Vitis **27**, 21—32 (1988)

Department of Viticulture and Enology, University of California, Davis, CA, USA

Kearney Agricultural Center, Parlier, CA, USA

Dry matter and nitrogen partitioning and root growth of young field-grown Thompson Seedless grapevines

by

F. J. Araujo[1]) and L. E. Williams

Die Verteilung von Trockensubstanz und Stickstoff und das Wurzelwachstum junger Freilandreben der Sorte Thompson Seedless

Zusammenfassung: Bei 2jährigen zurückgeschnittenen und nichtgeschnittenen Freilandreben der Sorte Thompson Seedless wurden die jahreszeitlichen Veränderungen des Trockengewichtes und der Stickstoffverteilung quantitativ bestimmt. Während der Vegetationsperiode wurden zwischen Austrieb und Traubenernte zu verschiedenen Terminen jeweils ganze Reben entnommen und aufgearbeitet. Das Trockengewicht und der N-Gehalt der Reben stiegen im Laufe der Vegetationsperiode bei beiden Varianten an, bei den zurückgeschnittenen Reben entwickelten sich beide Parameter jedoch langsamer und erreichten niedrigere Endwerte. Bei den zurückgeschnittenen Reben setzte der Zuwachs des Wurzel-Trockengewichtes gegenüber den nichtgeschnittenen Reben später ein; am Ende der Untersuchung bestand jedoch zwischen den beiden Varianten kein Unterschied im Wurzel-Trockengewicht. Bei beiden Varianten blieb der N-Gehalt der Wurzeln zu Beginn der Vegetationsperiode unverändert, später nahm er signifikant zu. Die N-Konzentration der Wurzeln ging infolge des zunehmenden Wurzel-Trockengewichtes zurück, dann pendelte sie sich in beiden Varianten infolge ähnlicher Steigerungsraten bei Trockensubstanz und N der Wurzel auf einen Wert von etwa 1,2 % ein. Die Ergebnisse stützen bei jungen Reben die Vorstellung von der Rolle der Wurzeln als wichtigstes N-Speicherorgan nicht, aus dem zu Beginn der Vegetationsperiode die übrigen Pflanzenorgane versorgt werden. Aus anderen Dauerstrukturen der Rebe wurden jedoch gleich nach dem Austrieb zwischen 14 und 26 % des für das Triebwachstum benötigten N zur Verfügung gestellt.

Key words: growth, nitrogen, translocation, root, pruning.

Introduction

The root's contribution to the total biomass of the vine and its growth throughout the season has yet to be quantified under field conditions. The lack of information on root growth may be due in part to the difficulty and time required to separate roots from the soil. Studies on vine root systems have centered on root distribution (Harmon and Snyder 1934; Perry *et al.* 1983) and the periodicity of new root initiation and turnover (Hiroyasu 1961; Freeman and Smart 1976; McKenry 1984). The sole study in which root biomass had been measured throughout the season was conducted on potted vines (Conradie 1980). It is unknown if the dynamics of growth for potted vines would be similar to vines in which the root system was unrestricted.

It has long been recognized that roots function as storage organs to include N reserves in woody perennials (Taylor 1967). Approximately 60—80 % of the stored N in 2-year-old dormant peach trees was found in the roots (Taylor and May 1967). Numerous experiments have been conducted to elucidate N partitioning and redistri-

---

[1]) Present address: FUSAGRI, Calle 76 No. 46-21, Maracaibo, Venezuela.

