

Plant N Fluxes and Modulation by Nitrogen, Heat and Water Stresses: A Review Based on Comparison of Legumes and Non Legume Plants

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1. Introduction

Nitrogen (N) is one of the most limiting mineral elements for plant growth and yield (Davidson et al., 2007). This element is an essential component of plant cells at the structural, genetic and metabolic levels, getting involved in many processes of plant growth and development which finally lead to yield as well as the quality of harvested organs (seeds or shoot biomass). While soil N availability can be enhanced in agricultural areas through fertilizers supply, under natural conditions mineral N generally limits plant growth because of spatial and temporal fluctuations in its availability in the soil. Moreover, in the context of climate change, plants will experience more abiotic stresses, including those impacting water availability (drought, flooding), extreme temperatures (chilling, heat), presence of heavy metals, nutrients availability, and soil structure, which can have dramatic consequences on yield and quality, as they directly or indirectly modify plant N acquisition and utilization. Among plants species, legumes have the capacity to acquire soil N *via* roots and, in addition atmospheric dinitrogen through symbiosis with bacteria. While in legumes both these N retrieval ways interact (the interaction being mediated by soil nitrate availability), they also complement for an optimum N nutrition. However, even in legumes, because of the high energy cost of N₂ fixation (Voisin et al., 2003b) and the high sensitivity of nodules to environmental factors (Salon et al., 2001; Serraj et al., 1999), N acquisition is also very frequently spatially and temporally limited. Hence, details concerning the differences between legumes and non-legume plants can set the foundation for the understanding of the stress impacts on plants.

One of the **biggest challenge for European agronomy** in the next years will be to cope with the necessary reduction/optimization of fertilizer use in order to minimize agricultural detrimental impacts on the environment (reducing fossil use energy and greenhouse gas emissions, maintaining/enhancing biodiversity through pesticides/herbicide use reduction) while producing more feed/food for the ever growing population. One way to solve this dilemma consists in the identification/selection of crops having **enhanced N use efficiency**

(NUE, yield per unit of soil N) in the context of increased abiotic constraints. Agroecological advantages of legume cultures are thus obvious, as they naturally enrich soil with N, leading to a high reduction of N amendments, and consequently avoiding pollutions linked to amendment synthesis, their transport and their spreading.

In this chapter, the main features concerning the physiological pathways involved in NUE, that is to say N uptake efficiency (NUpE) and N utilization efficiency (NUE) including assimilation, allocation and mobilization within/from plant organs will be described highlighting differences between legumes and non legume plants. **A first section** will depict the system when plants encounter no environmental constraints. **In a second section**, the main changes in the plant physiological mechanisms depicted in section 1, mediated by heat stress, water stress and soil N limitation will be illustrated using up to date literature. Using recent results from multidisciplinary integrative approaches we will illustrate how plants cope with these constraints during the different phases of their growth cycle.

2. Plant N fluxes without environmental constraints

2.1 Nitrogen forms available for plants

In soil, inorganic N forms are produced by soil microorganisms and represent less than 5% of total soil N which is mostly sequestered in soil organic matter. Nitrogen is acquired in a variety of forms by most plant species but inorganic N forms (*ie* nitrate and ammonium) are preferred over organic forms in most agricultural soils (Crawford & Forde, 2002; Harrison et al., 2007) and are the most abundant in temperate climatic conditions. Nitrate, unlike ammonium does not get adsorbed by soil and is very mobile. As such, and despite that reducing nitrate to ammonium requires more energy than the direct uptake of ammonium (Noctor & Foyer, 1998), plants from most of agricultural soils and/or dry environments privilege nitrate for their N nutrition while in forest habitats and humid environments the preference goes for ammonium. Because soil nitrate concentration highly varies according to the soil and its microbial content (Miller et al., 2007) plants have to set up a strategy to adapt to such spatially and temporally fluctuations of resource availability. Inorganic N nutrition mostly concerned nitrate and impressive results arose from molecular research on the model plant *Arabidopsis thaliana* (Gifford et al. 2008; Scheible et al., 2004). Several recent studies otherwise examined ammonium regulation of gene expression in various plant systems (Lopes & Araus, 2008; Ruffel et al., 2008).

