

Nitrogen Dynamics in Grapevine: Physiology and Modeling

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Within-plant distribution and seasonal dynamics of nitrogen as a prominent plant nutrient are reviewed. In perennial plants such as grapevines (*Vitis vinifera* L.), nitrogen available for allocation to different organs is supplied by either ammonium and nitrate uptake from the soil or internal translocation between plant parts. All grapevine organs are capable of reducing soil-supplied inorganic nitrate, the main forms of N involved in xylem transport are nitrate and amino acids. Arginine is the predominant amino acid not only for transport but also for storage, contributing up to 80% of the N reserves in the perennial structures. The partitioning of nitrogenous compounds to plant organs is source/sink driven. The N reserves located in the woody plant structures are an indispensable prerequisite for early spring growth, since grapevine relies entirely on stored N during the first weeks of vegetative growth, regardless of the soil N supply. Soluble N in the wood reaches a maximum just prior to budbreak, and thereafter the N content in the storage organs (roots, trunk and canes) decreases markedly until the beginning of fruit growth. The N concentration in the annual structures such as shoots, leaves, and grape berries decreases during the flush of growth as well, while the total incorporated N mass increases. Nitrogen may be internally remobilized and reallocated to grapes during fruit maturation. Before leaf fall, more than 40% of the N is mobilized in the senescent leaves and translocated to the woody storage organs. Thus, the N concentration of roots and trunk rises again at the end of the season as N reserves are built up for next year's budbreak. An overview of existing models for N distribution within plants is given. A model for grapevine growth and yield formation is used to demonstrate the dynamics of N partitioning and N development of the different plant organs.

Nitrogen is generally acknowledged to be one of the most important and most likely limiting nutrients because it is a constituent of important and common components such as proteins, enzymes, and coenzymes, nucleic acids, chlorophyll, and vitamins, and it is necessary in the process of oil and resin formation (54).

Considerable work concerning within-plant N distribution has been done on plants other than grapevines. Some of these results are valid for plant metabolism in general, while some are plant-specific. Therefore, one must be careful in applying data from other perennials or even from annual plants to grapevine. This study reviews the work done on transport, distribution, storage, and seasonal dynamics of nitrogen in grapevine (*Vitis vinifera* L.). Furthermore, an overview of models for N distribution in plants is given, and a grapevine model is used as a conceptual tool to understand the seasonal N dynamics in grapevines.

Nitrogen Transport

N compounds: Grapevines are capable of utilizing both nitrate and ammonium ions taken up from the soil (10). While Hill-Cottingham and Lloyd-Jones (24) re-

ported ammonium (NH_4^+) to be rapidly metabolized in the roots before being translocated to the shoots, Dintscheff *et al.* (11) found it to be one of the major N constituents reaching the shoots, leaves, and clusters. In grapevines, nitrate reductase activity indicating amino acid formation was shown to occur in the root tips, in the green plant parts, mostly the leaves (40), and even in berries (42). Thus nitrate is present in any part of the vine at any time (31). The transition of N from inorganic to organic forms, *i.e.*, nitrate reduction and amination, in grapevine organs at different developmental stages is illustrated in Figure 1. Proteins are synthesized from the amino acids in the cytoplasm, the chloroplasts, or mitochondria (6).

Nitrogenous compounds are transported in the xylem from the roots to the aerial parts. A small proportion of the N assimilates remains in the roots for storage or metabolic processes, while the vast majority moves to the upper plant parts. The ratio between organic and inorganic transport forms of N, as well as the composition of the organic fraction, are plant-specific. The proportion of nitrates in the xylem ranges from 0% to almost 100% of the total transported N among different

plant species (24). The organic N fraction of the translocation solutes is composed of only a limited number of amino acids. In the grapevine xylem, both inorganic nitrate and organic compounds are found. In the petioles, a tissue often used for assessing the nutritional status of a plant, the (NO_3^-) fraction amounts up to 2.3% dry weight and depends on the solar radiation and the grapevine cultivar (41). For efficiency reasons, a low C/N ratio is characteristic for organic nitrogenous compounds involved in N transport (6). Major amino acid constituents in the xylem of grapevines are aspartic acid, glutamic acid and its amide, and arginine (24), arginine having the lowest C/N ratio (1.5) of all common amino acids. It is synthesized from glutamine and aspartate. The xylem can contain a wide range of N solutes originating from root N reserves and being transported to the sinks. Phloem transport involves mostly the same N forms as xylem transport (6,36). The prevailing transport directions of N solutes during the season are depicted in Figure 1. A distinction is made between inorganic and organic transport which, however, is not equivalent to xylem and phloem transport.