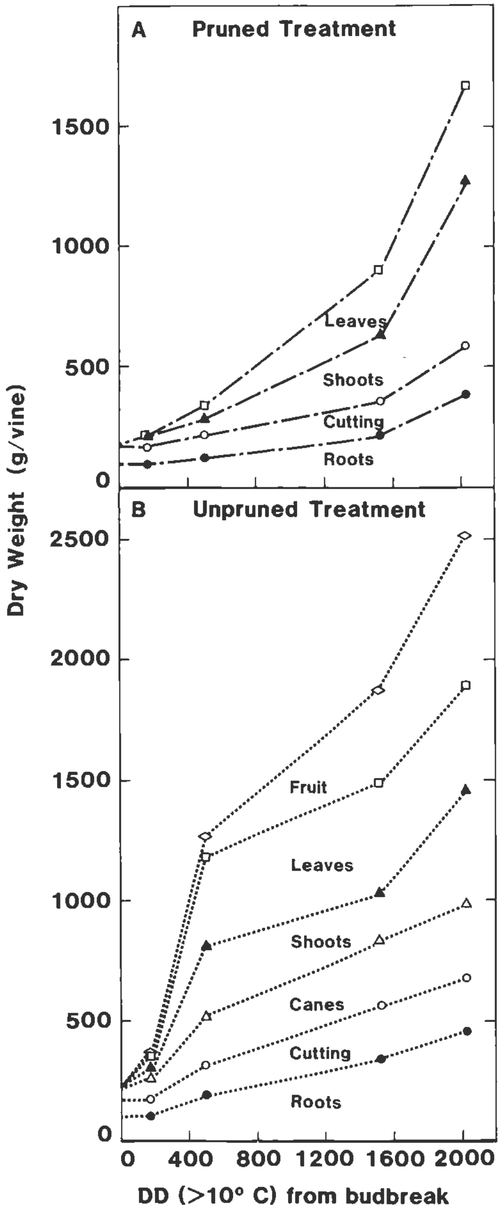

Fig. 1: The increase in dry weight among various organs of young Thompson Seedless grapevines as a function of degree days (> 10 °C) from budbreak. Vines were either pruned to a single two-bud spur (A) or left unpruned (B). Each point is the mean of 8 individual vine replicates. The curves are a result of the summation of the dry weights of each organ with those beneath on various harvest dates.

Die Zunahme des Trockengewichtes bei verschiedenen Organen junger Reben der Sorte Thompson Seedless als Funktion der Grad-Tage (> 10 °C) nach dem Austrieb. Die Reben wurden entweder auf einen einzigen Zweiaugenzapfen zurückgeschnitten (A) oder blieben ungeschnitten (B). Jeder Punkt ist der Mittelwert aus 8 Wiederholungen. Die Kurven resultieren aus der Summation der Trockengewichte für die einzelnen Organe mit allen darunter liegenden Trockengewichtswerten.

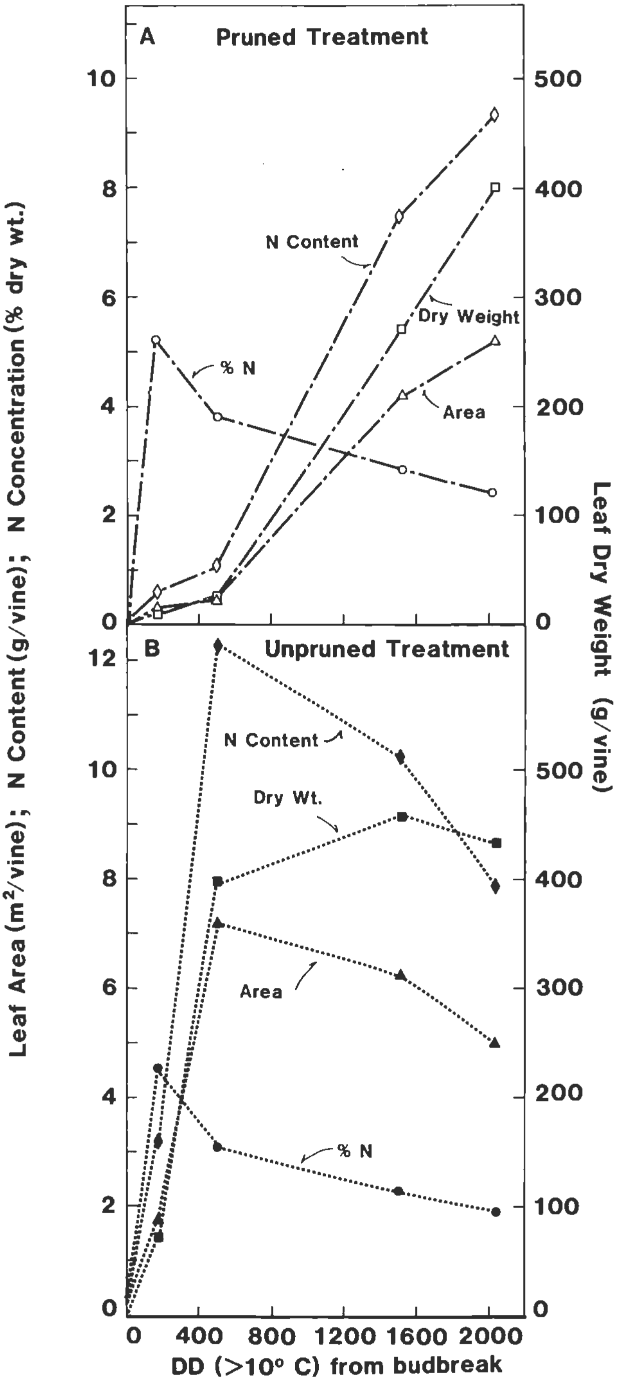

Fig. 2: The relationships between total vine leaf area, leaf N content, leaf N concentration and leaf dry weight and degree days for pruned (A) and unpruned (B) Thompson Seedless grapevines.

