

Distribution and Translocation of Nitrogen Absorbed During Late Spring by Two-Year-Old Grapevines Grown in Sand Culture

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Distribution and translocation of spring-applied nitrogen (N) were quantified for two-year-old Chenin blanc grapevines grown in sand culture. Vines were labeled with ¹⁵N over a four-week period stretching from the end of bloom to the end of rapid shoot growth. From this stage onwards, vines were fed unlabeled KNO₃, and entire vines were sampled eight times over a period of 11 months. Five samples were taken in the second and three during the third growing season. At the first sampling date (one week after the end of labeling), 55% of the labeled N was found in the vegetative growth, 20% in the bunches, and 25% in the permanent structure. Up to harvest, the total N content of shoots and leaves did not decrease, but the amount of labeled N showed losses of 48% and 21%, respectively. This indicated the importance of these organs as transitional reservoirs for N absorbed during late spring. Spring-applied N was also translocated from the permanent structure, resulting in the bunches containing 45% of the labeled N at harvest. Nearly 40% of the spring-applied N still present in the leaves at harvest was translocated to the shoots and the permanent structure during leaf senescence. At the end of dormancy, the fine roots, rootstock- and scion trunks contained similar concentrations of labeled N, but the rootstock trunk showed a larger proportion of soluble N. At the start of the third growing season, new growth utilized reserve N more readily from the permanent wood than from the roots, but roots played an important role at a later stage, *i.e.*, during bloom. The annual turnover of N for the whole vine appeared to be in the order of 80%, which is considerably higher than that of some other deciduous crops.

KEY WORDS: nitrogen, grapevine, distribution, translocation, spring-applied N

Research on the amount of N required by the grapevine has been done since the early part of the 20th century. However, the work of Conradie (5) on young, potted Chenin blanc grown outdoors and that of Araujo and Williams (2) on young, field-grown Thompson Seedless are the only known studies in which the absolute amount of N present in the entire vine was determined over the course of a full season. Results from both these trials and from several others done with woody perennials (1,7,12,18,20,22,23,27) stressed the importance of the permanent structure as a major storage organ for N to be utilized by new growth at the start of the next season. In the case of the potted trial (5), the roots played an important role as a storage organ for N, which was not the case for the field-grown vines (2). In the latter case, however, N from permanent wood supplied between 14% and 26% of the N required for shoot growth shortly after budbreak. Furthermore, remobilization of N from the vegetative parts to the bunches was found in the potted vines, while this was not the case for 15-year-old, field-grown Thompson Seedless vines (32). The differences between these trials may point to the dynamics of growth for potted vines with restricted root systems being different from field-grown vines (2). How-

ever, differences might also have been cultivar bound as Chenin blanc is a very productive variety (9) and normally less vigorous than Thompson Seedless which is known for continued growth after harvest in hot regions. The latter fact may prevent the accumulation of nutrients in perennial parts such as roots. Soil temperatures at the time of budbreak may also have a pronounced effect in stimulating active root growth. In the warmer inland areas of South Africa, root growth on sandy soil was found to commence four weeks before budbreak (16), in contrast to the Western Cape where root growth of field-grown vines commenced, as in the case of the potted vines, only four weeks after budbreak (26).

From the foregoing it is clear that our understanding of the N metabolism of the grapevine is far from complete. This is largely due to the impossibility of distinguishing with conventional methods between reserve N and newly absorbed N. However, by using isotopically labeled N, it was possible to distinguish, for deciduous and evergreen fruit trees, between an endogenous pool of previously assimilated N and currently available N (11,14,28,29). For grapevines, this technique has also been used to determine N utilization on two different soil types (7) and differences in N-uptake between different rootstocks (6).

The first objective of this study was to determine the distribution and translocation of N absorbed during a four-week period immediately after the end of bloom. This phenological stage was chosen because it entails the uptake of 12% to 15% of the grapevine's annual demand for N (5,7). Furthermore, cell division is actively taking place during this period, resulting in a

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characteristically high rate of berry growth, making optimization of N availability essential. Secondly, the aim was to differentiate between the utilization of reserve N from either the soluble or the insoluble pool. In this respect, there have been indications that the grapevine stores part of its reserve N as soluble low-molecular weight compounds (12), but soluble and insoluble proteins are utilized as well (20).

In order to quantify the translocation and utilization of spring-applied N, isotopically labeled KNO_3 was applied to potted, bearing grapevines over a period of four weeks after the end of bloom. This created a pool of labeled N designated as "spring N". Following this, the vines were fed normally, sampled periodically, and analyzed over a period of 11 months.

Materials and Methods

The research was conducted at the VORI experimental farm, Stellenbosch, with *Vitis vinifera* L, cv. Chenin blanc grapevines grafted on 99 Richter, grown outdoors in sand culture in 45-L earthenware pots with Hoagland's solution as nutrient medium, as already described (5). One-year-old nursery vines were planted during September 1980, allowed to develop normally for one year, spur-pruned to three 3-node spurs during the winter of 1981, and suckered after budbreak to retain eight shoots per vine. The 1981-1982 season (vines in their third leaf, i.e., one year in the nursery and the

second season in pots) was regarded as the second growing season and 1982-1983 as the third. In the second growing season, 32 vines were labeled with ^{15}N during a four-week period starting immediately after the end of bloom, as outlined in Table 1. This was obtained, as already described (7), by replacing part of the standard KNO_3 in Hoagland's solution with ^{15}N -labeled KNO_3 (9.87 atom % excess ^{15}N). Nutrient leachate was collected and reapplied daily during this period in order to maximize uptake of N. At the end of the labeling period, excess ^{15}N was leached from the sand over a period of one week, and vines received standard Hoagland's solution for the rest of the investigation period.