N concentration and composition change during transport in the xylem (36). Xylem tissue of apple trees was found to have metabolic capacity (24), *i.e.*, there is an exchange of N material between stem tissue and xylem fluid. Arginine, the main transport form of N other than inorganic nitrate in grapevine (40,43), is most readily absorbed by stem tissue from the xylem (6). The net decrease of the N concentration in the xylem in distant plant parts is compensated for by increased transpiration of the more distant leaves, while expanding, weakly transpiring leaves rely on phloem import (36).

Transport mechanisms: Transport in the xylem is essentially a one-way, passive transport driven by the water transpiration stream with active or diffusive loading and unloading of the solutes (5). It appears to be subject to a circadian rhythm with a maximum N output from the roots near noon (high transpiration) and a minimum at midnight. Conversely, N is translocated at night from shoots to the roots in the phloem, and there it builds up a pool for xylem transport at daytime (6).

The transport of N in the phloem most likely follows the bulk flow theory for carbohydrate movement (5), since C and N assimilation in the leaves are closely linked together (36); active loading of sugars and N compounds to phloem causes a low local osmotic potential that attracts water from the apoplast or the xylem. This hydrostatic pressure forces the phloem sap out of leaves. In the roots, the solutes are actively unloaded, and the water passes over to the xylem and moves back to the leaves. The translocation and distribution of carbohydrates, and most probably of N solutes, is driven by source/sink relations, *i.e.*, supply and demand via phloem loading and unloading (44).

Seasonal N Dynamics

The seasonal development of N mass and concentration in various grapevine organs has been described in

several studies (1,4,9,31,51,53). As a general overview and on a temporal basis, Figure 1 depicts input and output of N in grapevine organs at four distinct phases in plant development, while in the following review, the temporal development of N is presented on a plant organ basis, with special reference to nitrate and arginine. Figure 1 also illustrates this plant-part-based approach. A distinction will be made hereinafter between concentration (% dry weight) and content (mass in grams).

Perennial parts and N reserves: N reserves are located in the woody, perennial parts of the grapevine, *i.e.*, roots, trunk, and canes. The N dynamics of the woody plant structures and the reserves are tightly interrelated; therefore, they are treated together, starting in spring with a given initial quantity of N reserves.

A very intense phase of N reserve **mobilization** from the woody parts takes place from bleeding up to blooming time. Within this period, in five-year-old Müller-Thurgau vines, the total N mass in the woody structures was found to decrease by 76%, mostly from the one-year-old wood (43). Löhnertz (31) reported that in the cv. Riesling up to the 5- to 6-leaf-stage the grapevine depended almost entirely on its N reserves. Depending on soil temperature, the root growth may be retarded up to ten weeks after budburst (2,15), and during this period the plant depends mostly on its N reserves (8). By bloom time, a considerable amount of N reserves is mobilized from the roots, trunk, and canes and is transported to the growing organs, and the amount of total N in the woody parts reaches its minimum (43). In two-year-old vines, all nitrogen mobilized for new growth originated from the trunk (2). The N content of the roots remained constant at the beginning of the growth period, which may be due to lack of N reserves in these parts. Nitrogenous reserves for new shoot and leaf growth are most readily utilized from canes, then from the trunk, and last from the roots (9,30,39). This corresponds to findings of Faby and Naumann (12) in apple. They found high levels of reserves to be more extensively used than low reserves. N reserves were mobilized as long as they were readily available. In grapevines, Groot Obbink *et al.* (19) found that up to 65% of the N content of cuttings can be used for new growth, and soluble nitrogen was utilized before the proteins.

Before bloom, the mobilization is independent of the N supply from the soil (12,13,19,31,32,39,47). If the N demand of the growing parts during the flush of vegetative growth until veraison (beginning of rapid fruit growth, maturation, and coloration), and during grape maturation cannot be entirely met by the large quantities of N taken up from the soil (8), further mobilization of N from the wood may occur, which leads to a decline of N in the roots and the trunk and an increase in the canes (3,31).

