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FLUXES OF NITROGEN WITHIN DECIDUOUS FRUIT TREES

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Abstract. Nitrogen (N) nutrition is a major means of controlling growth and fruiting of trees. In EU Countries, society's expectations and political decisions have pushed for the adoption of sustainable ways to manage orchards. Guidelines for N management aim to limit fertiliser applications under threshold limits, in order to reduce N losses. Increasing the effectiveness of the recycling of the N present in the orchard is a basic step to reduce external N inputs. The availability of the stable isotope ^{15}N as experimental tool has made possible significant advances in the knowledge of the fluxes of N at tree and orchard level. This paper discusses the N fluxes occurring within the tree both between the years and within the year (root-shoot-root N recycle) and their role in the vegetative and reproductive cycle of fruit trees.

Key words: Nitrogen storage, nitrogen remobilization, shoot-root-shoot nitrogen recycling, xylem sap composition

INTRODUCTION

Nitrogen (N) nutrition is a major means of controlling growth and fruiting of trees. In EU Countries, society's expectations and political decisions have pushed for the adoption of sustainable ways to manage fertiliser application in agro-ecosystems. Guidelines for N management in orchards aim to limit fertiliser applications under threshold limits, in order to reduce N losses to the environment. Optimisation of the use of external as well as internal sources of N is needed if sustainable fruit production systems are to be developed. Adapting rates of fertilisers to mach tree needs, adopting highly efficient technology of nutrient supply (e.g. fertigation) and splitting nutrient rates are among the means to improve external N use.

Increasing the effectiveness of the recycling of the N already present in the orchard is a basic step to reduce external N inputs. Nitrogen is a rather mobile nutrient and is

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transferred quite easily between different compartments of the orchard ecosystem. Nitrogen fluxes from outside to inside occur in the form of N fertilisers, N deposition, N in the irrigation water and as N_2 fixation by leguminous plants whenever present in the alley. Nitrogen exits the orchard with fruit yields and by N losses due to volatilisation and leaching. Although N in the orchard has an open cycle, there is little doubt that a sustainable management of N nutrition would benefit from a greater degree of recycling of the available N within the orchard.

Two major processes of N cycling can be described: the cycling within the tree and the cycling between the tree and the soil (and *vice versa*). In this review we will concentrate only on the former type of N cycling, and we will discusses the N fluxes occurring within the deciduous trees both between the years and within the year (root-shoot-root N recycle), and their role in the vegetative and reproductive cycles.

NITROGEN SOURCES

There are two major sources of nitrogen contributing to vegetative growth and reproduction in the fruit trees, root uptake and internal cycling [Millard 1996]. The N available for root uptake can derive from external sources or from mineralization of native and recently added organic matter. The internal cycling of N (fig. 1) is an impor-

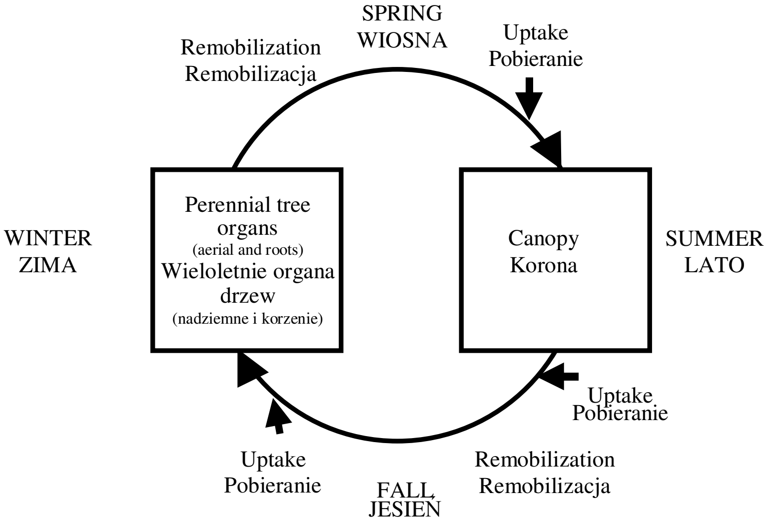

Fig. 1. The seasonal pattern of cycling of N between years in deciduous trees showing N fluxes and storage [Millard 1996]

Rys. 1. Sezonowy schemat obiegu N pomiędzy latami u drzew owocowych, przedstawiający przepływy i nagromadzanie azotu [Millard 1996] tant strategy developed by perennial plants to uncouple the growth process from the uptake of N by roots, therefore allowing growth in the absence (or with a low degree) of root N uptake. These situations occur: (a) at growth resumption in spring, when soil temperature is low, and, therefore, soil mineralisation rates are slow and (b) during periods of rapid growth when there is a high demand for N, such as during fruit maturation. The presence of storage pools of N in a plant is also important to allow them to recovery from herbivory.