Whole vines were sampled six times during the second season, i.e., end of bloom (before labeling), end of rapid shoot growth (one week after the end of labeling), veraison, harvest, start of leaf-fall, and end of leaf-fall (Table 1). Fallen leaves were collected quantitatively during leaf-fall. Vines were pruned to four 3-node spurs just before the start of the third season. This resulted in about 90% of the shoots (one-year-old wood) being removed. During this season, spurs were sampled together with permanent wood while new shoots were again sampled from 6 October (before bloom). Vines were sampled three times during the third growing season, i.e., budbreak, 200-mm shoot length (before bloom), and at the end of bloom (Table 1). Four labeled

Table 1. Outline of experiment

Date	Growth Stage of vines	Growth Season	N supplied	Sampling Date ^(a)	
21 October	Bloom	2nd Season	(Unlabeled)		
11 November			11 November ^(b)	11 November	
	Rapid shoot growth		(Labeled)		
18 December			10 December	18 December	
			(No N) ^(c)		
	Véraison			18 December	
4 January				8 January	
11 February	Harvest			11 February	
21 April	Leaf-fall			(Unlabeled)	21 April
20 June					20 June
30 August	Dormancy			30 August	
19 October	Bloom	3rd Season		6 October	
8 November				22 November	

(a) Thirty-two vines were labeled with ^{15}N from 11 November to 10 December.

(b) Five unlabeled vines were removed on 11 November, while one unlabeled and four labeled vines were sampled on all other dates.

(c) Excess ^{15}N was leached out during this period.

vines and one unlabeled control (for $^{14}\text{N}/^{15}\text{N}$ ratios) were lifted at each sampling and divided into the different organs as previously described (5,7). All samples (excluding bunches) were dried in a vacuum oven at 40°C, while bunches were freeze dried. After weighing and grinding, samples were stored at -10°C until analyzed.

Dried samples were digested by means of a salicylic acid modification of the regular Kjeldahl method in order to recover nitrates quantitatively (3). Total N concentration and ^{15}N abundance were determined as described in an earlier paper (6). Insoluble N was determined using the method of Tromp and Ovaas (25), whereby proteins were precipitated with trichloroacetic acid. The precipitate was then digested and analyzed for total N concentration and ^{15}N abundance as above. The absolute amounts of soluble N present in the various organs were calculated by subtracting the figure for insoluble N from the total N. This fraction may be accepted to consist mainly of amino acids but is not directly comparable to soluble N figures obtained through the extraction of plant material (12,20).

The amount of fertilizer-derived N ("spring-N") present in each organ at the various sampling dates was calculated from the isotopic composition and dry mass (6). At the first sampling of labeled vines (end of rapid shoot growth), the average amount of "spring-N" present in the whole vine came to 1132 mg. This was regarded as the pool of labeled N in all further calculations. All results were subjected to statistical analyses and significance of differences between sampling dates determined by means of a D-value based on the Student's Q test (21).

Results and Discussion

Roots: The pattern for accumulation of dry mass by medium and fine roots (Fig. 1a, 1b) showed, apart from a distinct dip between veraison and harvest, a steady increase to the start of leaf-fall. These findings are in agreement with the results from previous pot trials (5), while field-grown Colombar/99R also showed two maxima with very little growth occurring during mid-summer (16,26). The fine roots showed a loss in dry mass at the start of the third season (Fig. 1b). This is in agreement with the previous pot trial (5), but no indications of a reduction in dry mass after budbreak were found in a field trial with young, pruned Thompson Seedless (2). In the latter case, however, active root growth also started relatively late in the season, *i.e.*, not before 500 growing degree days (GDD). According to the figures for California (31), the 500 GDD stage is reached more than two months after budbreak, coinciding in the current trial with the end of bloom when active accumulation of dry material was starting to take place.

Changes in the absolute amount of total N in the medium roots correlated with that of the dry mass (Fig. 1c). For fine roots (Fig. 1d), no significant changes occurred up to harvest. The latter result differs from that found previously (5) but is in line with that found for young, pruned, field-grown vines (2). After harvest, however, the amount of total N increased as expected

while, similar to the dry mass, a reduction occurred after budbreak in the third season. Soluble N accumulated in both root fractions from harvest up to budbreak, which can be partly ascribed to hydrolysis of proteins (12,20,25). From budbreak to the end of bloom the soluble N concentrations were reduced significantly suggesting translocation to new growth.

In the case of "spring-N" (Fig. 1e, 1f), the amounts of total N up to harvest were reduced by 67% and 47% for medium and fine roots, respectively, in contrast to reductions of only 26% and 13% for the absolute amounts of N (Fig. 1c, 1d). Similar results have been obtained for citrus (14,15) and show that spring-absorbed N is utilized in preference to "older" reserves. Furthermore, differences in the partitioning of N between the soluble and insoluble pools were illustrated by the fact that, at harvest, 29% ($440/1540 \times 100$) of the absolute amount of N (Fig. 1d) in the fine roots was present in the soluble form (amino acids) as against only 17% ($20.2/115.5 \times 100$) of the spring-applied N (Fig. 1f). From harvest to the end of leaf-fall, the amounts of spring-applied N increased by 230% and 46% for medium and fine roots, respectively, resulting in the medium roots containing more "spring-N" than the amount present at the start of the experiment. This confirms the ease with which N can translocate within a plant (11) and also the importance of medium roots as organs for the storage of reserve N. In the third growing season, no "spring-N" from the roots was utilized for new growth immediately after budbreak (30 August to 6 October), but significant export occurred over the flowering period. This shows that reserve N accumulated during spring was still actively utilized one year after absorption. For almonds, the reproductive organs were also found to be highly dependent on the endogenous pool of stored N during the early developmental stages (27).

Permanent wood: For the permanent wood, *i.e.*, rootstock- and scion trunks, dry mass increased as expected (2,5) from the end of rapid shoot growth to the start of leaf-fall (Fig. 2a, 2b). In contrast to roots, the absolute amounts of N (Fig. 2c, 2d) did not decrease between veraison and harvest but showed an increasing trend. However, some recycling of N must have occurred during this period as the amounts of "spring-N" were reduced by 23% and 25% for the rootstock and scion trunks, respectively (Fig. 2e, 2f). The fact that an organ can absorb N and export it at the same time has also been found for citrus (14,15). During autumn and dormancy, absolute and "spring-N" increased, and as for medium roots, both trunk fractions ended the second season with more "spring-N" than the amounts initially present. For the rootstock trunk a large portion of the "spring-N" remained in the soluble form (Fig. 2e), and both fractions supplied N to new growth immediately at the start of the third season. This is in contrast to the roots and indicates that, as in the case of other deciduous fruits (17,24), the new growth utilizes reserve N more readily from organs closest to the point of new growth.