Die Beziehungen zwischen gesamter Blattfläche, Blatt-N-Gehalt, Blatt-N-Konzentration sowie Blatt-Trockengewicht und Grad-Tagen bei zurückgeschnittenen (A) und nichtgeschnittenen Reben (B) der Sorte Thompson Seedless.

bution within the plant relative to the contribution of storage organs to new growth (ALEXANDER 1957; OLAND 1959; NASSAR and KLIEWER 1966; KLIEWER 1967; TAYLOR and MAY 1967; TAYLOR and VAN DEN ENDE 1969; CONRADIE 1980). These studies suggest that roots accumulate N at the end of the season, which subsequently is utilized to support new growth the following year. However, most of these studies did not measure the absolute amount of N in the entire root system, with the exception of TAYLOR and MAY (1967) and CONRADIE (1980) who used potted trees and vines, respectively. Again, it is unknown if such data may be extrapolated to field conditions. It has become clear that without knowing the total biomass of the root system and its relation to root N concentration the results obtained in previous studies on N distribution are qualitative in nature.

This study was conducted to quantify dry matter and N accumulation of 2-year-old, field-grown Thompson Seedless vines in the San Joaquin Valley of California. It is during this year that vine training up the stake takes place (WINKLER *et al.* 1974). In addition, the role of the root system as a storage organ with respect to N mobilization during the growing season was determined.

Materials and methods

Cuttings of *Vitis vinifera* L. (cv. Thompson Seedless) were planted in the field at the University of California, Kearney Agricultural Center, near Fresno, California, on April 15, 1984. Vine and row spacing were 1.0 and 3.6 m, respectively. Normal vine spacing for raisin vineyards in this growing region is 2.1 m. Soil type was a Hanford sandy loam with a hardpan at a depth of 90—120 cm. Vines were furrow-irrigated every 3—4 weeks during the season. Prior to budbreak in 1985, approximately half the vines were pruned to a single two-bud spur, while the remaining vines were allowed to retain their first year's growth. No trellis system was used during the course of this study. Sets of pruned and control vines were randomly distributed throughout the experimental plot. Several times throughout the season, beginning with budbreak, entire vines were harvested. Roots were removed from the ground with a backhoe and then carefully separated from the soil by hand. The soil volume removed during this procedure was dependent upon the distribution of the vine's roots within the soil mass and generally increased throughout the season. The harvested roots were washed to remove any remaining soil particles. Vine organs were separated into leaves, new shoots, 1-year-old canes, cutting or trunk, roots and fruit in the case of the unpruned vines. All organs were dried at 70 °C in a forced air oven until no further decrease in weight was measured. Leaf area was measured with a LiCor area meter (Model 3100). Total nitrogen was measured by the Kjeldahl procedure. Ambient temperature was measured with a thermistor connected to a Campbell Scientific CR21 datalogger in a vineyard 200 m from the study site. The datalogger calculated degree days (DDs), using a minimum threshold temperature of 10 °C as described by WILLIAMS (1987).

Results

Total dry weight of vines in the pruned treatment was approximately 1670 g, 2000 DDs after budbreak (Fig. 1 A), compared to an average dry weight of 2500 g for vines in the unpruned treatment on the same date (Fig. 1 B). The pattern of dry weight accumulation differed between the two treatments. The greatest increase in dry weight occurred between 177 and 500 DDs for the unpruned vines, whereas the greatest increment of vine dry weight for the pruned treatment occurred between 1500 and 2000 DDs after budbreak. The greatest increase in leaf area and dry weight for vines in the pruned treatment occurred after 500 DDs (Fig. 2 A). While there was no significant increase in leaf area from 1500 to 2000 DDs for the pruned treatment, there was a significant ($P<0.05$) increase in leaf dry weight during this period. Leaf fall significantly ($P<0.05$) reduced leaf area for the unpruned treatment from 500 DDs until the