NITROGEN CYCLING BETWEEN YEARS

Winter storage of nitrogen. The ability to store N for future use is a characteristic feature of perennial plants. Young trees (with a small perennial frame in relation to their annual growth of leaves, roots and fruits) have a limited capacity of store N, which increases as trees ages and increase in size. A simple clue of the N storage capacity of a tree organ is its marked increase of N concentration in the winter as compared to summer. Deciduous fruit trees store N in the bark of twigs, branches and trunk as well as in the root system (fig. 1). Storage pools of N in the aerial organs are likely in the form of specific proteins which have been isolated from ray parenchyma cells and from the bark, while it is believed that major storage in the roots system occurs in the form of free amino acids, mainly arginine or of arginine rich proteins. While both fine and coarse roots are major winter storage sites for N in young trees [Tagliavini et al 1998], their role in larger trees has not been clearly determined. The synthesis and turnover) of specific storage proteins depends on photoperiod and nitrogen supply [Coleman et al. 1993]. In contrast, the main storage site for N in coniferous, evergreen trees is in the needles [Fife and Nambiar 1984, Millard and Proe 1992], often as the photosynthetic protein rubisco [Warren et al. 2003].

The first mechanism contributing to the build up of N storage pools is the N withdrawal from leaves during their senescence (fig. 1). The ability of different species to withdrawn N during leaf senescence ranges from 20 to 80% [Millard 1996]. In a mature peach orchard under Californian conditions, Niederholzer et al. [2001] have estimated that around 30 kg N ha^{-1} $year^{-1}$ are remobilised from leaves to perennial organs during leaf senescence; such amounts were considered by the authors to account for the majority of the N remobilised the following spring. Similar calculations for a mature apple orchard in Italy [Tagliavini et al., unpublished] indicate that N withdrawal from leaves contributes to some 20 kg N ha^{-1} $year^{-1}$. In apple, it has been demonstrated that leaf N withdrawal in autumn can be less than that N remobilised the following spring [Neilsen et al. 1999] and trees with a relatively high leaf concentration at the beginning of leaf senescence withdraw from the leaves a lower proportion of total leaf N than those receiving a moderate N supply (tab. 1). The timing of N supply affects the N withdrawal from leaves and that arriving late in the season to the leaves is more likely to be recycled than that accumulated in the leaves during the spring and summer [Sanchez et al. 1991, Tagliavini et al. 1999]. For example, foliar application of urea post harvest proved to augment N storage by increasing the amount of N withdrawal from sprayed leaves [Tagliavini et al. 1998, Rosecrance et al. 1998].

Table 1. Variation of leaf N content and net N withdrawal (per m^2 of leaf area) to perennial organs during leaf senescence in field-grown apple trees (cv. Mondial Gala on M9) subjected to differential N supply [Tagliavini et al., unpublished]

Tabela 1. Wahania zawartości N w liściach i ilość odprowadzonego N z liści netto (w przeliczeniu na m^2 powierzchni liści) do organów zdrewniałych w trakcie ich starzenia, u jabłoni (odm. Mondial Gala na M9), poddanych nawożeniu w różnych dawkach [Tagliavini et al., dane niepublikowane]

Level of N supply kg N ha^{-1} $year^{-1}$ Dawka nawożenia kg N ha^{-1} rok^{-1}	Leaf N concentration before senescence, % d.w. Koncentracja N w liściach przed starzeniem, % s.m.	Leaf N content before senescence Zawartość N w liściach przed starzeniem g N m^{-2}	Leaf N content of abscised leaves Zawartość N w liściach po opadnięciu g N m^{-2}	Net N withdrawal during leaf abscission Odprowadzenie N z liści netto w trakcie opadania g N m^{-2}
80	1.9	2.3	1.5	0.8
40	1.7	2.0	1.1	0.9

The second mechanism contributing to build up of N storage pools is N uptake in the autumn which is directly allocated to storage in the roots. Peach and pear trees partition a significant part of the N taken up in late summer early autumn directly into the N storage pools located in the fine and coarse roots, while that taken up in early spring-early summer is preferentially retained in the leaves during their senescence [Tagliavini et al. 1999].