The annual cycle of N in the permanent structure of

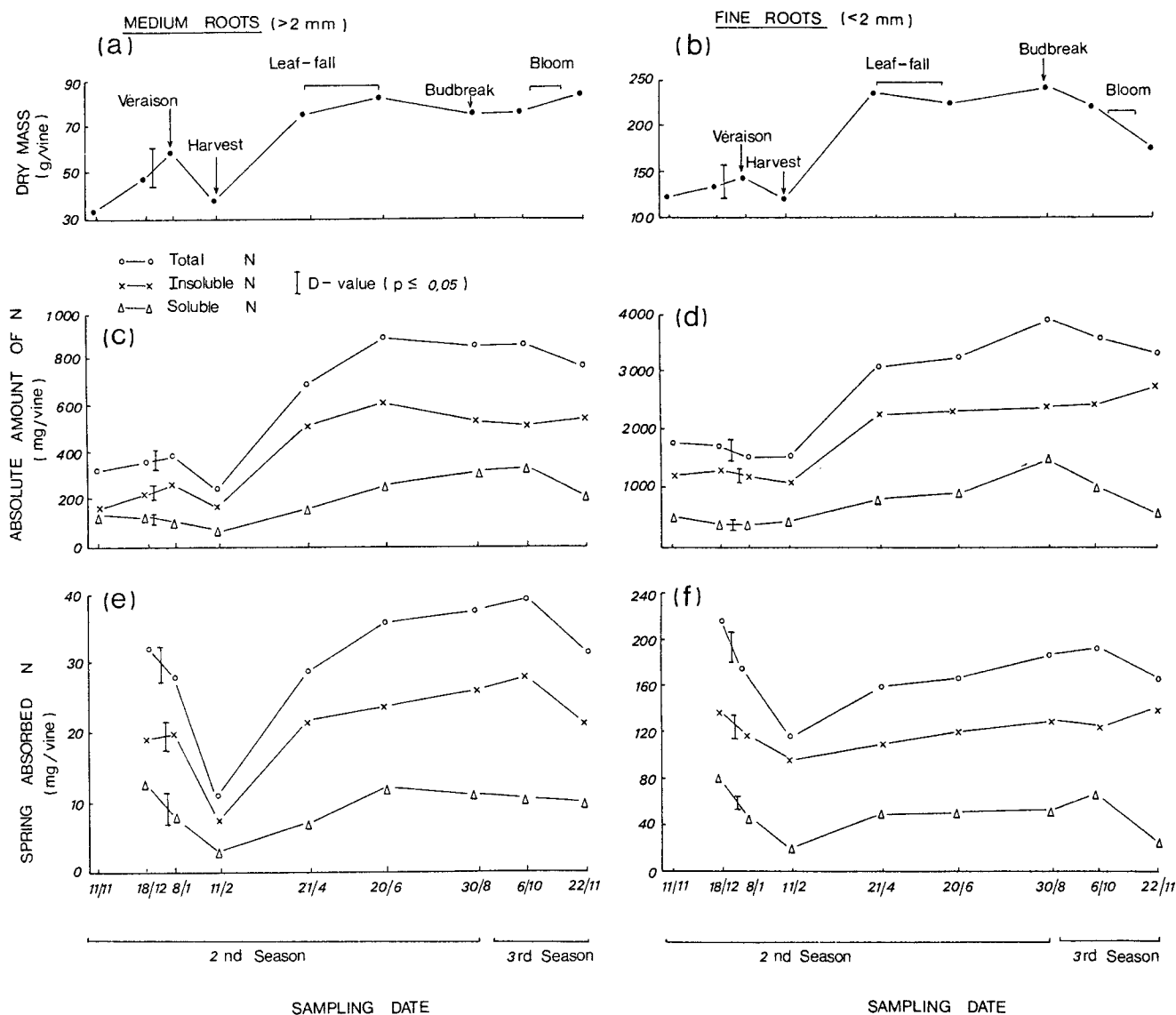


Fig. 1. Seasonal changes in dry mass, as well as absolute amounts of N and spring-applied N in the different nitrogenous fractions of roots of Chenin blanc/99R.

the vine (roots and wood), therefore, showed that a fraction of spring-applied N is retained in the roots, mostly as proteins, in spite of the vines being adequately nourished — as was the case in this experiment. Up to harvest, about half of the “spring” reserves from the roots (medium and fine roots combined) were utilized by the new growth against only a quarter from the permanent wood. In autumn, N is accumulated in all the permanent organs in both soluble and insoluble forms, with the rootstock trunk containing the highest proportion of soluble N. At the onset of the next season, reserve N from the wood is mobilized in preference to that from the roots. However, all the other permanent organs also showed decreases in soluble N contents during the stage of active growth. Similar indications have been obtained previously (12,20).

Shoots and leaves: Dry mass of shoots (current season's growth) increased linearly up to veraison, at a

slower rate to the start of leaf-fall, and showed a reduction of 37% during leaf-fall and dormancy (Fig. 3a). For leaves (Fig. 3b), dry mass showed a relatively rapid increase up to veraison and a slower rate to the end of leaf-fall, which is in agreement with previous results (5,31).

