Partitioning of Nitrogen in Grapevines during Autumn and the Utilisation of Nitrogen Reserves during the Following Growing Season

W.J. Conradie

Nietvoorbij Institute for Viticulture and Oenology (Nietvoorbij), Private Bag X5026, 7599 Stellenbosch, Republic of South Africa

Submitted for publication: March 1992
Accepted for publication: April 1992
Key words: Grapevine, nitrogen, post-harvest, autumn, distribution, reserves, translocation

The distribution and translocation of nitrogen (N) absorbed during autumn (post-harvest) were quantified for two-year-old Chenin blanc grapevines grown in sand culture. Vines were labelled with ^{15}N over a one-month period immediately after harvest. From this stage onwards vines were fed unlabelled Hoagland solution. Selected vines were destructively sampled over a period of seven months, *i.e.* twice at the end of the second season (start of leaf-fall and end of leaf-fall) and three times at the start of the third growing season (budbreak, before bloom and after bloom). Autumn-absorbed N accounted for 60% of the total amount of N-reserves present at the start of the third season. The utilisation of these N-reserves over the first part of the third season was compared to that of reserves originating from the previous spring and summer, respectively. All reserve pools were utilised equally with one quarter being translocated to new growth up to the end of bloom. At the latter stage one-year-old reserves accounted for at least 18% of the N-demand of the new growth. Newly absorbed N and reserve N were allocated to all the new organs in equal ratios. It was estimated that 50% of the N-reserves present at budbreak will be utilised up to harvest. After bloom, however, reserve N lost from the permanent structure was compensated for by newly absorbed N, which was not the case before bloom.

It is generally accepted that N-reserves, accumulated by the grapevine during the previous season(s), play an important role in sustaining new growth at the start of the next season (Alexander, 1957; Conradie, 1980, 1986, 1990, 1991; Löhnertz, 1988; Peacock, Christensen & Broadbent, 1989; Koblet & Perret, 1990). In a warm country like South Africa the major share of these reserves is accumulated during the post-harvest period when root growth, which may stop temporarily at véraison (Freeman & Smart, 1976; Conradie, 1980; Van Zyl, 1984), is normally resumed. In cooler countries, where grapes are harvested relatively late, accumulation of N in the permanent structure may already start before harvest (Löhnertz, 1988). This difference probably occurs because the bunches are a less competitive sink for N during the period immediately preceding harvest due to slower ripening. Accumulation of N-reserves during the later part of the growing season is therefore a common phenomenon under all climatic conditions. Even though it is known that the amount of N absorbed during the post-harvest period may vary from 27% (Conradie, 1986) to 34% (Conradie, 1980), the way in which this N is distributed and relocated between the different organs of the grapevine has not yet been described in detail. The first objective of this study was to clarify this aspect through the use of the ^{15}N isotope.

The quantitative role of stored N is difficult to assess with conventional methods because a specific organ may supply stored N to new growth, while soil-derived N is accumulated at the same time (Legaz *et al.*, 1982; Conradie, 1990, 1991; Habib *et al.*, 1989). The second objective of this study was to determine the way in which autumn-absorbed N, being the most important source of stored N, is utilised during the following season, and to compare this with the utilisation of storage pools accumulated during the previous spring (Conradie, 1990) and summer (Conradie, 1991), respectively.

The amount of N required by the grapevine for the production of a crop of a specific size has been investigated in several countries (Alexander, 1957; Lafon *et al.*, 1965; Conradie, 1980; Williams, 1987; Löhnertz, 1988). On average, each ton of fresh grapes removed 1,6 kg N, while the associated amount of N present in the vegetative growth amounted to 2,1 kg, implying that the bunches of a balanced vine should contain 43% of the total amount of N present in the new growth at harvest. The third objective of this study was to calculate the contribution of reserve N, accumulated during the previous season, to the abovementioned annual N-demand.

The study was carried out with two-year-old, potted, bearing grapevines. Isotopically labelled KNO_3 was applied during the first month after harvest. The pool of labelled N thus created was designated as "autumn N". After labelling, vines were fed with Hoagland solution and sampled periodically over a period of seven months.

MATERIALS AND METHODS

Utilisation of autumn-absorbed N: The study was conducted at the Nietvoorbij experimental farm, Stellenbosch,

Acknowledgement: Technical assistance by the staff of the Soil Science Section of Nietvoorbij is gratefully acknowledged.

