# Effect of Interior Canopy Defoliation on Berry Composition and Potassium Distribution in Thompson Seedless Grapevines

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The interior portion of the Thompson Seedless grapevine canopy was defoliated approximately 950 'growing degree days' (GDDs) after budbreak in 1983 and 1984. Leaf area removed at that time was 9 $m^2$ (1983) and 7 $m^2$ (1984), which represented 35% and 27% of the total vine leaf area, respectively. Solar radiation penetration, when measured directly beneath the vine's canopy at soil level, increased from 40 $\mu mol/m^2/s$ for the control to 100 $\mu mol/m^2/s$ for the defoliated treatment. The amount of leaf dry matter lost subsequent to 1000 GDDs after budbreak was greater for the control than for the defoliated treatment. Leaf removal from the interior of the vine had no significant effect on fruit maturation characteristics in either year. In addition, there was no treatment effect on berry potassium concentration. A net loss of K from the stems of the vine prior to fruit harvest was measured, while there was no loss of K from the leaves throughout the season that could not be accounted for due to leaf fall or shoot trimming. The results indicate that the majority of K in fruit of Thompson Seedless grapevines comes either from the soil or the permanent structures of the vines during the course of berry growth with little redistribution from the current season's growth of leaves or stems under the conditions of this study.

The amount of leaf area required to mature a given weight of fruit on grapevines has been studied extensively (4,9,10,11,15,24). Leaf area required per mass of fruit has been shown to vary from 0.7 to 1.7 $m^2$ per kg of fruit depending upon variety and experimental conditions. Kliewer and Weaver (11) concluded that *ca* 1.0 $m^2$ of leaf area is required per kg of fruit for Thompson Seedless grapevines, while May *et al.* (15) found that value to be 0.8 $m^2$ or slightly less for Sultana vines. One aspect often overlooked in field studies considering this relationship is the amount of functional leaf area per vine, or the area within a grapevine canopy, that accounts for the majority of the vine's fixed carbon. Smart (18) has determined that 70% of the direct light intercepted by the vine occurred in the first 0.1 m of canopy. In addition, this portion of the vine's canopy also accounted for the majority of the total carbon fixed by the vine. Thus, if one were to consider these data, then the amount of leaf area required by a field-grown vine to mature a crop may be less than the values already reported in the literature.

A factor related to the functional leaf surface of a grapevine is the amount of shaded leaves within a canopy. Recent studies have shown that the proportion of shaded leaves within a vine's canopy affects berry composition (20). Excessive shading caused increased pH and K content in must and wine from red and white wine cultivars, in both hot and cool climates (19,22). Hypotheses that account for the influence of shade within a canopy on berry composition are related to the redistribution of mineral elements out of the leaves, which readily turn yellow and abscise under extreme shaded conditions. It previously has been shown that mineral nutrients are translocated out of leaves prior to abscission from the plant (16). The mobile elements within leaves, to include potassium, would then become available for redistribution within the vine. It has been suggested that monovalent cations, especially potassium, are exchanged for hydrogen ions in the berry, with a resultant increase in juice pH (1,2,3) which may decrease the quality of the fruit.

The purpose of this study was *(1)* to determine if defoliation of the vine's interior resulted in any differences in fruit maturation characteristics over a two-year period with the cultivar Thompson Seedless, *(2)* to quantify the distribution of potassium within the grapevine to determine the amount of remobilization that takes place during the course of the normal growing season in the San Joaquin Valley, and *(3)* to quantify leaf fall for two consecutive years. Besides providing information regarding the amount of leaf area required to mature a crop, such defoliation would remove a potential source of K for redistribution to the clusters.