The absolute amount of N in shoots increased to the start of leaf fall (Fig. 3c), while leaves showed an increase up to harvest (Fig. 3d). This appeared to be in contrast to previous findings (1,5) and to support the view that an increase in cluster-N content does not occur at the expense of N remobilization from vegetative structures (32). However, the figures for “spring-N” (Fig. 3e,3f) showed, up to harvest, declines of 48% and 21% for shoots and leaves, respectively. This signifies a simultaneous influx and efflux of N and has already been substantiated for citrus (15), almond (29), and wheat (33). As in the case of apples (24), growing leaves

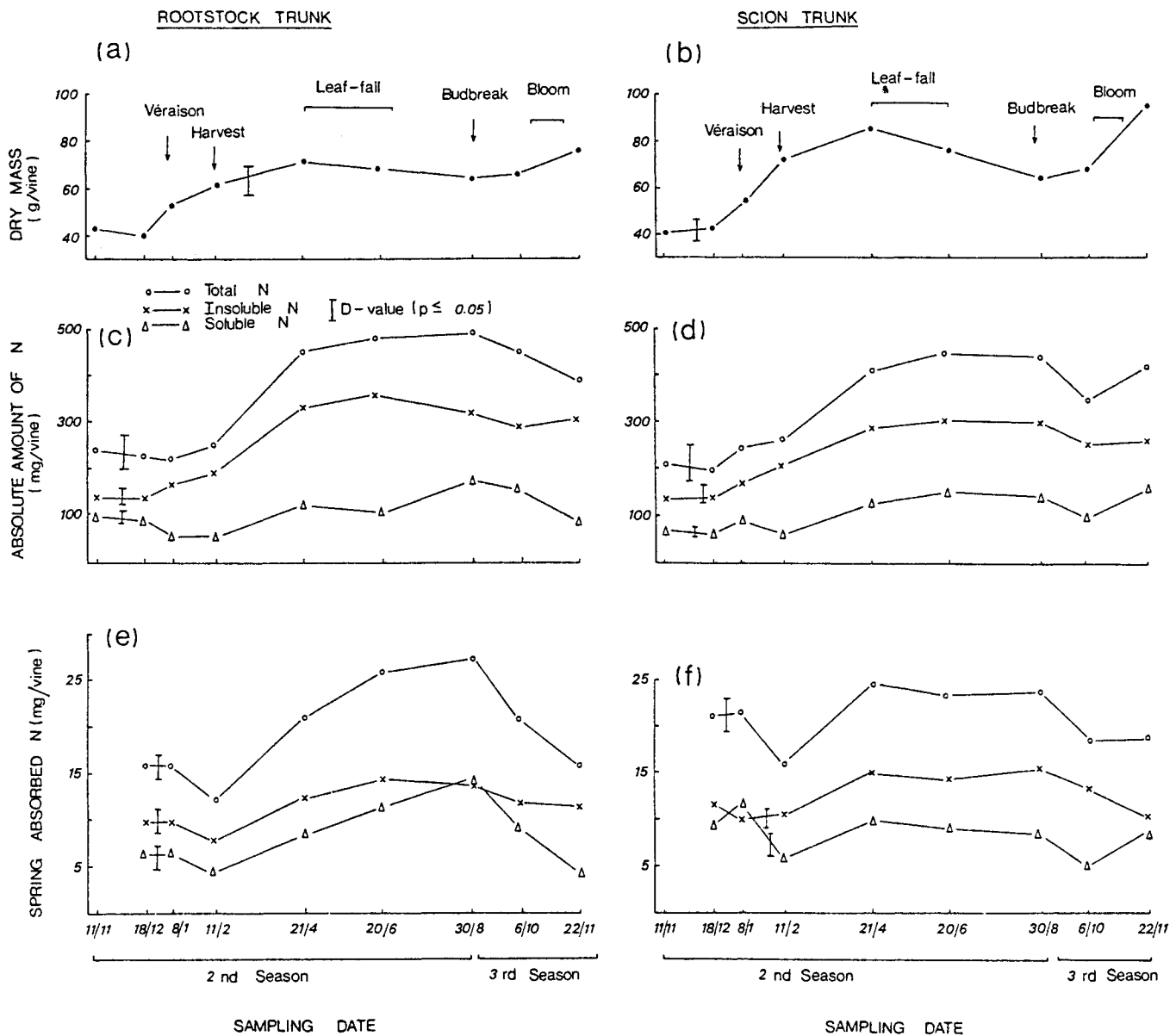


Fig. 2. Seasonal changes in dry mass, as well as absolute amounts of N and spring-applied N in the different nitrogenous fractions of the rootstock- and scion trunks of Chenin blanc/99R.

and shoots of grapevines, therefore, also effectively act as intermediate reservoirs of nitrogenous compounds imported from the roots. High turnover of spring-applied N takes place in these organs with a large fraction, initially present as proteins (Fig. 3e, 3f), being hydrolyzed and exported to the bunches. As expected (1,5,6,32), N migrated from leaves after harvest, with the total N showing a decline of 21% (Fig. 3d) against an even larger loss of 38% for “spring-N” (Fig. 3f). Part of this N was remobilized to the shoots which showed increases from harvest to the start of leaf-fall. However, as found for fruit trees (24), this gain of N by the shoots was only temporary, and migration, probably to the older wood and root system, occurred during leaf-fall and dormancy. Spring-applied N (Fig. 3e) was lost at a faster rate than absolute N (Fig. 3c)

Bunches and entire vine: The dry mass of

bunches increased relatively slowly up to the end of rapid shoot growth (18 December), after which a sharp, linear increase was observed up to harvest (Fig. 4a). A similar trend was found for other cultivars (2,9,31). The total N (Fig. 4c) and “spring-N” contents (Fig. 4e) of the bunches increased by 316% and 119%, respectively, from the end of rapid shoot growth up to harvest, which implied a reduction in the contribution of “spring-N” to the total N of the bunches from 30% to 16%. This indicated that, even though an appreciable fraction of spring-applied N is translocated, bunches were also largely dependent on other sources of N. At harvest, absolute N and “spring-N” were distributed evenly between the soluble and insoluble pools (Fig. 4c, 4e).