TABLE 1
Outline of experiment to determine the fate of N absorbed during the post-harvest period.

Date	Growth Stage of Vines	Growth Season	Type of N supplied	Sampling Date [a]
13 February	Harvest	Second season	(Unlabelled)	13 February
			21 February	
			(Labelled)	
			22 March	
			(Unlabelled)[b]	
			12 April	
			(No N) [c]	
21 April	Leaf-fall		21 April	21 April
20 June				20 June
	Dormancy			
30 August		Third season		30 August
			(Unlabelled)	6 October
19 October	Bloom			
8 November				22 November

(a) Four unlabelled vines were removed on 13 February, while one unlabelled and three labelled vines were sampled on all other dates.
(b) Unlabelled N was supplied over this period while leachate was recirculated.
(c) Pots were leached to remove any traces of labelled N from the root zone.

with *Vitis vinifera* L. cv. Chenin blanc grafted onto 99 Richter. One-year-old nursery vines were planted during September 1980, grown outdoors in sand culture in 45 L earthenware pots, and fed with Hoagland nutrient solution (Conradie, 1980). Vines were spur-pruned to three 3-node spurs during the winter of 1981 and the investigation was carried out during the last part of the 1981/82 and the first part of the 1982/83 season (second and third growing seasons, respectively). Fifteen vines were labelled with ^{15}N (Conradie, 1986) as outlined in Table 1. During a one-month period, starting one week after harvest, the standard Hoagland solution, applied twice per week, was enriched with ^{15}N labelled KNO_3 up to 7,35 atom % excess ^{15}N. To maximise the uptake of ^{15}N, nutrient leachate was collected and reapplied daily during this period and also over the next three weeks when standard Hoagland solution was applied. At the end of this period the sand was leached over a period of one week, and vines received standard Hoagland solution for the rest of the investigation period. Four whole vines were sampled before labelling (after harvest) while one unlabelled and three labelled vines were sampled at each of five further stages (Table 1).

During the second growing season the sampled vines were divided into roots, permanent wood (rootstock trunk and scion trunk plus cordons), shoots (current season's growth) and leaves (those on the vine plus fallen ones). Vines were spur-pruned before budbreak and from this stage onwards spurs were included with the permanent wood. During the third season, roots and permanent wood were sampled as before, while new growth was divided into leaves, shoots and bunches. Samples were dried, weighed and analysed for total N and insoluble N contents (Conradie, 1990). The ^{15}N concentration in both the total N and insoluble N fractions was determined as described by Conradie (1983; 1990). These values were corrected with the ^{15}N concentrations obtained for the unlabelled treatment, in order to obtain the ^{15}N enrichments for specific tissues. The amount of fertiliser-derived N (designated as "autumn N") present in each organ at the various sampling dates was calculated from the isotopic composition and dry mass (Conradie, 1991). At the first sampling of labelled vines (start of leaf-fall) the average amount of autumn-absorbed N present in a whole vine amounted 1830 mg. This was regarded as the pool of labelled N in all further calculations. The principle therefore entailed isotopic labelling of a portion of the N-fraction after which labelled N was washed from the root zone and the isotope subsequently "chased" with the normal fertilisation regime (Weinbaum & Muraoka, 1986). Time of sampling was expressed both as calendar date and growing degrees days (GDD) above 10°C. In the latter case, 1st September was regarded as the start of the growing season.

Utilisation of spring- and summer-absorbed N: The fate of N absorbed by two-year-old vines over a four-week period during late spring (end of bloom to the end of rapid shoot growth) was determined through labelling with ^{15}N in a way identical to that described for autumn-applied N. Distribution and translocation of the labelled pool were followed during the rest of the second and the first part of the third season through regular sampling. Details have

been published by Conradie (1990). In a separate experiment, two-year-old vines were labelled during early summer (end of rapid shoot growth to véraison) and the fate of this pool was followed into the third season (Conradie, 1991).