## Materials and Methods

Seventeen-year-old *Vitis vinifera* L. (cv. Thompson Seedless) vines grown at the University of California Kearney Agricultural Center near Fresno, California, were used in this study. Vines were own-rooted, head-trained, and cane-pruned on a single-wire trellis at a height of 1.3 m. Cultural practices were typical of those used for raisin production (25), including trimming shoots near the ground to facilitate soil preparation prior to laying the grapes to be dried. The vineyard was flood-irrigated when needed as determined by field station personnel. The vines were fertilized in March 1984 with 78 kg N/ha using UAN-32 (urea-ammonium-nitrate, 32% N).

Current year's growth of stems, leaves, and clusters was harvested from different sets of six individual vine replicates throughout the growing season. Leaf area was measured with a LiCor area meter (model 3100). All leaves on a vine were measured to determine area in 1983, while leaf area in 1984 was determined from subsamples. Dry weights were taken when there was no further decrease in weight of the vine parts after being placed in a forced air oven at 70°C. An additional 12 individual vine

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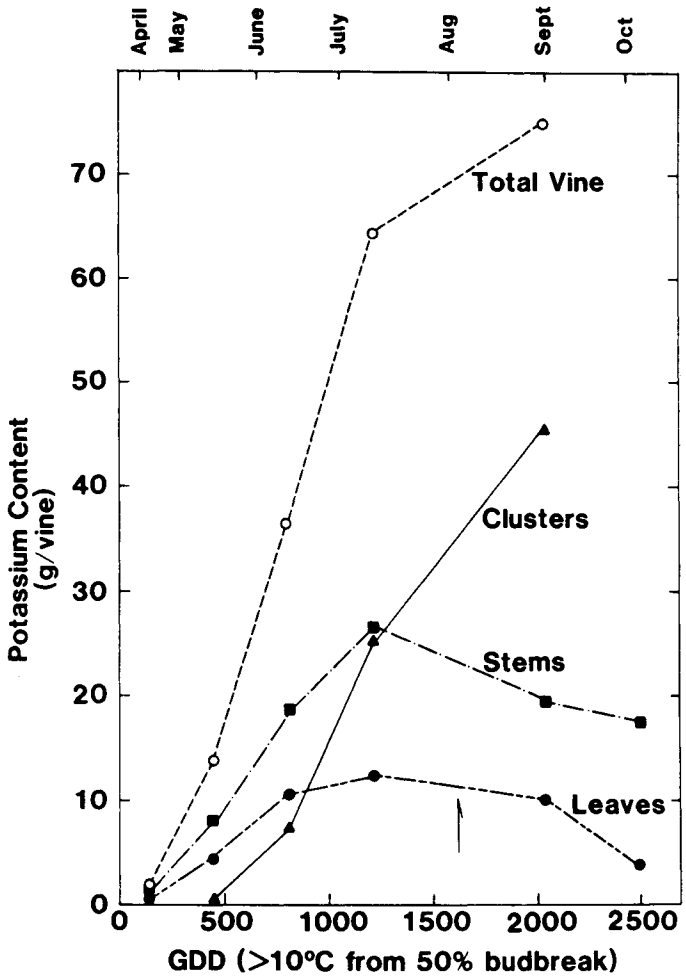


Fig. 1. Potassium accumulation throughout the 1984 growing season for Thompson Seedless grapevines. Each point is the mean of six replicate vines. Bloom occurred approximately 370 growing degree days after budbreak. The arrow represents the time at which the shoots were trimmed prior to soil preparation for laying grapes to be dried. The monthly abbreviations at the top of the figure are placed on the first day of the month.

replicates were defoliated just prior to full canopy development by removing leaves within the interior of the canopy. The objective was to leave at least two leaf layers remaining on the vine's exterior. Photosynthetic photon fluence rate (PPFR) was measured at the soil surface directly beneath control and defoliated vines with a LiCor line quantum sensor (model LI-191SB). Leaf fall was determined by collecting leaves beneath the 12 replicate vines per treatment once or twice a week from imposition of treatments until no leaves remained on the vine. An additional treatment consisted of removing all clusters at fruit set. 'Growing degree days' (GDDs) were calculated by a Campbell Scientific CR21 datalogger which was connected to a thermistor used to measure ambient temperature. The thermistor was housed in a shelter 0.3 m above the vine canopy in the vineyard. The lower temperature threshold was 10°C. Growing degree days were based on temperature readings taken every minute and then summed at the end of each 24-hour period. Budbreak represented the day when 50% of all buds on fruitng canes had burst.

