.4

[a]Primary bud T_{50}(°C)

Correlation Coefficients

1x4; r=+0.93 **
2x4; r=+0.95 **
3x4; r=+0.84 **

** significant at the 1% level

APPENDIX D

Table 1. Crop loads of treatment vines at the inception of the defoliation study, Aug. 1977.

Treatment	Clusters/node retained	Berries/cluster
Defruited	a	a
50% shade	1.09	37.8
100% defol.	1.29	35.1
Alt. cordon (Defol.)	1.34	32.4
Alt. cordon (Fol.)	1.55	36.4
Alt. shoot (Defol.)	1.18	37.9
Alt. shoot (Fol.)	1.16	36.6
Alt. leaf (Defol.)	1.74	34.7
Alt. leaf (Fol.)	1.65	35.0
Control	1.29	31.0
Laterals	1.20	33.0

[a]Not measured

APPENDIX E

Table 1. Comparisons of primary bud T_{50}, cumulative primary bud mortality, and minimum temperatures in the field for the period December 1977-April 1978.

Treatment	Critical temperature[a] 1-9-78	2-18-78	4-3-78	Percent primary bud mortality
Defruited	-26.7	-25.5	- 9.8	9.9
50% shade	-25.0	-23.8	- 8.8	7.3
100% defol.	-15.8	-16.8	- 5.5	88.4
Alt. cordon (Defol.)	-23.7	-22.5	- 9.0	41.4
Alt. cordon (Fol.)	-24.2	-25.4	- 9.2	13.3
Alt. shoot (Defol.)	-24.3	-23.2	- 9.5	14.8
Alt. shoot (Fol.)	-25.0	-25.3	- 9.9	11.6
Alt. leaf (Defol.)	-23.5	-25.5	- 9.0	8.1
Alt. leaf (Fol.)	-24.8	-25.5	- 9.5	7.8
Control	-26.0	-26.2	-11.3	6.6
Laterals	-25.3	-24.9	-10.9	12.4

MINUS 22 DEC. 11 — MINUS 20 JAN. 15 — MINUS 24 FEB. 4 — MINUS 24 FEB. 19 — MINUS 22 MARCH 2 — MINUS 3 APRIL 9

[a] °C

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