Although legumes also assimilate some soil mineral N by their roots, they indirectly acquire this element from atmospheric N₂ through endosymbiosis with N₂-fixing bacteria that involves the formation of a specific symbiotic organ (nodules) on roots. Interestingly, non legumes plants such as rice (Chi et al., 2005), wheat (Iniguez et al., 2004) or maize (Perin et al., 2006) are also able to interact with N₂ fixing bacteria for N acquisition (Kraiser et al., 2011; Rosenblueth & Martin-Romero, 2006). For instance, using ¹⁵N dilution methods, it has been demonstrated that wheat plants inoculated with *Klebsiella pneumonia* and cultivated under low mineral N conditions assimilated up to 49% of the plant N from the atmosphere while plants inoculated with mutant of *Klebsiella pneumonia* unable to fix N₂ presented symptom of N deficiency (Iniguez et al., 2004).

2.2 Nitrogen acquisition and assimilation

During plant vegetative stage, meristems and young developing organs need ample supply of N for synthesis and storage of their amino compounds, which are further incorporated in

proteins. Water and minerals diffuse osmotically in roots *via* both an apoplastic (extra cellular free spaces) and a symplastic (cytoplasmic channels) pathway up to the endodermis cells surrounding xylem and phloem. Reaching the endodermis, ions have to be actively pumped from the symplasm to tracheids of xylem as apoplastic transport is precluded by the Casparian strip (Enstone & Peterson, 2002). Ammonium and nitrate reduction/assimilation does not take place in the same tissue, ammonium being assimilated in roots, and sometimes translocated to shoots (Schjoerring et al., 2002). Nitrate reduction and further assimilation occurs in roots and/or shoots (most of the times) depending as example upon the plant species, the amount of available soil nitrate or energy.

Adapted to the fluctuating nitrate concentrations, root N uptake relies at the molecular level on nitrate transporters, whose affinity varies. For soil nitrate concentration below 1 mM, high affinity transport systems (HATS comprising the NRT2 gene family) are predominant, while for soil nitrate concentration higher than 1 mM, low affinity transport systems (LATS comprising the NRT1 gene family) are predominant. Both of these nitrate transports systems are inducible. Part of the LATS is the protein expressed by the gene NRT1.1 belonging to the NRT1 family (Tsay et al., 2007). NRT1.1 is also involved in the activation of nitrate-related genes (Ho et al., 2009), the signalling network for regulation of root development (Ho & Tsay, 2010) and auxin transport (Krouk et al., 2010). It is inducible and located in the epidermis of the root tip and in the cortex and endoderm of upper root parts (Huang et al., 1996). NRT1.2, which expression occurs in root hairs and epidermis of mature root parts (Huang et al., 1999), is a constitutive part of LATS. The main component of HATS (Li et al., 2007) is the plasma membrane protein expressed by the NRT2.1 gene (Filleur et al., 2001; Orsel et al., 2004) which in *Arabidopsis* (AtNRT2.1) occurs in the epidermis, cortex, and endodermis of mature root parts (Naoza et al., 2003). NRT2.1 protein is physically associated with the protein expressed by NAR2 (also named AtNRT3.1) with which it constitutes the nitrate transporter. The gene AtNRT2.2 is also, although for a minor part, involved in the HATS. Both NRT1 and NRT2 transport nitrate together with protons (Miller et al., 2007). Thereafter nitrate is reduced within root tissues to nitrite by nitrate reductase (NR) and then either reduced to ammonium by nitrite reductase (NiR) (Crawford & Forde, 2002) or translocated to upper plant parts for further assimilation or transient storage.

Plants can also uptake ammonium by ammonium transporters (AMT, Crawford & Forde, 2002), further assimilated into glutamate *via* the glutamine synthetase (GS)/glutamate synthase (GOGAT) cycle. Some plants such as legumes have the ability to establish symbioses with a bacterium housed within specialized plant organs (nodules) and acquire N through biological N₂ fixation. In nodules of legumes, atmospheric N₂ is converted to NH₃ by nitrogenase and diffuses from the nodule bacteroid alkaline protoplasm into the acidic peribacteroid space where it is converted to ammonium. Ammonium is then transported across the peribacteroid membrane into the cytoplasm of infected cells (Tyerman et al., 1995) and assimilated, as explained above, by the GS/GOGAT system.