The dry mass and absolute N content of the whole vine (Fig. 4b, 4d) increased until the start of leaf-fall, which is in general agreement with previous results (2,

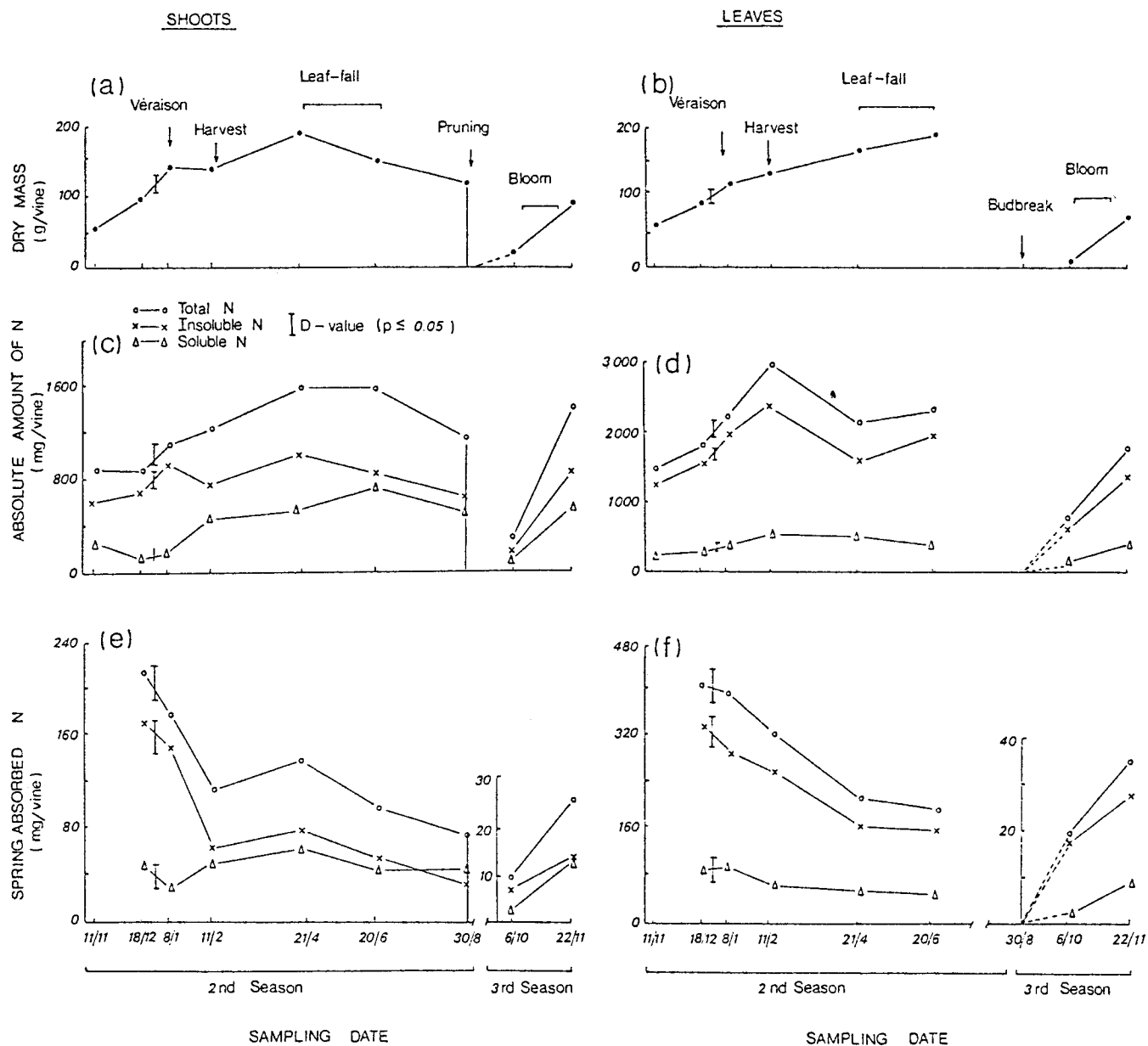


Fig. 3. Seasonal changes in dry mass, as well as absolute amounts of N and spring-applied N in the different nitrogenous fractions of the shoots and leaves of Chenin blanc/99R.

5). However, in the previous pot trials (5) as well as in field trials (13), uptake of N slowed down before harvest which was not the case in the present trial. In spite of this difference, the amount of N absorbed up to harvest, expressed as a fraction of the seasonal demand (73%), was comparable the 66% of the previous trial (5), indicating, for the same scion/rootstock combination, a fixed ratio for the uptake of N.

The total amount of spring-applied N present in the whole vine showed a loss of about 5% up to harvest (Fig. 4f). From this time onwards, only minor losses occurred, and at budbreak in the third season the amount of labeled N which could not be accounted for came to only 8% (7). Losses of ^{15}N on account of factors like the dieback of roots and root exudates was, therefore, negligible.

The suggestion that a linear relationship exists between the grapevine's accumulation of dry material and N (2) was confirmed in this trial (Fig. 4b, 4d). The N concentration of the entire vine was approximately 1% over the whole season, which is comparable to previous results (2,5,13).

The ratio for aerial/root dry mass (0.98), as measured at the end of leaf-fall, was comparable to the average figure (1.18) recorded in South Africa for 10-year-old field-grown vines (19). Root masses increased from the second to the third season (Fig. 1a, 1b) indicating that root growth was not restricted during the investigation period. Grafted grapevines, therefore, appear to be well suited to pot experiments for at least two seasons. In the case of Chenin blanc, a well balanced