Potassium content of dried vine parts was determined by the tetraphenylborate method (12). Plant material (250 mg dry wt) was digested with concentrated sulfuric acid and hydrogen peroxide over heat. Potassium was then determined on a diluted solution of the digested material at 650 nm with a Hach spectrophotometer (model DR/3). Berry juice K was determined by a Perkin Elmer atomic absorption spectrophotometer (model 2380) after a 1:200 dilution with distilled water.

## Results

There was a linear increase in total vine K content from 250 to 1250 GDDs after budbreak (Fig. 1). The majority of K was found in the leaves and stems early in the season, while at fruit harvest, clusters accounted for approximately 62% of the total K content. Approximately 7.0 g of K per vine was lost prior to harvest due to shoot trimming and leaf fall (Table 1). Interior canopy defoliation removed 9 and 7 $m^2$ of leaf area in 1983 and 1984, respectively (Table 2). This almost tripled PPFR measured beneath the defoliated vine's canopy when compared to that of the control. The defoliation was reflected in the leaf dry weight recovered during leaf fall. Vines that were

Table 1. Losses of potassium from control and defoliated Thompson Seedless grapevines throughout the growing season in 1984.

| | | g/vine |
|---|---|---|
| Before fruit harvest | | |
| | Canopy defoliation | 3.80[1] |
| | Shoot trimming[2] | |
| | Leaves | 2.40 |
| | Stems | 2.21 |
| | Leaf fall | 1.95 |
| After fruit harvest | | |
| | Leaf fall | 6.20[3] |
| | Prunings | 11.2 |

[1] This amount represents K removed by defoliating the interior of the vine. In 1983, 3.76 g K/vine were removed by this treatment.
[2] Vines were shoot-trimmed near the ground on 30 July to facilitate soil preparation prior to laying the grapes to be dried.
[3] The amount of K in fallen leaves was 5.87 g/vine in 1983.

Table 2. The effect of removing leaves from the interior of a grapevine's canopy on photosynthetic photon fluence rate (PPFR) beneath the canopy and leaf dry matter recovered during leaf fall in 1983 and 1984.[1]

| Year | Treatment | Leaf area removed[2] ($m^2$) | Leaf dry wt removed[2] (g) | PPFR[3] ($\mu mol/m^2/s$) | Leaf dry wt recovered during leaf fall[2] (g) |
|---|---|---|---|---|---|
| 1983 | Control | — | — | 47 | 1220 |
| | Defoliated | 8.8 | 408 | 131 | 899 |
| 1984 | Control | — | — | 32 | 1561 |
| | Defoliated | 6.9 | 338 | 85 | 1345 |

[1] Vines were defoliated on 14 July 1983 and 26 June 1984, which was 909 and 983 GDDs after 50% budbreak, respectively. Total maximum vine leaf area during the growing season was 24 and 28 $m^2$ in 1983 and 1984, respectively.
[2] Values represent the mean of 12 individual replicate vines.
[3] Values represent the mean of 24 measurements (one on either side of 12 vines) taken one day after treatments were imposed. Measurements were taken at solar noon.