The **build-up** of N reserves in grapevines begins as early as during maturation, and reserves continue to increase after harvest until the end of the vegetation period (31,43). In apples, N reserves are incorporated

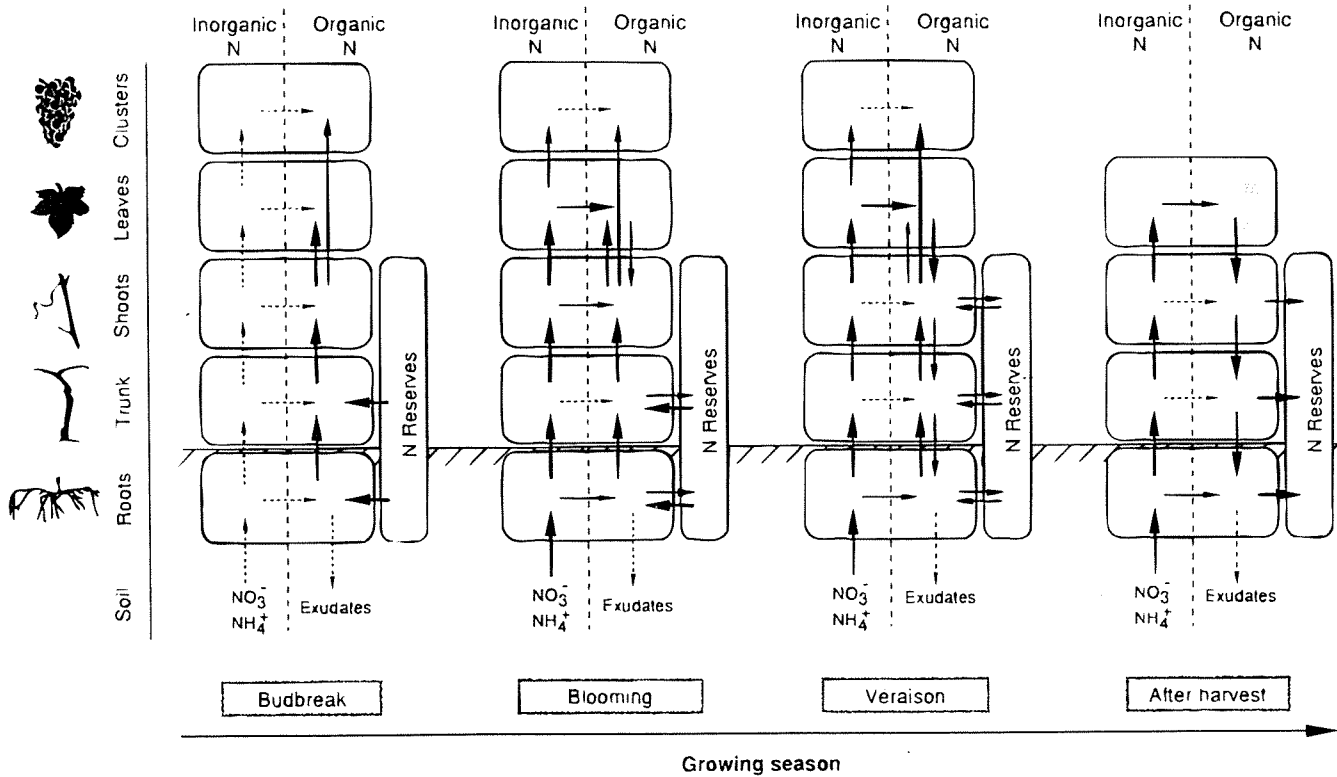


Fig. 1. Prevailing flows of inorganic and organic nitrogen within grapevine compartments and between plant and soil at four stages of development. Budbreak represents first one to two weeks of growth; blooming, the phase of rapid vegetative growth; and veraison, the phase of fruit maturation. Arrow width indicates relative magnitude of N flow.

primarily into the bark in August and into the wood even earlier (12). The N reserves pool in the woody structures, preferably the roots, is replenished - together with starch for the carbohydrate pool - by retranslocation of nitrogenous material from the aging parts and by N uptake from the soil even late in the season (1,8,31,43). In senescent leaves three to four weeks before leaf fall [apple; Oland, (35)], protein is hydrolyzed and organelles are broken down to form soluble nitrogenous compounds (6,11). More than 40% of the leaf N is mobilized and exported from the leaves (9,35,46). This affects the composition of the phloem sap in that carbohydrate predominance changes to amino acid predominance (6,36). N is more easily reallocated from older tissues than carbohydrates (37). Grape growth and reserve formation appear to have an antagonistic relation. Balasubrahmanyam *et al.* (3) found vines with low or no fruit yield to have larger N incorporation in canes than plants with a high yield. On the other hand, more nutrient reserves were mobilized from the wood carrying a heavy crop. In the Löhnertz study (31), 5% of the total N was located in the canes at the end of the vegetation period and was, therefore, largely lost with winter pruning.

Among the woody structures of the grapevine, roots have the highest and most fluctuating N concentration, ranging from 0.4% to 1.7% (1,31,43), and being lowest at veraison. They also have the highest concentration of free amino acids (33). During dormancy the concentration of soluble N in roots and other woody

tissues increases, reaching a maximum just prior to budbreak (29,43). Thereafter, the level of amino acid concentration (mainly arginine) in the roots decreases rapidly during heavy vegetative growth. It reaches a minimum at the beginning of fruit ripening and increases again during leaf senescence. Similarly, total N concentrations of trunk and canes (0.3% - 0.7%) decline slowly after budbreak and recover during fruit maturation.