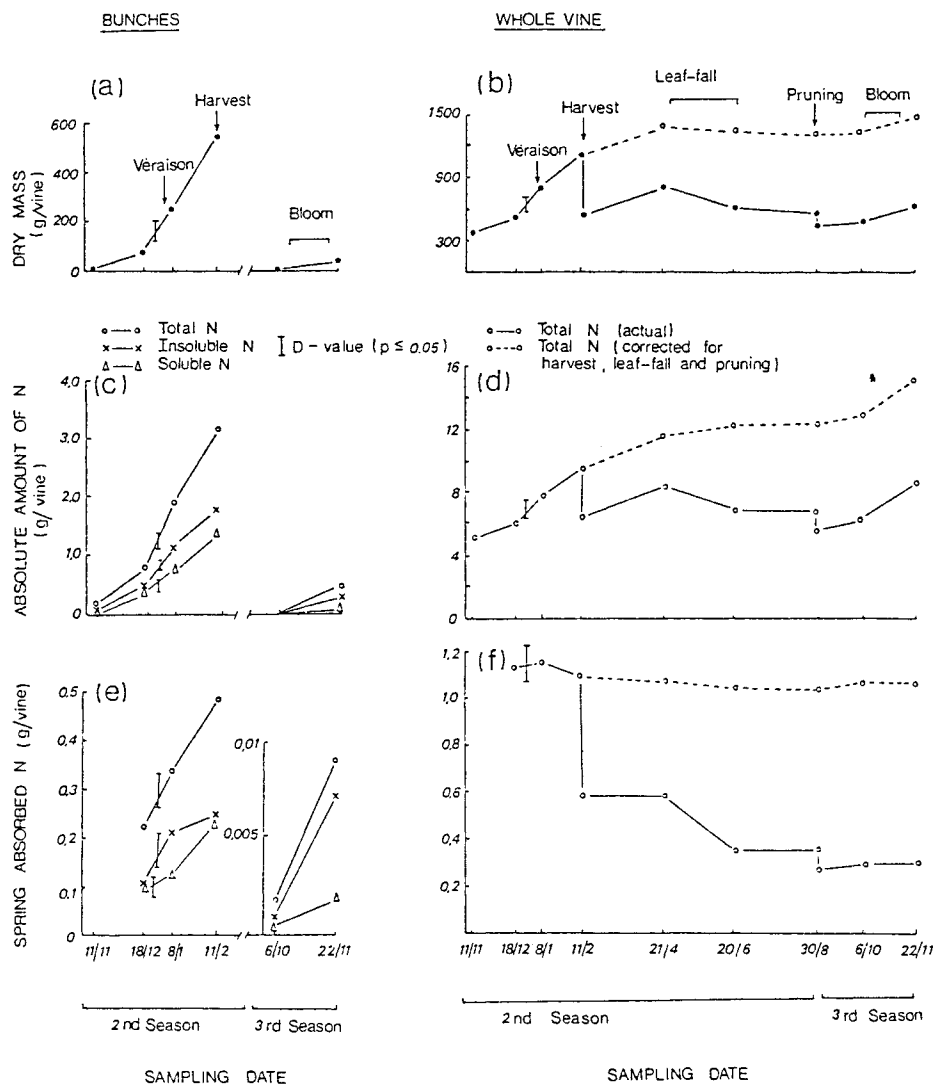


Fig. 4. Seasonal changes in dry mass, as well as absolute amounts of N and spring-applied N in the different nitrogenous fractions of the bunches and the entire Chenin blanc/99R vine.

plant with a realistic yield of about 3.5 kg/vine and a normal yield/shoot ratio of 7.5 (data not shown) was obtained. In general, the growth pattern observed in this study was similar to that reported for field-grown grapevines (9, 30).

Annual changes in N and ¹⁵N concentrations:

The N concentrations in all permanent parts showed a downward trend up to harvest (Table 2). From this stage up to the end of dormancy (30 August) the concentrations increased before starting to decrease as new growth commenced in the third season. Leaves and bunches, however, showed a decreasing trend throughout the season as was found by several other workers (4, 5, 13, 32). The N concentration in shoots increased from the start of leaf-fall to the time of pruning, probably partly due to a concentration effect on account of reduced dry mass (Fig. 3a). During this period, however, the concentration of insoluble N remained constant, pointing to the hydrolysis of proteins. In the case of permanent organs, insoluble N concentrations reached

minimum values from veraison to harvest.

At the first sampling date, the shoots, leaves, and bunches contained a higher concentration of labeled N than the permanent parts (Table 3). Similar results were obtained for citrus (8, 14) while N absorbed during spring by almond was also preferentially translocated to vegetative growth (27). The ¹⁵N concentration in the total N (TN) fraction of the permanent parts was reduced as the season progressed, and at the end of leaf-fall the fine roots, rootstock- and scion trunks reached a comparable value of ca 0.24 atom % excess ¹⁵N. When new growth commenced, the concentrations in the permanent wood again declined and at the end of the experiment the ¹⁵N concentration in the TN fraction was similar at ca 0.18% for medium roots, rootstock- and scion trunks, implying that all organs contributed equally to new growth and bunches. The fact that the fine roots contained a higher concentration of labeled N might have been a concentration effect on account of the reduction in dry mass (Fig. 1b)

Up to harvest, bunches showed a higher concentration of labeled TN than either shoots or leaves, confirming the dominating demand of bunches for N. The efflux of N, occurring from the shoots between harvest and pruning, was illustrated by a significant reduction in labeled TN concentration (Table 3). At the end of

bloom in the third season, new growth (shoots, leaves, and bunches) contained a similar amount of ca 0.08 atom % excess ¹⁵N in the case of TN. This indicated that N supplied during the previous spring (labeled N) and the N newly absorbed in the next spring were utilized in equal ratios by all the new organs. In general, labeled N concentrations tended to be lower in the insoluble N (IN) fraction than in TN, suggesting that spring-applied N made a larger relative contribution to the soluble pool (amino acids) than to the insoluble one (proteins). This was confirmed by the scion trunk with relatively low ¹⁵N concentrations in the IN fractions on 18 December and 8 January (Table 3) and large portions of spring-applied N present in the soluble form on these dates (Fig. 2f). However, it was clear that the translocation of labeled N cannot be judged from concentration figures alone, but that changes in dry mass should be taken into account as well.

Relative distribution of total N and “spring N”: From Figure 5a it can be calculated that, at the end

Table 2. Seasonal changes in total N (TN) and insoluble N (IN) concentrations in different organs of Chenin blanc/99 Richter (% dry mass).