Table 3. Leaf area per vine and leaf area per kg cluster weight at fruit harvest in 1983 and 1984.

| Year | Leaf area/vine[1] | Leaf area/fresh cluster weight[1] | Leaf area/fresh cluster weight of defoliated treatment[2] |
|---|---|---|---|
| | ($m^2$) | ($m^2$/kg) | ($m^2$/kg) |
| 1983 | 19.8 | 0.95 | 0.49 |
| 1984 | 21.6 | 1.07 | 0.65 |

[1]Each value is the mean of six individual replicate vines harvested from the same vineyard in which this study was conducted.
[2]These values were estimated by subtracting leaf area removed by defoliation (See Table 2) from the values in column 1 and dividing by the average cluster weight per vine of that treatment. Cluster weight in 1983 and 1984 for the defoliated vines averaged 22.4 and 22.7 kg/vine, respectively.

Table 4. Berry composition of control and defoliated vines at harvest.

| Year | Treatment | Wt/berry (g) | Soluble solids (°Brix) | TA (g/100mL) | pH | K (mg/L) |
|---|---|---|---|---|---|---|
| 1983 | Control | 1.77[1] | 20.2 | 0.59 | 3.90 | 1303 |
| | Defoliated | 1.80 | 19.1 | 0.58 | 3.90 | 1342 |
| 1984 | Control | 1.55 | 21.0 | 0.50 | 3.58 | 1524 |
| | Defoliated | 1.57 | 20.7 | 0.48 | 3.58 | 1475 |

[1] Each value is the mean of four three-vine replicates. Harvest took place on 28 August and 29 August in 1983 and 1984, respectively.

defoliated had less recovered dry weight than the control vines (Table 2). The estimated leaf area per fresh cluster weight for the defoliated treatment was approximately 0.55 $m^2$/kg (Table 3). Defoliation had no significant effect on berry weight, soluble solids, titratable acidity, pH, or K concentration either year (Table 4).

Cluster removal at fruit set dramatically increased the amount of dry weight partitioned to leaves and stems of Thompson Seedless grapevines at harvest (Table 5). While the increase in leaf dry weight was only 7%, primary stem dry weight of the vines in which clusters were removed was 67% greater than the control vines. Differences in dry weight between treatments were even greater when lateral stems and leaves were compared. Cluster removal also affected the amount of K in each vine part (Table 6). The K content of the parts of vines in which clusters had been removed were greater than the controls. The relative increase in K content among vine parts between the treated and control vines was greater than a similar comparison for dry weight (Table 5). This was due to greater K concentrations in leaves and stems of vines which had their clusters removed at set (Table 6).

Table 5. The effect of cluster removal on dry weight allocation to leaves and stems of Thompson Seedless grapevines at harvest.[1]

| Treatment | Leaves | | Stems | |
|---|---|---|---|---|
| | Primary | Lateral | Primary | Lateral |
| | g/vine | | | |
| Control | 1243 | 373 | 2171 | 142 |
| Fruit removed | 1335 | 670 | 3634 | 574 |
| % Increase in dry wt | 7 | 80 | 67 | 304 |

[1] Clusters were removed two weeks after bloom (25 May 1984). Neither treatment was shoot-trimmed. Each data point is the mean of six individual replicate vines.

Table 6. The effect of cluster removal on potassium distribution in leaves and stems of Thompson Seedless grapevines at fruit harvest.[1]

| Treatment | Primary leaves | Lateral leaves | Primary stems | Lateral stems |
|---|---|---|---|---|
| | g/vine | | | |
| Control | 10.1 (0.81)[2] | 2.5 (0.65) | 20.4 (0.94) | 1.6 (1.08) |
| Clusters removed | 12.9 (0.97) | 6.4 (0.94) | 38.4 (1.06) | 7.5 (1.31) |
| % Increase in K content | 28 | 156 | 88 | 369 |

[1] Each value is the mean of six individual vine replicates.
[2] Values in parentheses represent K concentration (% dry wt) of the respective vine parts.