RESULTS AND DISCUSSION

Utilisation of autumn-absorbed N: Between harvest and the start of leaf-fall, the total N content of the roots was doubled (Fig. 1A), while 58% of the labelled N was also accumulated in these organs (Fig. 1B). Even though leaves exported N during this period, part of the labelled N was also incorporated, with the major portion being present in the insoluble (protein) form (Fig. 1B). This showed that protein synthesis continued during senescence and that the decline in the total amount of leaf proteins from after harvest to the start of leaf-fall (Fig. 1A) represented the difference between synthesis and degradation (Titus & Kang, 1982). The amount of N which migrated from the leaves during the post-harvest period (23%) was comparable to figures obtained in other field and pot experiments (Williams, 1987; Conradie, 1990, 1991). Part of the N lost by the leaves was probably relocated to the shoots and permanent wood (Williams, 1987; Conradie, 1990, 1991; Wermelinger & Koblet, 1990); this showed an increasing trend up to the start of leaf-fall.

Up to the end of leaf-fall insoluble N accounted on average for 70% of both the total N and labelled N present in the entire vine (Fig. 1). However, the contribution from the soluble pool (total N - insoluble N) increased during dormancy and reached a maximum value of *c.* 40% at budbreak. This is in agreement with previous results (Kliewer, 1967; Tromp & Ovaa, 1971; Schaefer, 1981; Conradie, 1990).

Due to leaf-fall and pruning the grapevines lost 34% of the total amount of N present at the start of leaf-fall (Table 2). A nearly identical loss of 35% was found for autumn-absorbed N, resulting in 65% [not 68% as erroneously reported by Conradie (1986)] of autumn-absorbed N still being present at the start of the third season.

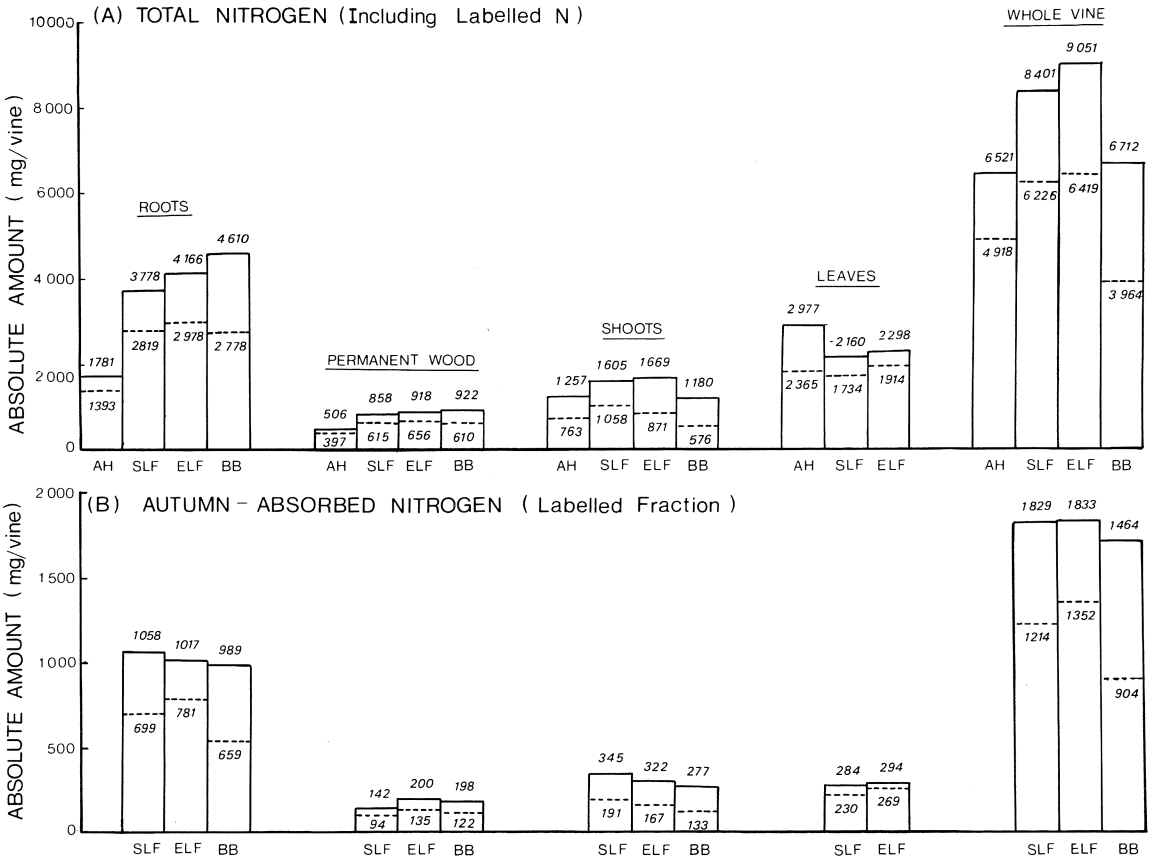

FIGURE 1

Seasonal accumulation of total nitrogen (A) and autumn-absorbed N (B) by different organs of the grapevine from harvest to budbreak. The dashed line indicates amount of insoluble N. AH = immediately after harvest; SLF = start of leaf-fall; ELF = end of leaf-fall; BB = budbreak.