Spring remobilisation of nitrogen. Remobilisation of stored nitrogen is used by many trees to augment the supply of nutrients from the soil [Millard 1996], and can provide the majority of nitrogen used for growth each year [Neilsen et al. 1997, Weinbaum and van Kessel 1998]. Despite only a few studies having described in detail the dynamics of this process, it is clear that in some species the majority of N remobilization occurs before root uptake starts [e.g., *Prunus persica*, Rufat and DeJong 2001; *Sorbus aucuparia*, Millard et al. 2001; *Malus domestica*, Dong et al. 2001; *Prunus avium*, Grassi et al. 2002], while in other species the two processes are concurrent [e.g *Juglans nigra* × *regia*, Frak et al. 2002]. The large variability of data reporting the contribution of remobilised N on total N in new growth (tab. 2) is due to both the different age of the trees, to their N status, to the soil fertility and to the period of the year when the assessment was made. The majority of N in present at bloom in the spur leaves of apple [Neilsen et al. 1997] and pear [Tagliavini et al. 1998] is derived from remobilisation, while the N taken up in spring is preferentially partitioned to the leaves of developing shoots.

The knowledge of the duration of the remobilisation period in spring is important for determining the timing of N supply to increase soil N pools for root uptake. While the remobilisation process is little affected by the amount of soil N available for uptake in spring, the duration of N remobilisation depends on the amount of stored N, being longer in trees with large storage pools. In cherry [Grassi et al. 2002] and apple [Guak et al. 2003] N remobilisation is almost complete within 40 days from bud burst, but it may last up more than 60 days if trees have sufficient N storage [Grassi et al. 2002] (fig. 2). The N stored in the aerial organs is likely remobilized toward developing organs before that stored in the root system [Tagliavini et al. 1998].

Table 2. Examples of the percentage contribution of remobilised N on total N recovered in the canopy of some tree species along the vegetative season

Tabela 2. Przykłady procentowego udziału remobilizowanego N w ogólnej ilości odzyskanego N z koron niektórych gatunków drzew w czasie okresu wegetacyjnego

Species Gatunek	Remobilised N/total N[1] Stosunek remobilizowanego N do ogólnego N, %	Reference Źródło
Juglans nigra × regia	88–92	Frak et al. 2003
Juglans regia	58	Weinbaum and VanKessel 1998
Malus domestica	18–92	Neilsen et al. 1997, 2001
Betula pendula	50–80	Wendler and Millard 1996
Fraxinus excelsior	72–77	Marmann et al. 1997
Picea sitchensis	43–76	Millard and Proe 1991, 1993
Pinus sylvestris	30–70	Millard et al. 2001
Acer pseudoplatanus	40–62	Millard and Proe 1991
Prunus persica	38–46	Tagliavini et al. 1998
Nothofagus fusca	30–40	Stephens et al. 2001
Prunus avium	12–27	Grassi et al. 2002
Pyrus communis	88	Tagliavini et al. 1997

[1] Values represent the range measured experimentally using ^{15}N labelling techniques on young, immature trees often grown in sand culture and are presented to demonstrate the range of possible values obtained. The range was often affected by differing levels of N supply so direct comparison between the different species is not possible.

Wartości te reprezentują zakresy wyznaczone eksperymentalnie, przy użyciu znaczonego ^{15}N na młodych drzewach, często uprawianych w kulturze piaskowej, i są przedstawione jako możliwe zakresy. Zakresy te często zależały od różnych poziomów odżywiania N. W związku z tym bezpośrednie ich porównywanie nie jest możliwe.