Date	Phenological stage	Medium roots (> 2 mm)		Fine roots (< 2 mm)		Rootstock trunk		Scion trunk		Shoots		Leaves		Bunches	
		TN	IN	TN	IN	TN	IN	TN	IN	TN	IN	TN	IN	TN	IN
11 November	End of bloom	0.99	0.51	1.49	0.97	0.55	0.32	0.50	0.34	1.53	1.10	2.63	2.14	2.19	1.16
18 December	End rapid shoot growth	0.76	0.49	1.30	0.91	0.55	0.34	0.45	0.32	0.91	0.75	2.33	1.89	0.95	0.53
8 January	Veraison	0.67	0.49	1.07	0.75	0.42	0.32	0.46	0.30	0.83	0.68	2.19	1.81	0.74	0.46
11 February	Harvest	0.64	0.45	1.27	0.91	0.40	0.30	0.36	0.28	0.90	0.55	2.49	2.05	0.56	0.32
21 April	Start of leaf-fall	0.94	0.72	1.32	1.02	0.65	0.45	0.48	0.34	0.84	0.55	1.33	1.07	-	-
20 June	End of leaf-fall	1.09	0.76	1.50	1.00	0.69	0.52	0.58	0.40	0.99	0.56	1.30 ^b	1.08 ^b	-	-
30 August	Budbreak	1.15	0.74	1.67	1.09	0.77	0.49	0.67	0.44	1.01 ^a	0.56 ^a	-	-	-	-
6 October	Before bloom (200 mm shoots)	1.15	0.69	1.58	1.07	0.68	0.43	0.52	0.37	1.81	1.18	3.44	2.87	2.82	2.10
22 November	Two weeks after bloom	0.93	0.68	1.89	1.56	0.52	0.39	0.42	0.29	1.66	1.00	2.71	2.19	1.41	1.01
	D value ($p \leq 0.05$)	0.12	0.11	0.14	0.13	0.09	0.08	0.09	0.07	0.14	0.13	0.18	0.14	0.24	0.21

^aOne-year-old shoots removed through pruning just before budbreak.

^bFallen leaves collected during leaf-fall.

Table 3. Seasonal changes of ¹⁵N concentrations in the total N (TN) and insoluble N (IN) fractions of different organs of Chenin blanc/99 Richter (atom % excess ¹⁵N).

Date	Phenological stage	Medium roots (> 2 mm)		Fine roots (< 2 mm)		Rootstock trunk		Scion trunk		Shoots		Leaves		Bunches	
		TN	IN	TN	IN	TN	IN	TN	IN	TN	IN	TN	IN	TN	IN
18 December	End of rapid shoot growth	0.406	0.392	0.553	0.486	0.326	0.280	0.510	0.430	1.199	1.130	1.051	1.009	1.352	1.202
8 January	Veraison	0.339	0.331	0.442	0.406	0.328	0.268	0.378	0.295	0.688	0.687	0.796	0.754	0.878	0.865
11 February	Harvest	0.207	0.212	0.344	0.354	0.231	0.192	0.295	0.235	0.393	0.380	0.481	0.498	0.706	0.637
21 April	Start leaf-fall	0.185	0.200	0.246	0.243	0.227	0.178	0.269	0.235	0.386	0.345	0.434	0.426		
20 June	End leaf-fall	0.185	0.200	0.248	0.261	0.239	0.186	0.238	0.221	0.275	0.283	0.402 ^b	0.382 ^b		
30 August	Budbreak	0.186	0.214	0.235	0.241	0.234	0.190	0.251	0.236	0.263 ^a	0.243 ^a	-	-		
6 October	Before bloom (200 mm shoots)	0.201	0.228	0.245	0.238	0.213	0.185	0.242	0.241	0.133	0.137	0.124	0.133	0.145	0.141
22 November	Two weeks after bloom	0.180	0.187	0.234	0.231	0.182	0.169	0.206	0.185	0.085	0.077	0.080	0.094	0.081	0.094
	D value ($p \leq 0.05$)	0.042	0.040	0.064	0.072	0.030	0.029	0.035	0.036	0.130	0.150	0.131	0.139	0.077	0.083

^aOne-year-old shoots removed through pruning just before budbreak.

^bFallen leaves collected during leaf-fall.

of rapid shoot growth, "spring N" accounted for 19.3% (1132/5853 × 100) of the vine's total N. In comparison to the distribution of total N, the vegetative growth and bunches contained a larger fraction of "spring N". A relatively high partitioning of spring-applied N to the new growth has also been found for other crops (10,11). Up to harvest (Fig. 5c), the fraction of total N contained in the vegetative growth remained constant at ca 44%. The fraction of the "spring N" in the vegetative growth, however, was reduced from 55% at the end of rapid shoot growth to 41% while the fraction in the bunches was concomitantly increased from 20% to 45%. This again confirmed the fact that a large fraction of spring-applied N was first translocated to leaves and shoots, where N turnover occurred, followed by export to bunches (15, 29). At harvest, spring-applied N consti-

tuted only 11.2% (1076/9582 × 100) of the vine's total N, but contributed 15.6% to the N-content of the bunches (Fig. 4c, 4e). As found for citrus (11,14), a relatively small fraction of spring-applied N was translocated to the permanent parts which contained, at harvest, only 15% (12 + 3) of the spring-applied N as against 24% (19 + 5) of the total N (Fig. 5c). From this stage onwards, spring-applied N was redistributed at a relatively fast rate from the shoots and leaves, resulting in the permanent parts showing equal distribution for total N and "spring-N" at the start of the third growing season (Fig. 5f). At this point it can be calculated that spring-applied N accounted for only 4.8% of the vine's total N content. The 273 mg of "spring-N" still present constituted 24% of the labeled N initially present. This compares well with the 21% retained in the case of summer-applied N