TABLE 2
Total N and autumn-absorbed N as determined in Chenin blanc/99 Richter from harvest to budbreak.

Sampling time	Total N (mg/vine)(a)	Autumn-absorbed N (mg/vine)(b)
Immediately after harvest	6521 (801)	-
Start of leaf-fall	8401 (870)	1830 (201)
End of leaf-fall	6753 (753)	1539 (195)
Budbreak	5532 (624)	1187 (184)

(a) Figures in parentheses represent the SE of four replicates.
(b) Figures in parentheses represent the SE of three replicates.

In the current experiment the N-content of the vines was not measured at the start of the second growing season. It was, therefore, not possible to estimate the amount of N-reserves accumulated over the whole of the second growing season. The experiment with spring-absorbed N, however, was carried out with identical vines over the entire 1981/82 season and showed a seasonal N gain amounting to 2700 mg/vine (Conradie, 1990). It can, furthermore, be expected that at least 65% of the N (650 mg) absorbed during the period of active leaf-fall (Fig. 1A) will also be retained in the permanent structure, resulting in N absorbed during the post-harvest period contributing 1609 mg (1187 + 422) to the N-reserves present at the start of the third season. This amount constitutes 60% of the amount of N-reserves accumulated during the second season. In the case of older field-grown vines the amount of N-reserves accumulated during a specific season will probably constitute a smaller fraction of the total N-content. However, the general growth pattern of young, potted vines was found to be identical to that of mature vines (Löhnertz, 1988; Conradie 1990, 1991) and autumn-absorbed N should always be the main contributor to the N-reserves of grapevines, irrespective of age and cultivar.

At the start of the third growing season, total N and labelled N were distributed similarly between roots and permanent wood, with roots containing the major share of *c.* 83% (Table 3). Nearly identical distributions were found for spring-absorbed N (Conradie, 1990) and summer-absorbed N (Conradie, 1991). It can therefore be assumed that the roots of a two-year-old, pot-grown vine will contain *c.* 80% of the total N present at the end of the season, irrespective of the time during which the N was absorbed.

Utilisation of N during the second season after accumulation: From budbreak up to the 200 mm shoot length stage (before bloom) the permanent parts lost 6,2% of their total N while a slightly higher fraction (9,9%) of autumn-absorbed N was translocated (Table 4). At the end of bloom the difference between these two figures was even higher with 10,8% of the total N being lost from the permanent structure against 26,5% of the autumn-obsorbed N. In view of the fact that the total N in the permanent structure (stored N) is largely comprised of autumn-absorbed N, these figures clearly indicate that the N-content of the permanent parts was replenished with soil-derived N. It is generally accepted that perennial crops are strongly dependent on stored N during the first weeks after budbreak, while soil-derived N is the primary source during the rest of the season (Titus & Kang, 1982; Weinbaum *et al.*, 1984; Millard & Neilsen, 1989; Sanchez *et al.*, 1990). The above results, however, also indicate that reserve N may well be utilised over the course of the whole season. The extent to which these losses are compensated for by soil-derived N can be expected to increase as the season progresses from budbreak onwards. The fact that soil-derived N plays an increasing role during the later parts of the season is supported by the total N figures (Table 4) which indicated that the permanent structure supplied 30,5% of the N-demand exhibited by the new growth (shoots, leaves, and bunches) prior to bloom while it accounted for only 16,3% at the end of bloom.

TABLE 3
Relative distribution of total N and autumn-absorbed N among different organs of the grapevine, as measured from harvest to budbreak.

Organ	Total N (%)				Autumn-absorbed N (%)		
	AH (a)	SLF (b)	ELF (c)	BB (d)	SLF	ELF	BB
Roots	28,6	43,2	62,1	83,0	57,8	66,1	83,3
Permanent Wood	8,5	10,0	14,1	17,0	7,8	13,0	16,7
Shoots	21,0	22,5	23,8		18,9	20,9	
Leaves	41,9	24,3			15,5		
	100,0	100,0	100,0	100,0	100,0	100,0	100,0

(a) AH = Immediately after harvest.
(b) SLF = Start of leaf-fall.
(c) ELF = End of leaf-fall.
(d) BB = Budbreak.