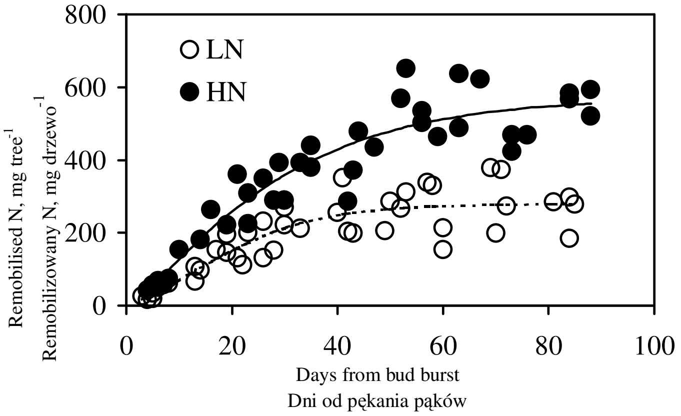

Fig. 2. Typical pattern of N remobilisation in spring toward developing shoots. Data refer to cherry trees with moderate (LN) or high (HN) N storage pools [Grassi et al. 2002]

Rys. 2. Typowy schemat remobilizacji N wiosną w kierunku rozwijających się pędów. Dane odnoszą się do drzew czereśni z umiarkowanym (LN) lub wysokim (HN) zapasem azotu [Grassi et al. 2002]

Measurement of the N storage capacity of a tree is difficult, and studies have usually involved the use of isotopic tracers, coupled with sequential destructive harvesting [Millard 1996]. Such studies are often restricted to small trees growing in sand culture. Unfortunately, N budgets constructed for larger trees growing in soil are often imprecise. An alternative approach to measuring N remobilisation by deciduous trees has been to consider the flux of N in the xylem during flushing. Several studies have measured a sharp peak in the concentration of N in the xylem sap during bud burst, which was attributed to N remobilisation [Glavac and Jockheim 1993, Schneider et al. 1994, Drambrine et al. 1995]. Use of ^{15}N tracers to label N storage pools in young trees has confirmed that remobilisation in *Betula pendula* [Millard et al. 1998] and *Malus domestica* [Malaguti et al. 2001] coincides with these peaks in xylem sap amino acid concentrations. Specific amino acids and amides have been identified in sap as being translocated due to remobilization, as shown by their ^{15}N labeling pattern [Millard et al. 1998, Malaguti et al. 2001, Frak et al. 2002, Grassi et al. 2002] (tab. 3). Subsequently, the flux of remobilized N in the xylem has been calculated by measuring sap flux and the concentration of amino acids translocated during remobilization to determine the flux of N.

Table 3. Nitrogen compounds found in the tree xylem sap and responsible for remobilisation of stored N. The major form of N translocated during remobilization is underlined

Tabela 3. Związki azotu znalezione w soku ksylemowym drzew, odpowiedzialne za remobilizację zgromadzonego N. Najważniejsze formy azotu translokowane w trakcie remobilizacji podkreślono

Tree species Gatunek drzew	Aminoacid Aminokwas	Reference Źródło
Betula pendula	Citrulline, Glutamine	Millard et al. 1998
Juglans nigra × regia	Arginine, Citrulline, Glutamine	Frak et al. 2002
Nothofagus fusca	Glutamine	Stephens, Personal communication
Prunus avium	Glutamine, Asparagine, Aspartic acid	Grassi et al. 2002
Populus trichocharpa	Glutamine, Asparagine	Millard, Personal communication
Malus domestica	Asparagine, Aspartic acid, Glutamine	Malaguti et al. 2001, Guak et al. 2003
Acer plasudoplatanus	Asparagine, Glutamine	Millard, unpublished data

This new approach to quantifying remobilization gave good agreement with quantification using ^{15}N and destructive harvesting for young *Prunus avium* and *Juglans nigra × regia* grown in sand culture [Grassi et al. 2002, Frak et al. 2002] and young *Malus domestica* grown in soil [Guak et al. 2003]. Such an approach for quantifying remobilization has a potential for application in the context of field experiments, particularly to measure the N storage capacity of trees. Recent evidence [Millard et al., submitted] suggests that the N translocation pattern found in small poplar and cherry trees during remobilization is similar to that also found in larger, more mature trees growing in soil. This suggests that there is the potential to scale up the technique in order to assess the amount of N remobilized by large, orchard grown-trees.