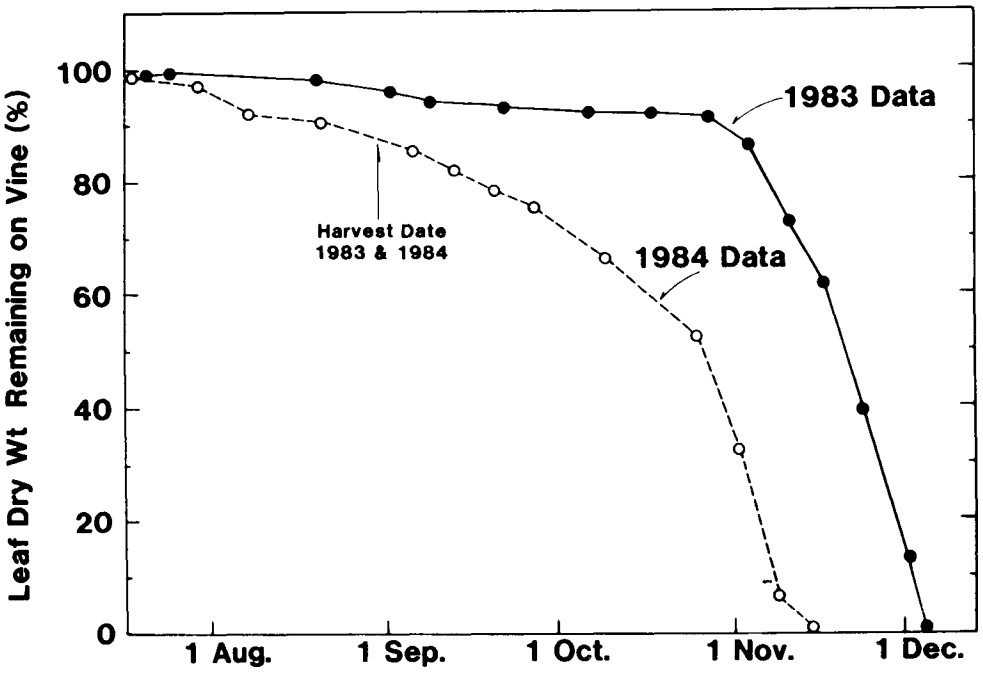


Fig. 2. The percent leaf dry weight remaining on Thompson Seedless grapevines as a function of calendar days. Fruit harvest occurred on 28 and 29 August in 1983 and 1984, respectively.