TABLE 4
Seasonal changes in total N, autumn-absorbed N and ^{15}N concentrations in different organs of Chenin blanc/99 Richter from budbreak to the end of bloom in the third growing season[a].

Organ	Total N (mg/vine)			Autumn-absorbed N (mg/vine)			Atom% excess ^{15}N[b]		
	BB[c]	BBL[c]	ABL[c]	BB	BBL	ABL	BB	BBL	ABL
Medium Roots (>2 mm)	879(110)	881(101)	787 (93)	187(19)	180(15)	149(13)	0,340(0,013)	0,336(0,017)	0,292(0,034)
Fine Roots (≤ 2 mm)	3731(313)	3520(356)	3359(401)	802(79)	738(81)	647(59)	0,330(0,035)	0,332(0,047)	0,299(0,034)
Rootstock Trunk	489 (75)	441 (46)	383 (57)	115(13)	97(11)	38 (5)	0,355(0,021)	0,333(0,028)	0,155(0,017)
Scion Trunk plus Cordons	443 (61)	349 (35)	408 (39)	83 (9)	55 (7)	39 (6)	0,294(0,022)	0,235(0,019)	0,147(0,012)
Shoots	-	319 (33)	1448(171)		46 (6)	114(13)		0,243(0,016)	0,130(0,009)
Leaves	-	746 (65)	1749(162)		86(11)	153(14)		0,200(0,023)	0,132(0,011)
Bunches	-	52 (11)	446 (49)		7 (2)	41 (5)		0,228(0,026)	0,141(0,015)
Total	5532	6308	8580	1187	1209	1181			

(a) Figures in parentheses represent the SE of three or four replicates.
(b) Vines were labelled with ^{15}N immediately after harvest.
(c) BB = Budbreak, BBL = Before bloom (200 mm shoot length), ABL = After bloom.

During the initial growth stages leaves were the main sink for N, containing 66,8% of the total N and 61,8% of the labelled N present in new growth at the 200 mm shoot length stage. At the end of bloom these fractions were reduced to 48,0% and 49,7% for total N and labelled N, respectively. The fact that leaves contained equal fractions of total N and labelled (reserve) N indicated that newly absorbed N and reserve N must have been allocated in equal ratios to all the new organs in spite of leaves being a much stronger sink than either bunches or shoots up to the end of bloom. This was confirmed by the fact that the ^{15}N concentrations in all new organs (leaves, shoots and bunches) were comparable at each sampling date (Table 4). The above figures also confirm that a major fraction (up to 60%) of the annual N-demand of leaves is accumulated up to the end of bloom (Conradie, 1980; Löhnertz, 1988). This fraction is structural rather than photosynthetically functional and it may be difficult to remobilise during senescence (Sanchez & Righetti, 1990). In contrast, N accumulated in leaves after the end of bloom was readily translocated during the post-harvest period (Conradie, 1986).

Up to the 200 mm shoot length stage, labelled N accumulated during the previous spring, summer and autumn (1841 mg) contributed 206,9 mg towards the N-demand of the new growth, thus accounting for 18,9% (Table 5). The total amount of one-year-old reserves (2700 mg) should contribute 27,7% (18,9 x 2700/1841) towards the N-demand of new growth. It should be borne in mind, however, that sampling occurred more than five weeks after budbreak and that the relative contribution of stored N towards the N-demand of new growth may well have been considerably higher during the initial growth stage.

TABLE 5
Contribution of labelled N, accumulated over three specific stages during the second season, to the N-demand of new growth at the beginning of the third season.

Stage in second season during which labelled N was accumulated	Amount of labelled N present at the start of the third season (mg/vine)	Growth stage in third season					
		Before bloom (200 mm shoot length)			Two weeks after the end of bloom		
		Total N in new growth) (mg/vine)	Labelled N in new growth (mg/vine)	Labelled N as a fraction of total N(%)	Total N in new growth (mg/vine)	Labelled N in new growth (mg/vine)	Labelled N as a fraction of total N(%)
End of bloom to end of rapid shoot growth (spring)	273	1097[a]	29,6	2,70	3782[b]	68,8	1,82
End of rapid shoot growth to véraison (summer)	381	1097	37,9	3,45	3782	80,3	2,12
After harvest (autumn)	1187	1097	139,4	12,71	3782	307,7	8,14
Total for three stages	1841		206,9	18,86		456,8	12,08

(a) Total N in new growth varied from 1077 mg to 1117 mg in the different experiments, with 1097 mg being the average.
(b) Total N in new growth varied from 3643 mg to 4059 mg in the different experiments, with 3782 mg being the average.