The N storage forms consist of an insoluble and a soluble fraction; the former is usually larger (9). A number of authors (29,33,40,43) found arginine to be the principal storage form of soluble N, amounting to more than 60% of the total soluble nitrogen in roots and woody tissues. Another important soluble form for N storage was reported to be aspartic acid (3). The dynamics of free arginine mass in the woody parts shows the same pattern as that of total nitrogen. There is a slight increase just prior to budbreak, and during the subsequent decline it composes up to 100% of the total N in the wood (43). The lowest amount of arginine is found at bloom, and thereafter it slowly increases. In apples, N is stored in the bark mainly in protein form (80%), and in the wood of the perennial frame in equal parts as soluble amino acids (arginine) and proteins (12,13,34,49).

The quantity of nitrates in a tissue is influenced by the uptake and reduction of nitrate in the roots, the velocity of transport, and the nitrate reduction activity of the leaves (31). Both the amount and concentration of

NO_3^- in the roots, trunk, and canes generally show a similar temporal pattern. Starting before budburst, a steep increase (more than 100%) in NO_3^- concentration in the roots occurs, peaking before blooming at approximately 800 ppm, followed by a rapid decrease until veraison. This is possibly due to augmented nitrate reduction in the growing root tips. During grape maturation and post-harvest time, the nitrate concentration stays low. The nitrate concentration in the trunk is generally lower than in the roots and peaks shortly before blooming at 250 ppm and declines thereafter to almost nil, as during the flush of growth, the transport to the shoots and leaves increases. The NO_3^- dynamics of the canes behaves similarly to that of the trunk but on a higher level. After harvest, both amount and concentration of NO_3^- start to increase again in both roots and trunk. The maximum nitrate concentration in perennial plant parts, as well as in annual parts, is reached two weeks before bloom (31).

Annual structures: In the Löhnertz experiments (31), about 30% of the final N mass was allocated to the annual structures (shoots, leaves, reproductive organs) by blooming time, of which about 20% originated from the N reserves of the perennial parts. Other experiments indicated that even 30% to 40% of the N present in annual structures at bloom time came from reserves (43). The bulk of the nitrogen was incorporated during the third and fourth week after blooming. During these two weeks another 30% of the final N mass was allocated to the annual structures; 8% of this mass originated from the reserves. During grape maturation, total N present in shoots and leaves slightly decreases due to the commencement of retranslocation of vegetative N to the woody structures and the onset of leaf fall.

Vegetative organs: The shoot N concentration and protein content (11) decrease steadily after budbreak. The decrease continues from bloom to veraison, but at a slower rate, while total N in the shoots increases. After veraison, the concentration rises slightly again, and total N mass peaks at the end of the vegetation period (1,9,31,51,53) due to retranslocation of N from the leaves to the shoots and perennial parts. During this last period, synthesis of proteins in the shoot increases (11). Shoots represent an N sink until the end of the main vegetative growth (approximately four weeks after blooming); then they become instead a source until the beginning of maturation, and they terminate the season as a sink (31). Generally, shoots have a lower C/N demand than roots because they possess a higher N concentration in the apex, and roots have higher C losses due to respiration (37). The proportion of shoot N in lateral shoots depends on the training system and pruning practices; their N concentration compares to the primary shoots.

The shoots have a much higher nitrate concentration [up to 4500 ppm (31)] than the woody tissues. NO_3^- concentration peaks shortly before blooming and decreases until veraison. The maximum amount of nitrate in the shoots, however, is reached later - at the end of the vegetative growth.

The N concentration of individual leaves, irrespective of their time of generation, initially decreases rapidly during their time of expansion, then decreases more slowly for 600 degree days $> 10^\circ\text{C}$ (51). It declines again at the beginning of grape maturation as proteins are broken down to amino acids (11) which are exported from senescent leaves. The export of N out of senescent leaves is also reflected by an increase in the cane N concentration. More than 40% of the nitrogen in leaves is recycled (9,35). Grapevine leaves have an average concentration of approximately 1.25% to 1.5% after shedding. The maximum amount of N in the leaf is reached at full leaf expansion; afterwards it remains constant until senescence. Total leaf mass represents a sink until the end of the main vegetative growth period (pea-size berries); thereafter, it is an N source. Ninety-five percent of the final leaf N mass is allocated to the leaves within a period of only four weeks around bloom (31). During much of the season, the nitrogen in the leaves greatly exceeds shoot levels. Dry matter, however, is located to a larger extent in the shoots than in the leaves (51). Both shoots and leaves have a high N turnover and seem to act as intermediate N reservoirs between root and berry (9).