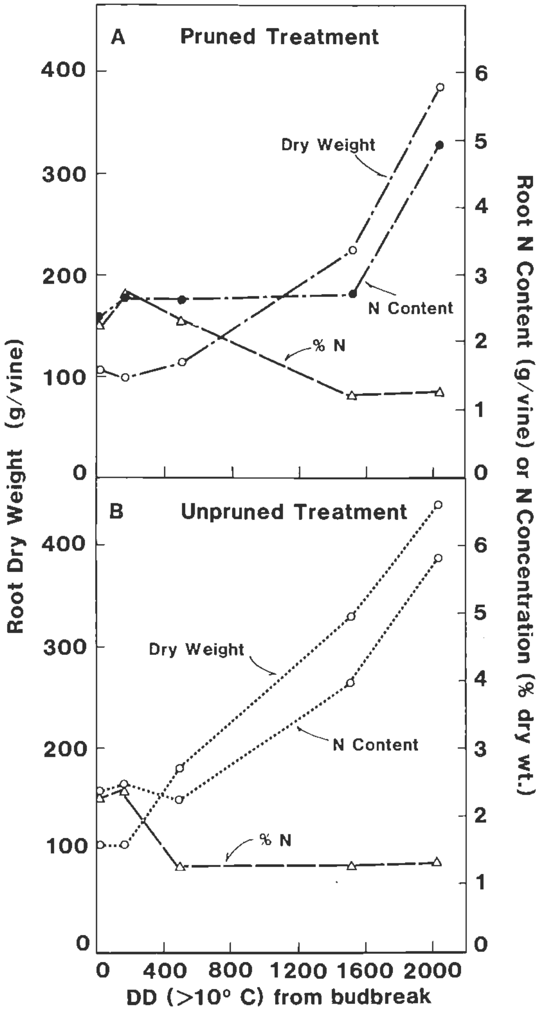

Fig. 3: The accumulation of root dry weight and N content and the resulting root N concentration throughout the growing season for 2-year-old Thompson Seedless grapevines.

Die Entwicklung des Wurzel-Trockengewichtes, des Wurzel-N-Gehaltes und der sich hieraus ergebenden Wurzel-N-Konzentration im Verlauf der Vegetationsperiode bei 2jährigen Reben der Sorte Thompson Seedless.

last harvest, but there was no significant decrease in leaf dry weight during that time (Fig. 2 B). Weight per unit leaf area (W_L) calculated on a whole vine basis increased from 38 to 78 g/m² and 42 to 85 g/m² for the pruned and the unpruned treatments, respectively, between 177 and 2000 DDs after budbreak. There were no significant differences in leaf area or leaf dry weight between treatments on the last harvest date.

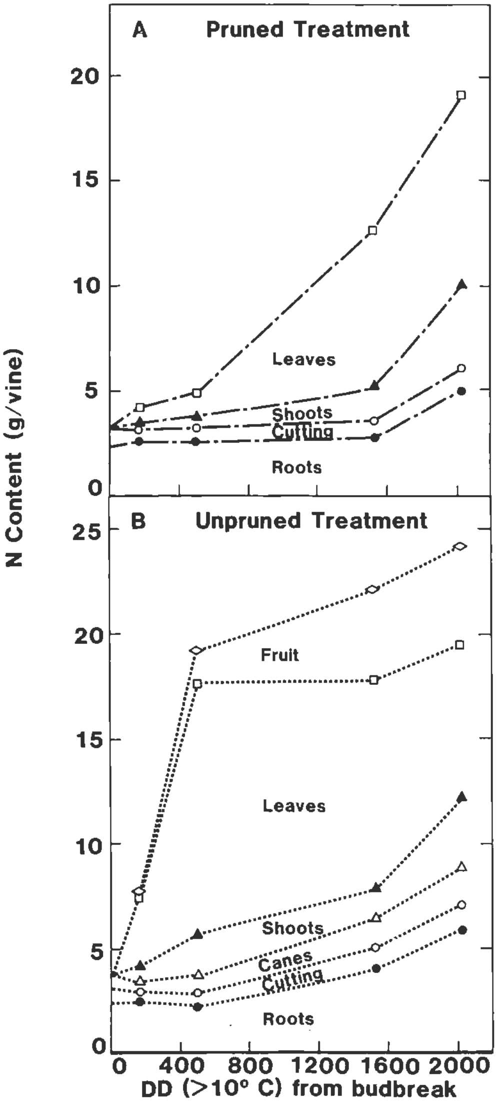

Fig. 4: The increase in N content among various organs of young Thompson Seedless grapevines throughout the growing season. Other information as given in Fig. 1.

Die Zunahme des N-Gehaltes in verschiedenen Organen junger Reben der Sorte Thompson Seedless im Verlauf der Vegetationsperiode. Für weitere Erläuterungen s. Fig. 1.

There was little increase in root dry weight before 500 DDs for vines in the pruned treatment (Fig. 3 A). There were significant ($P < 0.05$) increases in root dry weight for the unpruned vines at each harvest subsequent to the one on April 4, 147 DDs after budbreak (Fig. 3 B). Root dry weights of the two treatments were significantly different ($P < 0.05$) on the third and fourth harvest dates, 498 and 1517 DDs after budbreak, respectively.

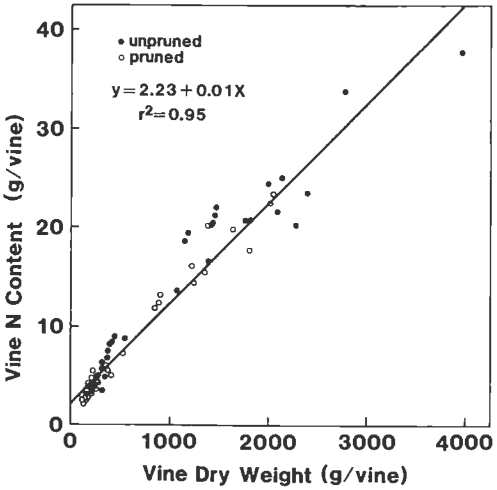

Fig. 5: The relationship between vine dry weight and vine N content. Data points represent individual vines of the pruned and unpruned treatments harvested throughout the experimental period.