From budbreak to the end of bloom labelled N contributed 12,08% towards the N-demand of new growth (Table 5). The contribution from all the one-year-old reserves can thus be estimated at 18% (12,08 x 2700/1841). At both sampling stages the contribution from one-year-old reserves was therefore comparable to the estimates obtained from the total N figures in Table 4 (30,5% and 16,3%, respectively), apparently indicating that the permanent structure functioned as a source of N only and that no soil-derived N was accumulated. However, if it is accepted that all N present in the vine at budbreak (5532 mg according to Table 4) will be utilised equally, the total contribution of stored N to the N-demand of new growth may be as high as 36% (12,08 x 5532/1841) at the end of bloom. This again indicates that active influx/efflux of N occurs in the permanent organs and that newly absorbed N compensates partly for reserve N lost to new growth. The uptake of N from the soil is largely affected by soil temperature (Sanchez *et al.*, 1990) and it can be speculated that the contribution from this source will vary from year to year, depending on climatic conditions.

Contribution of reserve N to the annual N demand of grapevines: When calendar days were used as a basis for comparison, new growth (leaves, shoots and bunches) utilised stored N from all three labelled pools linearly up to the end of bloom (*c.* 73 days after budbreak). It has been established that the utilisation of reserve N is affected by the time during which it was accumulated. In the case of roots, for example, summer-absorbed N is utilised from the start of the next season (Conradie, 1991) while no spring-absorbed N is relocated during the first five weeks after budbreak (Conradie, 1990). At the end of bloom, however, these differences did not appear to be of practical importance with about one quarter of labelled reserves having been relocated to new growth from all three pools (Fig. 2). A similar trend, *i.e.* a linear depletion of reserves during the first year after labelling, was also indicated for almonds (Weinbaum, Klein & Muraoka, 1987). Assuming that this linear trend will continue up to harvest, the best least square fits are presented in Figure 2. Previous experience has shown that Chenin blanc is normally harvested 165 days after budbreak, corresponding to *c.* 1 500 degree days. At this point the amount of labelled N utilised from the spring-, summer- and autumn-absorbed pools by the new growth of each vine can be estimated at 135 mg, 160 mg and 603 mg, respectively (Fig. 2). These amounts constituted 49%, 42% and 51% of the total amounts of labelled N present at budbreak for the spring, summer and autumn applications, respectively (Table 5), indicating that *c.* 50% of N reserves accumulated during the previous season were used up to harvest (Conradie, 1986; Weinbaum *et al.*, 1987).

About one third of the N-reserves present at the end of bloom could be utilised by new growth up to harvest (Table 4, Fig. 2). When the amount of reserve N utilised by new growth was plotted against growing degree days, a different linear relationship was obtained (not shown). The amounts of labelled N estimated, by means of this relationship, to be present in the new growth at harvest (1475 degree days) were nearly identical to those obtained by using calendar days (Fig. 2). The use of degree days as a criterion for expressing the seasonal accumulation of N, therefore, appeared to have little advantage over calendar days.

The vines used in this investigation were well-balanced, albeit young, and a realistic ratio for fruit/vegetative growth was maintained. The N-redistribution pattern for potted vines (Conradie, 1986, 1990, 1991) may, therefore be expected to be comparable to that of field-grown vines (Löhnertz, 1988). Up to the time of harvest, stored N originating from the previous spring, summer and autumn probably contributed a total of 898 mg N towards the demand of the vines used in the present study (Fig. 2) with the contribution from all one-year-old reserves estimated at 1317 mg. Previous work (Conradie, 1986) with potted Chenin blanc vines showed that the N present in the bunches at the time of harvest consistently amounted to *c.* 3250 mg, *i.e.* 43% of the N present in the new growth. One-year-old reserves will, therefore, supply 17,4% of this amount. If all stored N present at budbreak (5532 mg) is taken into account the relative contribution of reserve N (one year and older) can be as high as 35,7%. These estimates are virtually identical to the figures obtained two weeks after the end of bloom. From the end of bloom, however, reserve N lost from the permanent structure is replaced with newly absorbed N, which is not the case before bloom.