The nitrate concentration of leaf petioles is often used as an indicator of the N supply status of the vine. It fluctuates more than other tissues and reaches maxima before bloom (7) and at veraison and a minimum at bloom. All NO_3^- present in the leaves before leaf fall is supplied by uptake from the soil (11). Leaves in the upper layers of the vine plant have lower nitrate concentrations than lower ones (31).

Reproductive organs: The concentration of nitrogen in the young inflorescences starts at the same level as that of vegetative tissue and slowly decreases as the season progresses (31,51,53). Significant N partitioning to growing grape berries begins after bloom. There are two phases of intense N incorporation: the first one takes place during the two weeks before the "pea-size" stage of the berries, the second one starts one month later at the beginning of maturation and lasts another two weeks (31). In this last period, 50% of the final N mass is accumulated in the grape berries. The two periods correspond to the peaks of grape dry mass formation (31,54). Towards the end of fruit ripening large amounts of free amino acids (arginine and proline, the latter possibly synthesized in the fruit) are transported from the roots to the berries, and the concentration of soluble, as well as total nitrogen, increases again (29,33). By harvest, half of the N present in the annual structures of the grapevine is located in the reproductive parts (1,31,51).

Nitrate is present in small amounts at all times in the reproductive organs. The concentration is strongly influenced by soil management. A distinct NO_3^- maximum is reached in the grapes before veraison. Most of the N reaching the berries consists of soil-supplied ammonium and amino acids provided by leaves and shoots (11). The dynamics of nitrate content and total N content in the reproductive organs are similar, implying

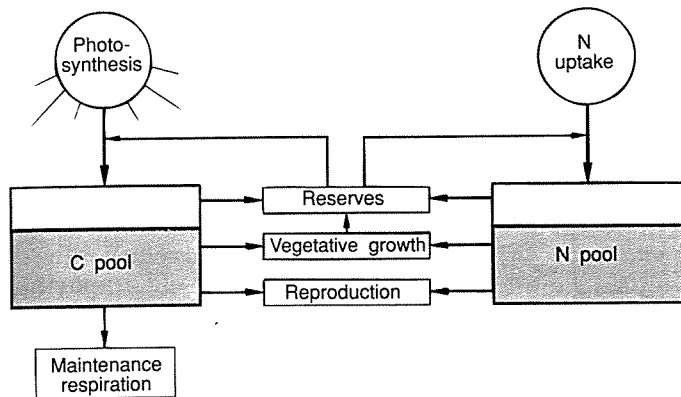


Fig. 2. Metabolic pool concept of the grapevine model.

a relatively constant ratio of $\text{NO}_3^-/\text{total N}$. However, nitrate content fluctuates more in the petioles than in the berries (31).

Plant Models

A model is defined as a set of equations which represents the behavior of a system. Models can be empirical; *i.e.*, they describe data or a process mostly on a single level without furthering the understanding of the system, or they are mechanistic, trying to explain the underlying mechanisms of interactions on one or several levels. Thereby, assumptions and hypotheses have to be made based on empiricism (14). Models may be static or dynamic depending on the inclusion of chronological or physiological time as a variable.

The goal of developing a plant model is not to mimic the complete physiology of a plant on a real scale, but to represent one or several specific processes (nutrient uptake, photosynthesis, translocation, growth, yield, formation, *etc.*) by empirical equations or a mechanistic concept. A mechanistic model allows the incorporation of the diversity of numerous physiological details in an underlying concept.

N allocation models: There exists a wide number of plant growth models that treat N uptake by the plant or fertilization effects on growth and yield. Only a few are concerned with nitrogen distribution within the plant. Some models calculate an overall plant N concentration based on N uptake and carbon production, as for example those of Johnson and Thornley (25) on grass, Greenwood *et al.* (18) on annual species, and Graf *et al.* (17) on rice. The model of Seligman *et al.* (45) for annual plants includes, in addition, N translocation from vegetative tissue to seeds. The models by van Keulen and Seligman (27) and van Keulen *et al.* (28) for wheat and other annual plants partition the nitrogen between organs in proportion to their relative demand, and include depletion of vegetative parts and N translocation to grains. A cotton model by Jones *et al.* (26) distributes N to the organs according to allocation functions and includes N reallocation and reserves. Similarly, the cassava model of Gutierrez *et al.* (20) allocates N according to a priority scheme to the organs or reserves. The only model for N distribution in the

grapevine (52) follows basically the same approach and is summarized in more detail below. The above models of cassava, rice, and grapevines have the metabolic pool concept in common.