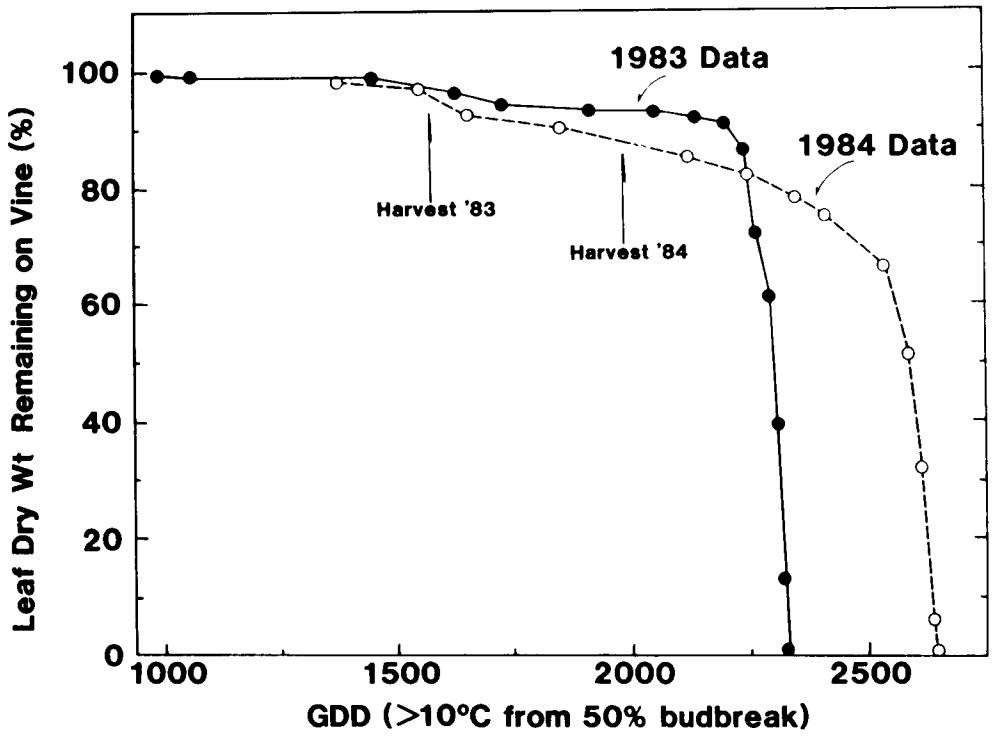


Fig. 3. The percent leaf dry weight remaining on Thompson Seedless grapevines as a function of growing degree days (GDDs) greater than 10°C from 50% budbreak.

The pattern of leaf fall for defoliated vines was similar to vines which were not defoliated both years (data not shown). The pattern of leaf fall for the control vines in 1983 and 1984 differed considerably regardless of whether time was expressed on a calendar or growing degree day basis (Fig. 2, 3). When time was expressed on a calendar basis, all leaves had fallen from the vine by 15 November in 1984, but not until 4 December in 1983. Conversely, when GDDs were used, leaves remained on the vine longer in 1984 than in 1983. Freezing air temperatures occurred on 4 and 11 November in 1983, while in 1984 air temperature did not fall below 2°C before all leaves had fallen from the vine.

## Discussion

The data presented in this paper demonstrated that the amount of leaf area required to mature the fruit of field-grown Thompson Seedless grapevines was considerably less than that reported in the literature. Approximately 1.0 $m^2$ of leaf area per kg cluster weight was present at harvest in 1983 and 1984 for the control vines (Table 3). This ratio, when estimated for the defoliated treatment, was reduced to 0.5 and 0.6 depending upon the year. May *et al.* (15) also demonstrated that fruit maturation by Sultana vines, *i.e.*, berry weight, soluble solids, and yield per node, was maximized in most instances at a leaf area to fruit ratio of *ca* 0.5 $m^2$/kg. They suggested that this was possible due to an increase in the photosynthetic efficiency of the remaining leaves on the vine after defoliaton. Since the external leaves of the canopy were not disturbed in the present study, there would have been little difference in the amount, location, or age of leaves exposed to most of the direct solar radiation between treatments. Thus, there would not have to be an increase in the photosynthetic efficiency of the leaves on the defoliated vines in this study. Even though PPFR measured beneath the vine at soil level tripled after defoliation, this level of PPFR still was only 5% of full sunlight (Table 2), indicating most of the direct sunlight was absorbed by the two leaf layers remaining on the vines. Since there was no significant delay in fruit maturation either year due to defoliaton, it would appear that the vines in this study needed a maximum of *ca* two-thirds of their leaves for normal growth and development of the fruit. The data also support estimates of vine canopy photosynthesis with regards to location within the canopy where the majority of solar radiation absorption and carbon fixation takes place (18).

Potassium content of the current years's new growth was greater than 70 g per vine with approximately 60% of that total found in the clusters at harvest (Fig. 1). This percent of the total in clusters at harvest was similar to that found by Lafon *et al.* (13) and Smart *et al.* (21) for field-grown vines. Conradie (6) found that 66% of the total amount of K within potted vines was in the cluster component at harvest. Lafon *et al.* (13) and Conradie (6) both observed appreciable translocation of K from the shoots and leaves to other structures of the vine, while Levy *et al.* (14) found no redistribution of K within the vine prior to harvest. When the amount of K in fallen leaves prior to harvest and leaves removed by shoot trimming (Table 1) was added to leaf K content at fruit harvest (Fig. 1), there was no net loss of this mineral element from these organs when compared to the whole vine harvest 1200 GDDs after budbreak. Thus, it appeared that there was little, if any, remobilization of K from the leaves to other parts of the vine. A loss of K from the stems (7 g/vine) during the same time period indicated that they may have been a possible source of K for redistribution within the vine. Since the permanent structures of the vine were not harvested, it is unknown

whether K from the stems may have been redistributed principally to the clusters or elsewhere.