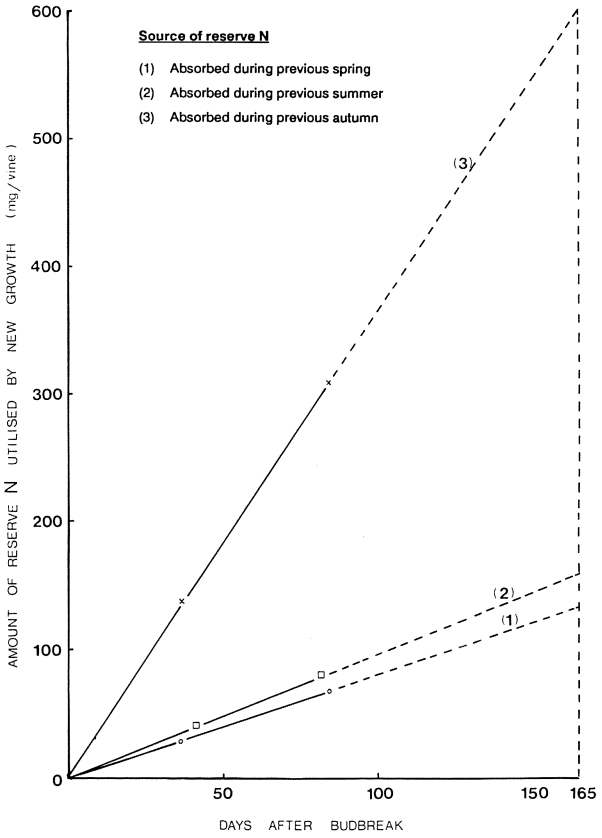

FIGURE 2
Utilisation of reserve N, originating from three different sources, during the following growing season.

CONCLUSIONS

This study showed that, in a warm country like South Africa, the major share (60%) of N-reserves present in a grapevine at the start of a growing season originates from N absorbed during the post-harvest period. A relatively early ripening cultivar (Chenin blanc) was used in the investigations and in the case of a later ripening cultivar, or in cooler countries, this accumulation may already start before harvest. A sufficient N-supply in the root-zone during this period is essential in order to prevent N-deficiencies during the next season.

It is generally accepted that perennial crops are strongly dependent on stored N during the first few weeks after budbreak while soil-derived N is the primary source during the rest of the season. In agreement with this, the new growth of grapevines used in the present study depended on reserve N, accumulated during the previous season, for *c.* 30% and 20% of their N-demand up to five weeks after budbreak and the end of bloom, respectively. Over these two stages soil-derived N did not replenish the reserve N lost by the permanent structure. From the end of bloom up to harvest, reserve N from the previous season was still contributing 18% to the N-demand of new growth, but this loss is completely compensated for by newly absorbed N. This shows that N is extremely mobile within the plant and with simultaneous influx/efflux of N occurring in most organs, the quantitative importance of reserve N is difficult to gauge. It can be expected that losses of reserve N will be replenished to a much smaller degree in N-stressed vines. This aspect should be investigated.

LITERATURE CITED

ALEXANDER, D. McE., 1957. Seasonal changes in the nitrogen content of the Sultana vine. *Aust. J. Agric. Res.* **8,** 162-178.

CONRADIE, W.J., 1980. Seasonal uptake of nutrients by Chenin blanc in sand culture: I. Nitrogen. *S. Afr. J. Enol. Vitic.* **1,** 59-65.

CONRADIE, W.J., 1983. The uptake and distribution of ^{15}N-enriched nitrate by three rootstock cultivars grafted to Chenin blanc. *S. Afr. J. Enol. Vitic.* **4,** 45-47.

CONRADIE, W.J., 1986. Utilisation of nitrogen by the grapevine as affected by time of application and soil type. *S. Afr. J. Enol. Vitic.* **7,** 76-83.

CONRADIE, W.J., 1990. Distribution and translocation of nitrogen absorbed during late spring by two-year-old grapevines grown in sand culture. *Am. J. Enol. Vitic.* **41,** 241-250.

CONRADIE, W.J., 1991. Distribution and translocation of nitrogen absorbed during early summer by two-year-old grapevines grown in sand culture. *Am. J. Enol. Vitic.* **42,** 180-190.