WITHIN YEAR N RECYLING (shoot-root-shoot recyling)

Once remobilization ceases, root uptake then provides the remainder of the N used for growth that year. Regulation of N uptake by roots involves several factors, including the concentration of nitrate and ammonium in the soil solution, soil temperature and the availability of current photsynthtates for translocation to the roots. As an inverse correlation has been found between the concentration of amino acids and amides in phloem saps and nitrate uptake by the roots of several trees including *Prunus dulcis* [Youssefi et al. 2000] it has been hypothesised that shoot- root cycling of N can act as an important regulatory mechanisms for N uptake, as it has been demonstrated for S and Fe [Marschner et al. 1996]. Shoot-root phloem transport of mineral elements is a normal feature of vascular plants and may serve other functions, such as the maintenance of cation-anion balance in the shoot [Pate 1975]. A considerable amount of the nutrients translocated to the roots can be loaded again into the xylem and translocated back to the shoot, i.e. they are "recycled" within the plant [Marschner 1995]. While it has been demonstrated for several herbaceous species that part of the N in the xylem sap represents a recycled fraction [Cooper and Clarkson 1989, Jeschke and Pate 1991, 1992], there is a paucity of data for tree species. Moreover, while qualitative evidence of this process are available, there is a lack of quantitative data, mainly due to methodological problems. Our current knowledge is mainly based on detailed analyses of phloem and xylem sap in different shoot parts of individual plants and the corresponding mineral element contents in the shoot parts at sequential harvests [Jeschke and Pate 1991, 1992].

A quantitative estimate of the amount of N recyling in trees was presented by Grassi et al. [2003]. Their approach was that the occurrence of this cycling implies that a cumulative measure of N flux through xylem should overestimate the amount of N effectively recovered in the new biomass. Using cherry trees subjected to destructive harvests and measurements of transpiration and N concentration in the xylem sap, these authors demonstrated that: 1) shoot-root-shoot recycling was negligible (or at least could not be measured) during the period when roots remobilise their stored N to new growth (first 40–60 days from bud burst); 2) when remobilization finished and trees relied on root N uptake, there was an intense phloem flux of N back to the root system, which is followed by N reloading to the xylem; 3) on average each atom of N fluxed 1.8–2.8 times in the xylem sap in a period of about 50 days and 4) root uptake of N was lower in trees that recycled back to the roots higher amounts of N.

CONCLUSIONS

The adoption of stable isotope techniques in tree physiology has led to significant improvements in our understanding of cycling of N in trees. It is clear that nitrogen has a very high mobility in the tree and that its initial partitioning to a target organ does not necessarily represent its final destination.. The better understanding of the role of internal tree cycling of N has allowed a fine tuning of N supply. Late winter N supplies (before bud burst) are now discouraged, while N is postponed to meet the more intense root demand. Small amounts of N are now often supplied in order to augment storage and subsequent remobilization. In such respect it must be taken into account that supplemental soil post-harvest N is not always needed as mature trees replenish storage pools mainly by withdrawing N from senescent leaves. Considering the low amounts required in post harvest, foliar supply can be preferred to soil N, especially under those condition leading to increased risks of N leaching in autumn.

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PRZEPŁYWY AZOTU WEWNĄTRZ DRZEW OWOCOWYCH KLIMATU UMIARKOWANEGO

Streszczenie. Odżywianie azotem (N) stanowi główny czynnik kontrolujący wzrost i owocowanie drzew. W krajach UE oczekiwania społeczeństwa i decyzje polityczne wymuszają przyjęcie odnawialnych sposobów prowadzenia sadów. Wskazania odnośnie gospodarki azotem są nakierowane na zastosowanie nawozów w progowych dawkach, w celu zredukowania strat N. Wzrost efektywności obiegu N obecnego w sadzie stanowi podstawowy krok w kierunku ograniczenia zewnętrznego wkładu. Zastosowania izotopu ^{15}N jako narzędzia doświadczalnego umożliwiło znaczny postęp w poznaniu przepływów azotu w obrębie drzew i w ogóle w sadzie. W pracy dyskutowane są przepływy N wewnątrz drzewa – pomiędzy latami i w obrębie roku (obieg korzenie–pędy–korzenie) oraz ich znaczenie dla cykli wzrostowych i reprodukcyjnych drzew owocowych.

Słowa kluczowe: magazynowanie azotu, ponowne uruchamianie azotu, obieg azotu pędy–korzenie–pędy, skład soku ksylemowego

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