Die Beziehungen zwischen Trockengewicht und N-Gehalt der Reben. Jeder Punkt repräsentiert eine einzelne Rebe der geschnittenen und nichtgeschnittenen Variante.

The greatest N concentration in all vine parts occurred at the beginning of the season and then decreased throughout the remainder of the study for both treatments (unpublished data). Nitrogen content of the vine, though, increased throughout the season for both treatments (Fig. 4 A and B). When the study was terminated the difference in the amount of N accumulated between treatments was 5 g. The pattern of vine N accumulation throughout the season differed between the two treatments. There was little increase in vine N content before 500 DDs for the pruned treatment while the unpruned treatment had accumulated almost 80 % of its N by that date. The original cuttings of the pruned treatment lost a significant ($P < 0.05$) amount of N (0.3 g/vine) on the second harvest date when compared with their N content at budbreak. All vine parts increased in N content by the end of the study with the exception of the leaves for the unpruned treatments. The cuttings and canes in the unpruned treatment lost a significant ($P < 0.05$) amount of N (0.5 g/vine) 177 DDs after budbreak when compared with the harvest at budbreak. The root N content for both treatments remained constant early in the season before increasing later on (Fig. 3 A and B). However, root N concentration in both treatments decreased during the same time frame due to an increase in root dry weight and then leveled off at about 1.2 %.

There was a linear relationship between vine dry weight and N content when data from both treatments were combined (Fig. 5). In addition, there were linear relationships between leaf dry weight and vine N content and vine dry weight (Fig. 6).

Discussion

The data obtained in this study extend the early classic works of WINKLER (1929, 1931, 1958). The earlier and greater accumulation of dry weight in the unpruned vines compared with the pruned vines was associated with a larger leaf area earlier in the season (Fig. 2). It was previously demonstrated that unpruned vines have the capacity of developing a larger canopy earlier in the season (WINKLER 1958). In addition, the linear relationship between leaf and vine dry weight offers indirect evidence for the dependence of vine dry weight on the size of the canopy (Fig. 6 B). Consequently, the greatest increase in vine dry weight for the pruned treatment occurred between 1500 and 2000 DDs after budbreak, when the vines had reached 80 % of their total leaf dry weight and 90 % of their total leaf area.

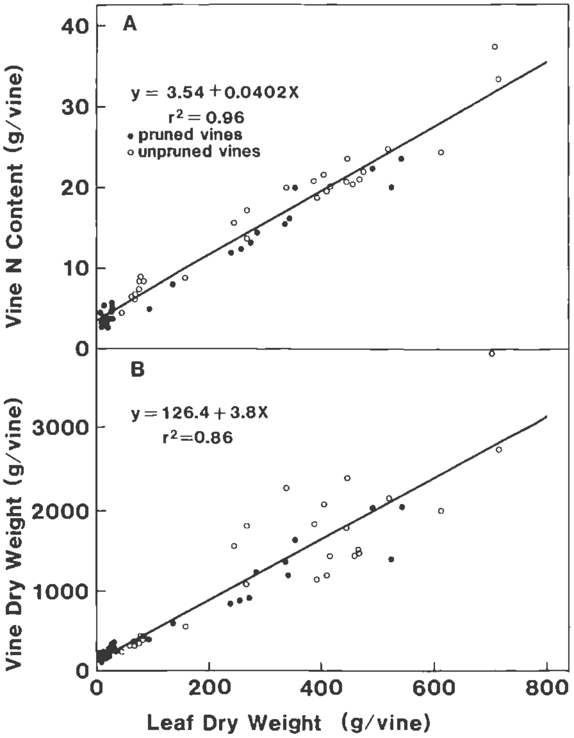

Fig. 6: The relationships between leaf dry weight and vine N content (A) and total vine dry weight (B). Data points represent individual vine replicates of both treatments.

Die Beziehungen zwischen Blatt-Trockengewicht und N-Gehalt der Reben (A) bzw. Blatt-Trockengewicht und gesamtem Trockengewicht der Reben (B). Jeder Punkt repräsentiert eine einzelne Rebe der beiden Versuchsvarianten.

CONRADIE (1980) reported that the total dry weight production of 2-year-old vines during a single season was approximately 870 g. Those vines were similar to the unpruned vines in this study in that they had not been pruned prior to the year the experiment was conducted. Dry weight of the unpruned vines in this study was almost

3 times larger than that reported by CONRADIE, indicating a possible detrimental effect that a confined root system could have on the growth of potted vines. There was no significant increase in root dry weight in the potted study, whereas root dry weight quadrupled for vines grown in the field (Fig. 3).