Models with a more physiological approach deal with source-sink relations between organs. Thornley (48) covered the theoretical aspects of modeling the nitrogen fluxes from roots to shoots based on their concentrations. Habib and Monestiez (21) and Habib *et al.* (22,23) presented a model for N distribution in peach. The N transfer between organs depends on the availability in the source organ and the demand in the sink organs. A model of nodulated lupins (37,38) simulates the net transport of fixed N between organs based on the C/N ratios of xylem and phloem flows.

Grapevine model. Features: The VIMO-model (vine model) used for the subsequent analysis was presented in elaborate detail by Wermelinger *et al.* (52). It is a dynamic, stochastic population model; *i.e.*, it includes variability of the life spans of the plant parts. The driving variables required to run the model are the local weather data, namely daily solar radiation and minimum and maximum temperatures. Assimilation of C and N is driven by the resources as well as by the plant's demand for these resources on a physiological time basis (degree day concept). The daily demand for N is proportional to the demand for carbohydrates. This demand is given by maximum dry matter growth rates, which in turn are affected by N availability. The core of this mechanistic model is the metabolic pool concept [reviewed by Graf *et al.*, (16)] which is depicted in Figure 2. The allocation of the daily available C and N from the pool to the different sinks occurs according to a priority scheme which attributes priorities in decreasing order to maintenance respiration (only for C), fruit, vegetative organs (leaves, shoots, roots, trunk, canes), and reserves. Before bloom, reproductive organs have the same priority as vegetative tissue. The organ populations (subunits) are age-structured, which means, for example in the case of leaves, that each of 30 age classes accommodates a certain number of leaves and their dry and N mass. Thus, the foliage of a vine plant is structured into leaves of different ages and N concentrations. The transition from one age class to the next is degree-day-driven and stochastic. The seasonal dynamics of the N concentration of a subunit is the net result of two opposite processes: new growth of a tissue zone with high N concentration and a subsequent N export out of the aging zones of the same organ. The export is a constant rate per degree day. The growing apical part of a shoot, for example, grows at a maximum N concentration, while from the more proximal parts (*i.e.* parts of older age classes), N is extracted and reallocated to the reserves. The average concentration of the shoot is eventually determined by the proportions of shoot mass and their N concentrations in each age class.

The object of this model is to gain further insight into the yield formation processes in grapevine and into the plant behavior under abiotic (N, light, pruning) and biotic (phytophagous pests) stress. The model is not a

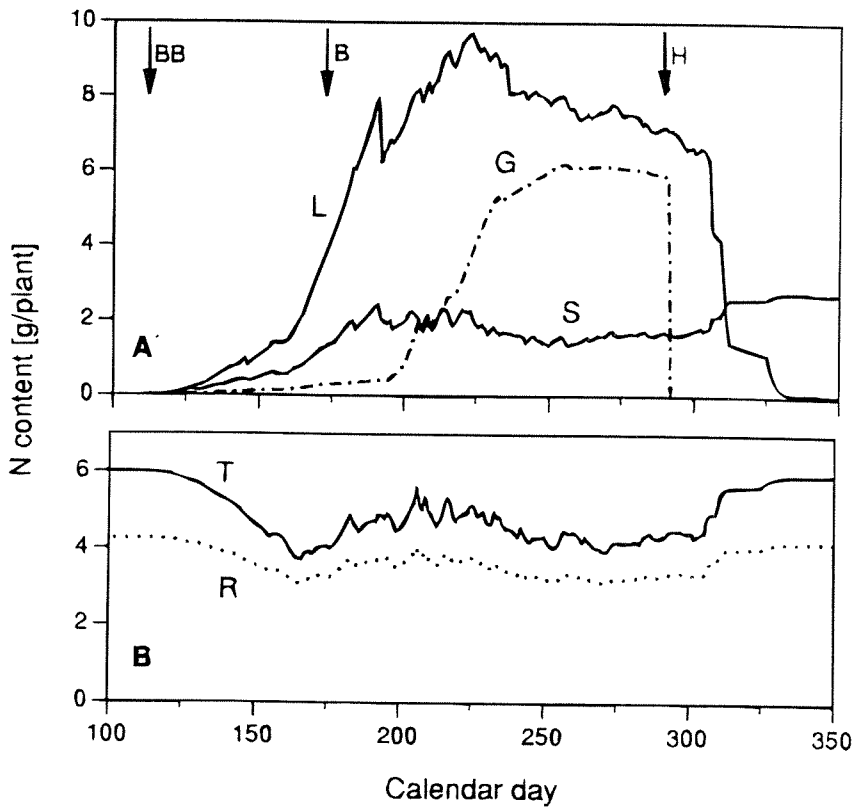


Fig. 3. Seasonal nitrogen distribution in annual (A) and perennial (B) parts of grapevine (L = leaves, G = grapes, S = shoots, T = trunk + canes, R = roots).