The amount of shade within a grapevine canopy has been correlated with must composition. A canopy with dense interior shading has been shown to produce must compositions of reduced sugar content and higher malic acid and K concentrations and pH (19,20,22). Boulton (3) has shown that the exchange of hydrogen ions by monovalent cations, principally K, accounted for the majority of the pH change in the grape juice, and ultimately, the wine. Defoliation of the vine's interior canopy, the portion of the canopy that is constantly in the shade, did not significantly reduce the potassium concentrations of the berry juice (Table 4). While the leaf area removed in both years represented approximately 30% of the total maximum leaf area, this procedure only removed 3.8 g K/vine (Table 1). This amount of K would be equivalent to 8% of the total K accumulated by the clusters on each vine. This would indicate that the major proportion of K in the fruit of Thompson Seedless grapevines must have come either from the soil or the permanent structures of the vine. The recent extraction and characterization of a potassium-stimulated ATP phosphohydrolase (EC 3.6.1.3) in grapevine roots (23) could indicate that the active uptake of K from the soil would be the driving force for K accumulation in the fruit as suggested by Boulton (2).

The increased K concentration for the various organs of the vines in which clusters had been removed shortly after bloom compared to the control vines (Table 6) would indicate remobilization from the stems and leaves to the clusters for this element on vines with clusters. An alternate explanation would be that the greater concentration of K for the treatment vines was due to greater shoot growth (Table 5), in which stem elongation and new leaf production occurred later in the growing season (after fruit set). Data obtained in this study (results not given) and elsewhere (5,8) have shown that K concentration declines throughout the season in both stems and leaves. Thus, younger vine tissues would have greater K concentrations than older vine tissues. Vines in which clusters were removed had more new growth occurring later in the season and would therefore have had a greater K concentration on a whole-vine basis as found in Table 6.

The senescence of leaves from perennial plants and their ultimate abscission late in the growing season has been viewed as a means to recover mineral nutrients and carbohydrates from these organs (7,16). The stimulus that controls senescence and abscission of leaves on grapevines is unclear. According to Osborne (17), adverse environmental conditions provide the signal for leaf senescence, and subsequently, this is the stimulus for leaf abscission. The data presented here indicate two very different patterns of leaf fall in 1983 and 1984 depending on whether data were plotted against calendar (Fig. 2) or growing degree days (Fig. 3). There was little difference in leaf dry weight remaining on the vine between years when growing degree days were used up to *ca* 2250 GDDs after budbreak. It was at this time that a freeze occurred in 1983. However in 1984, the amount of leaf dry matter remaining on the vine decreased at a more rapid rate than in 1983 when time was measured as a function of calendar days (Fig. 3). This would indicate that day length probably did not play an important role in inducing senescence or abscission of grapevine leaves in the San Joaquin Valley. Leaf senescence and abscission from grapevines in this study may have been a function of leaf age based upon GDDs. Leaves in 1984 were older based upon GDDs even though on a calendar basis, they were younger than the leaves were in 1983. Further research is needed to resolve what the actual stimulus is for these processes in grapevines.

Data presented here demonstrate the large K requirement for clusters of Thompson Seedless grapevines. However, little if any of this requirement appears to come from remobilization of K out of the stems or leaves. The reduction in K concentration of leaves and stems throughout the season doesn't necessarily indicate remobilization of K to the clusters. Thus, studies in which canopy microclimate is altered to influence fruit composition need to quantify total vine nutrient or carbohydrate contents in order to determine the actual cause for subsequent responses.

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