Root growth depends upon a current supply of photosynthates from the shoots (BOWLING *et al.* 1985). The partitioning of carbohydrates to roots depends upon their sink strength relative to other organs of the plant (TROMP 1983). The accumulation of root dry matter did not occur until the canopy was well developed for both treatments. Once root growth was initiated, it was maintained throughout the remainder of the season (Fig. 2 and 3). The shoot and root growth dynamics for both treatments were consistent with the model of root-shoot interaction proposed by RAPER *et al.* (1978). The earlier root growth of the unpruned vines compared with the pruned vines probably was due to the earlier development of the canopy in the former treatment which was able to support root growth. Root growth may take place only when excess photosynthates are available from the vine's leaves. The absence of fruit may explain the large increase in root biomass during the last part of the season for the pruned treatment such that there was no significant difference in root dry weight between treatments at the end of the study (Fig. 3).

There was a significant decrease in leaf area for the unpruned vines due to leaf senescence and abscission. Once full canopy has been achieved during the season, factors such as shading, water stress, or higher proportion of older leaves, can result in earlier leaf senescence and subsequent abscission (SMART and COOMBE 1983). The increase in W_L throughout the season has been demonstrated before by WILLIAMS (1987). CONRADIE (1980) also reported an increase in leaf dry weight per unit area at leaf fall. The increase in W_L seems to be a phenological characteristic of most plants until the last stages of leaf senescence at which time there is a decrease in W_L (OLAND 1959).

Despite the increase in vine N content throughout the growing season, the N concentration of the entire vine steadily decreased in both treatments such that vine N concentration was 1 % at fruit harvest. This indicated that vine dry weight accumulation was faster than N accumulation and was similar to that described by RAPER *et al.* (1978) for annual plants. The reduction in N concentration has been associated with changes in the pattern of growth as the season progresses, i. e. decrease in cell division and proportion of cytoplasm per cell to an increase in the proportion of cell wall material and non-growing tissue (MOORBY and BESFORD 1983). Nitrogen concentration of the entire vine calculated from CONRADIE's study (1980) also was 1 % at fruit harvest. In addition, the combined N concentration of fruit, leaves and shoots at fruit harvest calculated from the LAFON *et al.* study (1965) was approximately 1 %. The linear relationship between dry weight and N content of the vine in this study was based on the maintenance of an overall N concentration of approximately 1 % (Fig. 5). The maintenance of a specific concentration in these studies supports the critical N concentration hypothesis proposed by GREENWOOD *et al.* (1986).

The uptake of most nutrients by the roots, including N, is an active process which needs a supply of photosynthates from the shoots (EPSTEIN 1972; GLASS and SIDDIQI 1984; BOWLING *et al.* 1985). The increase in vine N content early in the season, when the amount of photosynthetic tissue was small, indicates that roots may have utilized their own carbohydrate reserves for N uptake. Quantification of the root N pool showed root N content remained constant before increasing later in the season. Mobilization of N from other permanent parts of the vine, such as the cutting and canes, to support shoot growth has been shown to occur (GROOT OBBINK *et al.* 1973). Nitrogen loss by the cutting of the pruned vines and cutting and canes for the unpruned vines between 0 and

177 DDs accounted for 26 and 14 %, respectively, of the total amount of N gained by the rest of the vine during that time period. This compares favorably with results of CONRADIE (1986) using ^{15}N. The remaining N required for shoot growth would have come from the soil. While the absolute amount of N mobilized from cuttings and canes was small, this may have been important for the initiation of growth early in season.

While it appeared no root N was mobilized to support shoot growth, N may have been remobilized within the root system to support new root growth. The growth of the grape root system has been separated into two events: 1. primary development which includes the production of new roots and their growth during the current season and 2. secondary development, which includes the resumption of cell division and elongation in overwintering root terminals and the secondary thickening of the persistent roots associated with the resumption of cambial activity (PRATT 1974; RRICHARDS 1983). The relative contribution of each type of growth to the increment in root dry weight was not determined in this study, both, however, include the production of new tissue. New root production or flushing has been observed to occur in grapevines during spring/early summer and after fruit harvest (HIROYASU 1961; PRATT 1974; MCKENRY 1984; VAN ZYL 1984). The increase in root dry weight before any increase in N content indicated that redistribution within the root N pool must have taken place. Mobilization of N from the vacuole to support new growth would not impair cell functioning as long as the cytoplasmic homeostasis was maintained (LEIGH and WYN JONES 1986).