physiological model in the sense of simulating the processes of transfer of nitrogenous compounds between organ populations on a biochemical level, but it does include the metabolic pool model as an overall mechanistic concept for N allocation.

plant anyway. The development of N in the perennial structures, trunk (plus canes), and roots (Fig. 3B), are very similar. After budbreak (day 111), a distinct depression of N is observed, since at the beginning of growth these organs are the only N source for the first flush of vegetative growth. After a minor recovery before the beginning of fruit growth (bloom, day 171), another N reserve drawing phase follows during ripening. Already before harvest, the reserve pool in the perennial structures starts being refilled by N reallocation from the leaves and uptake from the soil. The pronounced fluctuations are the result of the sensitive reaction of the model to N allocation and remobilization processes. While the simulations of the development of the above-ground plant parts are well supported by field data, it must be pointed out that data on root mass are difficult to obtain in the field; therefore, the dynamics of root N in this study was not validated, and values may possibly be underestimated. However, the simulated pattern is similar to the one described by Löhnertz (31) with cv. Riesling. The minimum trunk N at bloom compares well to findings by Conradie (9). He reported increasing

This model has previously been used to evaluate the effect of N deficiency on the allocation pattern of photoassimilates to different sinks such as maintenance respiration, reproductive and vegetative growth, as well as on the age structure and N composition of the leaves (50). In this study the absolute and relative distribution of N in 18-year-old grapevines is simulated under standard conditions.

Results: The absolute N mass accumulated in the annual growth of a grapevine is depicted in Figure 3A. The shape of the seasonal N growth curves corresponds to that of the dry matter curves (52). Throughout the season, most N is located in the leaves. The incisions on days 191 and 235 are caused by summer prunings (hedging and topping). The N mass comprised in the shoots remains at a fairly constant level after the initial build up. It slightly increases at the end of the vegetation period due to N mobilization in the leaves and its transport to the perennial structures. However, due to the winter pruning, most N in the shoots is lost to the

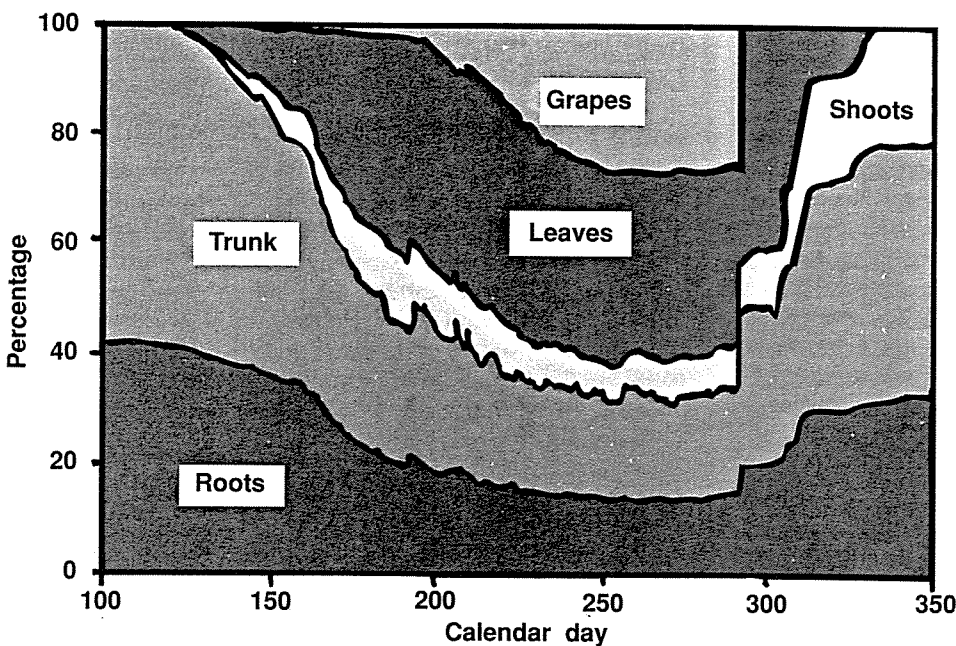


Fig. 4. Seasonal relative nitrogen distribution in grapevine.