FREEMAN, B.M. & SMART, R.E., 1976. A root observation laboratory for studies with grapevines. *Am. J. Enol. Vitic.* **27,** 36-39.

HABIB, R., DE COCKBORNE, A-M., MONESTIEZ, P. & LAFOLIE, F., 1989. An experimental test of a nitrogen uptake and partitioning model for young trees. *Tree Physiology* **5,** 403-421.

KLIEWER, W.M., 1967. Annual cyclic changes in the concentration of free amino acids in grapevines. *Am. J. Enol. Vitic.* **18,** 126-137.

KOBLET, W., & PERRET, P., 1990. Beziehung zwischen Triebwachstum, Wurzelentwicklung und Assimilatwanderung in Topfreben. *Wein-Wiss.* **45,** 93-96.

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.

LEGAZ, F., PRIMO-MILLO, E., PRIMO-YUFERA, E., GIL, C. & RUBIO, J.L., 1982. Nitrogen fertilization in citrus. I. Absorption and distribution of nitrogen in Calamondin trees (*Citrus mitis* Bl.) during flowering, fruit set and initial fruit development periods. *Plant and Soil* **66,** 339-351.

LÖHNERTZ, O., 1988. Nährstoffelementaufnahme von Reben im Veraluf eines Vegetationszyklus. *Mitt. Klosterneuburg* **38,** 124-129.

MILLARD, P. & NEILSEN, G.H., 1989. The influence of nitrogen supply on the uptake and remobilization of stored N for the seasonal growth of apple trees. *Annals of Botany* **63,** 301-309.

PEACOCK, W.L., CHRISTENSEN L.P. & BRAODBENT, F.E., 1989. Uptake, storage and utilization of soil-applied nitrogen by Thompson Seedless as affected by time of application. *Am. J. Enol. Vitic.* **40,** 16-20.

SCHAEFER, H., 1981. Der jahreszeitliche Verlauf de Stoffwechsels der loslichen und unloslichen proteine in den verholtzten Rebenorgane. *Wein-Wiss.* **36,** 3-20.

SANCHEZ, E.E. & RIGHETTI, T.L., 1990. Tree nitrogen status and leaf canopy position influence postharvest nitrogen accumulation and efflux from leaves. *J. Amer. Soc. Hort. Sci.* **115,** 934-937.

SANCHEZ, E.E., RIGHETTI, T.L., SUGAR, D. & LOMBARD, P.B., 1990. Seasonal differences, soil texture and uptake of newly absorbed nitrogen in field-grown pear trees. *J. Hort. Sci.* **65,** 395-400.

TITUS, J.S. & KANG, S., 1982. Nitrogen metabolism, translocation and recycling in apple trees. *Hort. Rev.* **4,** 204-246.

TROMP, J. & OVAA, J.C., 1971. Spring mobilization of storage nitrogen in isolated shoot sections of apple. *Physiol. Plant.* **25,** 16-22.

VAN ZYL, J.L., 1984. Response of Colombar grapevines to irrigation as regards quality aspects and growth. *S. Afr. J. Enol. Vitic.* **4,** 19-28.

WEINBAUM, S.A., KLEIN, I., BROADBENT, F.E., MICKE, W.C. & MURAOKA, T.T., 1984. Effects of time of nitrogen application and soil texture on the availability of isotopically labelled fertilizer nitrogen to reproductive and vegetative tissue of mature almond trees. *J. Amer. Soc. Hort. Sci.* **109,** 339-343.

WEINBAUM, S.A., KLEIN, I. MURAOKA, T.T., 1987. Use of nitrogen isotopes and a light-textured soil to assess annual contributions of nitrogen from soil and storage pools in mature almond trees. *J. Amer. Soc. Hort. Sci.* **112,** 526-529.

WEINBAUM, S.A. & MURAOKA, T.T., 1986. Nitrogen redistribution from almond foliage and pericarp to the almond embryo. *J. Amer. Soc. Hort. Sci.* **111,** 224-228.

WILLIAMS, L.E., 1987. Growth of 'Thompson Seedless' grapevines: II. Nitrogen distribution. *J. Amer. Soc. Hort. Sci.* **112,** 330-333.

WERMELINGER, B. & KOBLET, W., 1990. Seasonal growth and nitrogen distribution in grapevine leaves, shoots and grapes. *Vitis* **29,** 15-26.