WILLIAMS and SMITH (1985) found a N concentration of 1.25 % in leaves that had fallen from Thompson Seedless grapevines. Using this value in combination with W_L and the reduction in leaf area, N loss, due to leaf fall for the unpruned treatment (Fig. 2), was estimated to be approximately 1.8 g. With a total reduction of approximately 4.4 g in leaf N content between 500 and 2000 DDs (Fig. 2), the difference between these two N contents (2.6 g) was probably translocated to the vine prior to leaf abscission. Nitrogen remobilization from the leaves to the plant prior to abscission has been suggested by others in previous studies (ALEXANDER 1957; OLAND 1959; NASSAR and KLIEWER 1966; KLIEWER 1967; TAYLOR 1967; TAYLOR and VAN DEN ENDE 1969). The reduction in N content measured in shoots between 500 and 1500 DDs in unpruned vines also may have been attributed to translocation to other parts of the vine (Fig. 4).

The continuous increase in vine N content throughout the growing season in both treatments indicated that there was also a concomitant N uptake from the soil (Fig. 4). The largest increments in vine N content coincided with the largest accumulations in leaf biomass for both treatments (Figs. 2 and 4). Leaves were the main recipient of N in the vine (Fig. 4) as a consequence of their high N concentration (Fig. 2). The linear relationship between vine N content and leaf dry weight suggests that the leaves are an important factor in determining the bulk of the vine N content (Fig. 6 A). An explanation for this relationship would be the already mentioned relatively high N content of leaves and, in an indirect manner, the dependence of biomass production on photosynthates supplied by the leaves (Fig. 6 B).

The results of this experiment question the role of the root system as a storage organ for supplying N to the rest of the plant in 2-year-old grapevines grown in the field. Rather, the data indicate that the roots retain their N for their own growth. The results also indicated that root growth occurred during most of the growing season and, once initiated, was maintained in accordance with the growth of above ground parts of the vine. Lastly, part of the N required for shoot growth shortly after budbreak was supplied by the original cutting and woody canes for vines under the conditions of this experiment.

Summary

Seasonal changes in dry weight and nitrogen distribution were quantified on 2-year-old pruned and unpruned Thompson Seedless grapevines grown in the field. Entire vines were harvested several times during the growing season from budbreak to fruit harvest. Vine dry weight and N content increased throughout the season for both treatments, however, the accumulation of both parameters was delayed and of a smaller magnitude for the pruned vines. The increase in root dry weight of the pruned vines occurred later in the season when compared to the unpruned vines, but there was no difference in root dry weight between treatments at the end of the study. Root N content remained constant early in the growing season followed by a significant increase later in the season for both treatments. The root N concentration decreased as a result of an increase in root dry weight, then it leveled off at about 1.2 % for both treatments due to similar rates of root dry matter and N accumulation. The results do not support the role of roots as the major storage organ of N to supply the rest of the plant early in the season for young grapevines. However, N from other permanent structures of the vine supplied between 14 and 26 % of that required for shoot growth shortly after budbreak.

Acknowledgements

The authors acknowledge the technical assistance of P. J. BISCAY, D. C. HARRELL, S. A. WILLIAMS, D. ATAIDE and D. PATTIGAN.

References

1. ALEXANDER, D. MCE.; 1957: Seasonal changes in the nitrogen content of the Sultana vine. Austral. J. Agricult. Res. **8**, 162—168.
2. BOWLING, D. J. F.; WATSON, B. T.; EHWALD, R.; 1985: The effect of phloem ringing on root growth and potassium uptake by *Helianthus annuus*. J. Exp. Bot. **36**, 290—297.
3. CONRADIE, W. J.; 1980: Seasonal uptake of nutrients by Chenin blanc in sand culture: I. Nitrogen. S. Afr. J. Enol. Viticult. **1**, 59—65.
4. — — ; 1986: Utilisation of nitrogen by the grapevine as affected by time of application and soil type. S. Afr. J. Enol. Viticult. **7**, 76—83.
5. EPSTEIN, E.; 1972: Mineral Nutrition of Plants: Principles and Perspectives. John Wiley and Sons, New York.
6. FREEMAN, B. M.; SMART, R. E.; 1976: A root observation laboratory for studies with grapevines. Amer. J. Enol. Viticult. **27**, 36—39.
7. GLASS, A. D. M.; SIDDIQI, M. Y.; 1984: The control of nutrient uptake rates in relation to the inorganic composition of plants. In: TINKER, P. B.; LÄUCHLI, A. (Eds.): Advances in Plant Nutrition, Vol. **1**, 103—147. Praeger, New York.
8. GREENWOOD, D. G.; NEETESON, J. J.; DRAYCOTT, A.; 1986: Quantitative relationship for the dependence of growth rate of arable crops on their nitrogen content, dry weight and aerial environment. Plant and Soil **92**, 281—301.
9. GROOT OBBINK, J.; ALEXANDER, D. MCE.; POSSINGHAM, J. V.; 1973: Use of nitrogen and potassium reserves during growth of grapevine cuttings. Vitis **12**, 207—213.
10. HARMON, F. N.; SNYDER, E.; 1934: Grape root distribution studies. Proc. Amer. Soc. Hort. Sci. **32**, 370—373.
11. HIROYASU, T.; 1961: Nutritional and physiological studies on the grapevine [Jap.]. J. Jap. Soc. Hort. Sci. **30**, 111—116. [Abstr.: Hort. Abstr. **32**, 2677.]