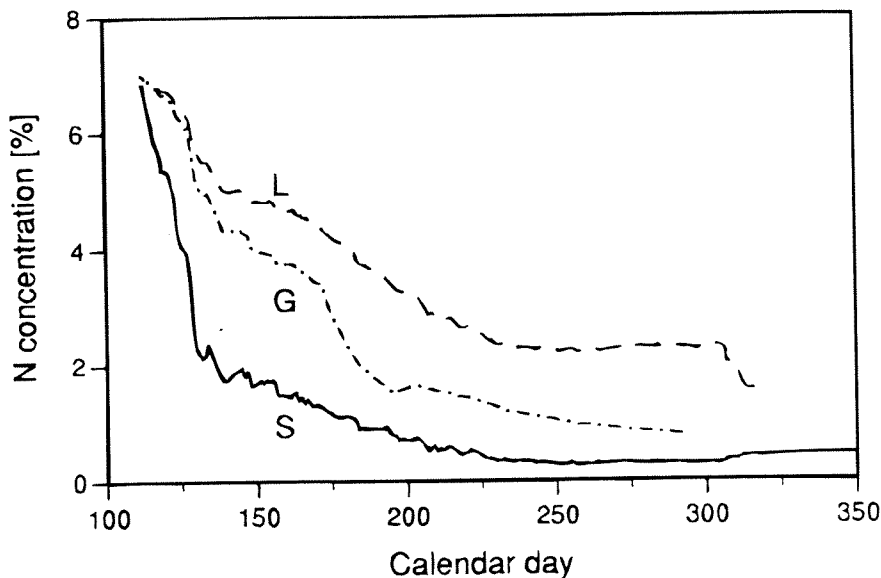


Fig. 5. Seasonal changes in nitrogen concentration of leaves (L), grape berries (G), and shoots (S) in grapevine.

trunk N up to leaf fall in two-year-old grapevines, while in our simulation, trunk N suffered another depression during fruit maturation.

Plotting the percentages of N present in the different organs illustrates the relative N distribution in a grapevine (Fig. 4). It is obvious that at the beginning of the season all nitrogen in the plant is located in the perennial structures, roots, and trunk (including canes). In mid-season, leaves possess the same amount of N as roots and trunk together. At harvest, more N is in annual than in perennial structures, and roughly 25% of total vine N is removed at harvest with the fruit. Most of the N in the shoots at the end of the year is lost by winter pruning.

The concentrations of the annual organs show a common decreasing pattern (Fig. 5). All young parts start with very high N concentrations which rapidly decrease, but at different rates. Leaves continuously mobilize nitrogen with a final drop in concentration before their abscission. Grapes and shoots have higher mobilization rates. After harvest (day 291), the N concentration of the lignified shoots slightly rises due to reserves allocation. The corresponding field data compare well to these simulations (52).

Discussion

The role of N reserves in early spring growth and during shortfalls in N supply from the soil was repeatedly emphasized. More information is needed on the exact localization of these reserves, on their compensation capacities, and on the multiseasonal behavior of reserves and resulting vine performance under stress conditions. The seasonal changes of concentration and content of nitrogen in individual plant parts is well investigated and documented. Less details are known on the temporal and spatial distribution pattern of N taken up from the soil and the distribution priorities. In

general, N is directed mainly to vegetative growth before bloom, while after the build-up of the vegetative frame, N is preferably allocated to the reproductive organs and reserves. Simultaneous influx and efflux processes occur in all organs (9), an approach which was also chosen for the N dynamics in the grapevine model (52).

A controversy may arise concerning the significance of physiological research versus modeling. However, the issue is rather physiology and modeling than physiology or modeling. Detailed work on specific physiological processes and chemical pathways are essential components contributing to our understanding of the plant metabolism. Plant modeling can neither replace physiological work nor field experiments, but both are prerequisites for constructing models.

The often confusing abundance of detailed results may be best compiled in a model. Moreover, a conceptual model like the grapevine model forces the researcher to focus on overlying patterns, on potential driving mechanisms ruling the general behavior of plant growth and yield formation. This gives rise to further insight into the basic processes and may demand new hypotheses on the underlying mechanisms which can be tested in the field. Models have to serve the purposes they were built for and, therefore, need to be viewed from this aspect. For example, it makes no sense to use an N-uptake model for evaluating the effects of various light intensities.

This grapevine model has proven to be a valuable tool for assessing the role of nitrogen in crop performance. Furthermore, a plant model is almost a necessity in analyzing population dynamics and interactions on different trophic levels. It compiles the available knowledge on single system components and this makes it indispensable for the analysis of complex systems. The fact that the structure of this grapevine model is also applicable to arthropod models makes a link between different trophic levels easy. Therefore, this grapevine model was also used to analyze interactions between spider mites and their host plant and to assess the role of nitrogen in this multitrophic system.

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