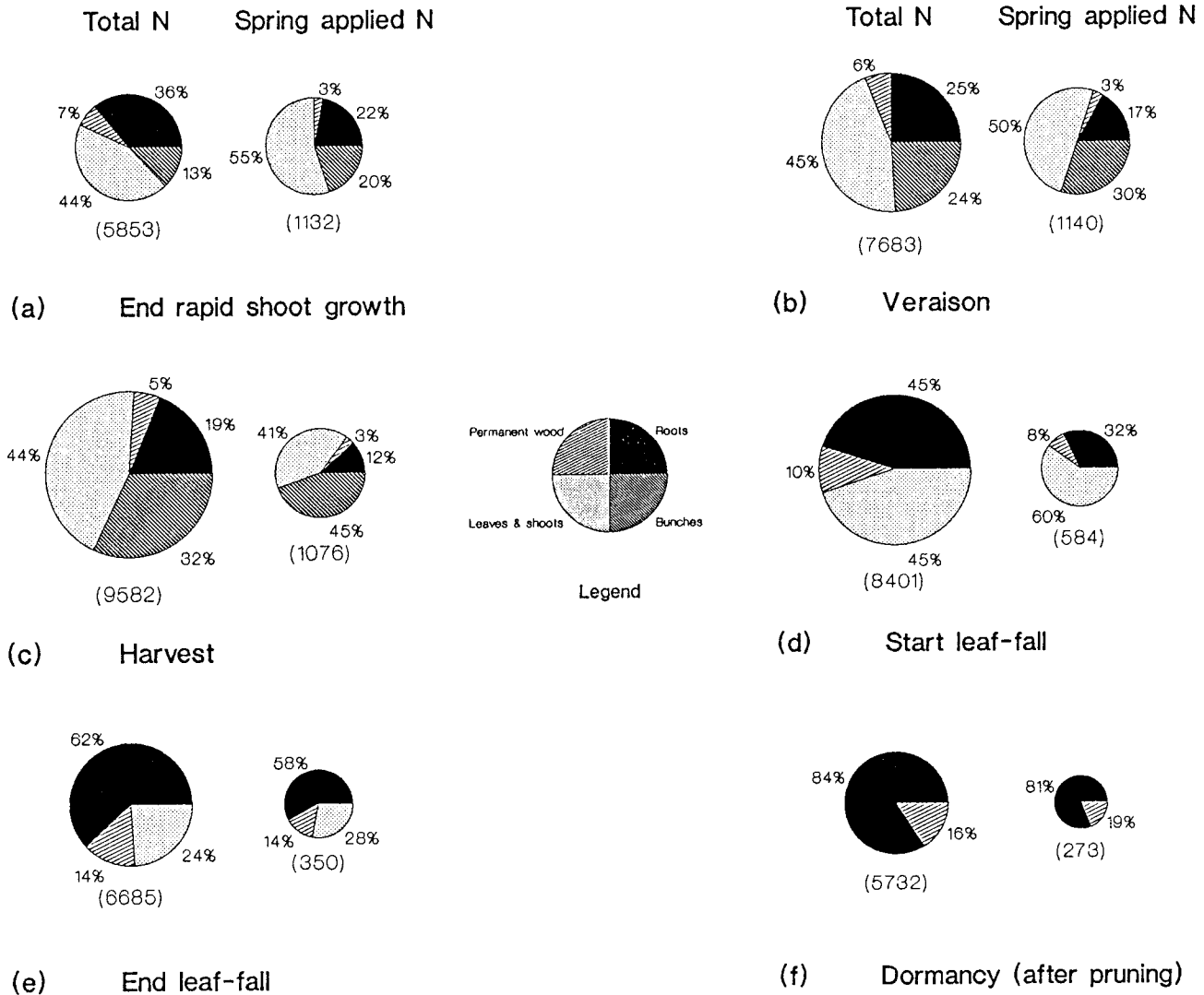


Fig. 5. Relative distribution of total and spring-applied N at different phenological stages of Chenin blanc/99R. Figures in brackets denote absolute amount of N in mg/vine.

(7) and the average figure of 19% obtained for N absorbed during the course of a season (5). In the case of N absorbed after harvest, however, the fraction retained in the permanent structure can be expected to be much higher (7,11). The annual turnover of N in young vines must, therefore, be in the order of 80% which is much higher than the 50% estimated for almond (28). The high turnover found for grapevines is probably partly due to the cultivation method whereby virtually the whole season's new growth is removed through cropping, leaf-fall, and especially pruning. Furthermore, the growth pattern of the grapevine differs from that of most other deciduous fruits on account of the period of bloom occurring six to eight weeks after budbreak, whereas for other fruit crops, blossoms are the first organs signifying the end of dormancy. This is probably the reason why such a high proportion of labeled N was recovered in the bunches, whereas for almond, soil-derived fertilizer N is preferentially translocated to vegetative growth in the year of application (27). The distribution of labeled N be-

tween bunches, shoots, and leaves, as found in the current trial, was comparable to that found for spring-applied N in a field trial on a sandy soil with a low N-supplying capacity (7).

Conclusions

Nitrogen is one of the most important nutrients as far as growth, production, and fruit quality of grapevines is concerned. However, hardly any research on the N metabolism has been done, primarily on account of the difficulty in distinguishing by conventional methods between reserve N and newly absorbed N. In this investigation, use of the ¹⁵N isotope made it possible to quantify the distribution and translocation of spring-applied N, and it can be seen as a first step towards obtaining a clear picture of the N dynamics of the grapevine. It was firmly established that roots, permanent wood, leaves, and shoots all play an important part in satisfying the N demand of bunches, even with an adequate supply of soil N being available. Under conditions where the supply of soil N is insufficient, these organs can be expected to play

an even more significant role.

In the case of the grapevines in this study, reserves of spring-applied N played an important role in supplying bunches at the start of the next season. However, the relative importance of this contribution will be affected by soil temperature, indicating that this aspect should be investigated in more detail.

It has been shown that the role played by N absorbed during spring in the N-metabolism of the grapevine differs from that of N absorbed during other stages in the season (total N). The fate of N absorbed during these other periods should, therefore, be determined in a similar way in order to get a complete picture of the pathway of nitrogen nutrition. Different scion/rootstock combinations may also be expected to react differently.

This study has also indicated that most of the reserve N is stored as proteins and that amino acids play only a minor role. However, this point should be investigated in more depth.

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