12. KLIEWER, W. M.; 1967: Annual cyclic changes in the concentration of free amino acids in grapevines. Amer. J. Enol. Viticult. **18**, 126—137.
13. LAFON, J.; COUILLAUD, P.; GAY-BELLILE, F.; LEVY, J. F.; 1965: Rythme de l'absorption minérale de la vigne au cours d'un cycle végétatif. Vignes Vins **140**, 17—21.
14. LEIGH, R. A.; WYN JONES, R. G.; 1986: Cellular compartmentation in plant nutrition: the selective cytoplasm and the promiscuous vacuole. In: TINKER, P. B.; LÄUCHLI, A. (Eds.): Advances in Plant Nutrition, Vol. **2**, 249—279. Praeger, New York.
15. MCKENRY, M. V.; 1984: Grape root phenology relative to control of parasitic nematodes. Amer. J. Enol. Viticult. **35**, 206—211.
16. MOORBY, J.; BESFORD, R. T.; 1983: Mineral nutrition and growth. In: LÄUCHLI, A.; BIELESKI, R. L. (Eds.): Encyclopedia of Plant Physiology, New Series, Vol. **25 B**, 481—527. Springer, Berlin.
17. NASSAR, A. R.; KLIEWER, W. M.; 1966: Free amino acids in various parts of *Vitis vinifera* at different stages of development. Proc. Amer. Soc. Hort. Sci. **89**, 281—293.
18. OLAND, K.; 1959: Nitrogenous reserves of apple trees. Physiol. Plant. **12**, 594—648.
19. PERRY, R. L.; LYDA, S. D.; BOWEN, H. H.; 1983: Root distribution of four *Vitis* cultivars. Plant and Soil **71**, 63—74.
20. PRATT, C.; 1974: Vegetative anatomy of cultivated grapes — a review. Amer. J. Enol. Viticult. **25**, 131—150.
21. RAPER, C. D.; OSMOND, D. L.; WANN, M.; WEEKS, W. W.; 1978: Interdependence of root and shoot activities in determining nitrogen uptake rate of roots. Bot. Gaz. **139**, 289—294.
22. RICHARDS, D.; 1983: The grape root system. In: JANICK, J. (Ed.): Horticultural Reviews. Vol. **5**, 168—172. AVI, Westport, Conn.
23. SMART, R. E.; COOMBE, B. G.; 1983: Water relations of grapevines. In: KOZLOWSKI, T. T. (Ed.): Water Deficits and Plant Growth, Vol. **VII**, 137—196. Academic Press, NY.
24. TAYLOR, B. K.; 1967: Storage and mobilization of nitrogen in fruit trees: a review. J. Austral. Inst. Agricult. Sci. **33**, 23—29.
25. — —; MAY, L. H.; 1967: The nitrogen nutrition of the peach tree. II. Storage and mobilization of nitrogen in young trees. Austral. J. Biol. Sci. **20**, 389—411.
26. — —; VAN DEN ENDE, B.; 1969: The nitrogen nutrition of the peach tree. IV. Storage and mobilization of nitrogen in mature trees. Austral. J. Agricult. Res. **20**, 869—881.
27. TROMP, J. N.; 1983: Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen. Plant and Soil **71**, 401—403.
28. WILLIAMS, L. E.; 1987: Growth of 'Thompson Seedless' grapevines: 1. Leaf area development and dry weight distribution. J. Amer. Soc. Hort. Sci. **112**, 325—330.
29. — —; SMITH, R. J.; 1985: Net CO_2 assimilation rate and nitrogen content of grape leaves subsequent to fruit harvest. J. Amer. Soc. Hort. Sci. **110**, 846—850.
30. WINKLER, A. J.; 1929: The effect of dormant pruning on the carbohydrate metabolism of *Vitis vinifera*. Hilgardia **4**, 153—173.
31. — —; 1931: Pruning and thinning experiments with grapes. Calif. Agricult. Exp. Sta. Bull. **519**, 1—56.
32. — —; 1958: The relation of leaf area and climate to vine performance and grape quality. Amer. J. Enol. Viticult. **9**, 10—23.
33. — —; COOK, J. A.; KLIEWER, W. M.; LIDER, L. A.; 1974: General Viticulture. 2nd Ed. University of California Press, Berkeley.
34. ZYL, J. L. VAN; 1984: Response of Colombar grapevines to irrigation as regards quality aspects and growth. S. Afr. J. Enol. Viticult. **5**, 19—28.

Eingegangen am 24. 4. 1987

Dr. L. E. WILLIAMS
Kearney Agricultural Center
9240 S. Riverbend Avenue
Parlier, CA 93648
USA