In legume plants, the two N nutrition pathways of display complementarities for N uptake while they are antagonist for C use within the plant. Indeed, on the one hand, N₂ fixation occurs in situations of low nitrate availability in the soil: as a result, N₂ fixation in nodules decreases as nitrate availability in the soil increases, while nitrate assimilation by the roots increases (Voisin et al., 2002b). On the other hand, bacteria provide the plant with reduced N₂ through nitrogenase activity, while the energy needs for nodule synthesis and functioning are sustained by plant photo assimilate supply to nodules (Kouchi & Yoneyama, 1984). Nodules are strong sinks for assimilates within the plant (Hacin et al., 1997), that

compete for C assimilates both with the shoot and the roots (Schulze et al., 1994, 1999; Voisin et al., 2003a,2003b). As such, it has been shown that N₂ fixation globally induces higher C requirements for the plant, as compared to nitrate assimilation (Ryle et al., 1979; Schulze et al., 1994, 1999; Silsbury, 1977). Therefore, the C budget at the plant level can be unfavourable when plant N nutrition relies exclusively on symbiotic N₂ fixation (Minchin et al., 1981). Nevertheless, interactions between legume plant, N source (N₂ fixation or nitrate assimilation) and C metabolism can be species- or genotype-dependent (Bethlenfalvays et al., 1978; Radin, 1983; Ryle et al., 1979; Vos et al., 2005). How acquisitions of NO₃⁻, NH₄⁺ and N₂ in legumes are co-ordinately regulated to fulfil the plant N demand is not known. The fact that the assimilatory pathways involved in the acquisition of these N sources share the same end-product suggests that the three pathways might be under a general control exerted by a systemic signalling pathway related to the level of downstream product of N assimilation in the whole plant (Forde, 2002). Split-root experiments were used to induce short term fluctuations of N availability supplied on a localized part of the roots, and to evaluate the systemic responses triggered at the whole plant level that are revealed on the untreated side of the root system. Supplying a high level of NH₄NO₃ to one part of the root system of *Medicago truncatula* induced a strong repression of the apparent N acquisition capacity of the other side, whatever the N source (NO₃⁻, NH₄⁺, N₂) (Ruffel et al., 2008). This demonstrates that the three pathways are controlled by feed-back repression mechanisms, which involve systemic signalling pathways. This regulation results in the adjustment of the acquisition capacities of the roots to the N demand of the whole plant. At the molecular level, a transcriptomic study has revealed that gene networks involved in these responses are rather specific of the N source (Ruffel et al., 2008).

Plants are also capable of taking up amino acids available in the rhizosphere. Indeed, some amino acid transporters have been identified. They seem rather specific, as for example cationic amino acid transporters (CAT) or lysine/histidine transporter (LHT) (Chen et al., 2001; Liu & Bush, 2006; Rentsch et al., 1996; Scheible et al., 2004; Stacey et al., 2002). LHT1 has a dual role, participating in the uptake of neutral and acidic amino acids in root and providing of leaf mesophyll cells with xylem-derived amino acids (Hirner et al., 1998). An early rice nodulin gene (OsENOD93-1) has been implicated in amino acid accumulation in roots and transport towards the shoot (Bi et al., 2009). Oligopeptide transporters (OPT) seem to have a role for peptide and amino acid transport during the early phase of embryo development (Stacey et al., 2002). Amino acid permeases (AAP) are involved in phloem-loading with various implications in amino acids transport (Sanders et al., 2009; Schmidt et al., 2007).

2.3. Distribution of N compounds within the plant

2.3.1 Amino compound transport

Long distance transport of water and ions from roots to shoots is apoplastic under tension and occurs through mass flow across xylem cells, driven by the shoot evaporative loss of water. In addition, the uptake of water following that of ions creates root pressure which mainly helps re-establishing flow continuity in xylem vessels when transpiration rate is either very high or in some plants reduced due to high air humidity. In *Arabidopsis*, nitrate is transported in roots either passively into the xylem or at the site of pericycle cells by the AtNRT1.5 nitrate transporter while the AtNRT1.8 acts in both root nitrate loading and unloading from root or shoot xylem vessels (Li et al., 2010). The compounds exported by roots in xylem come not only from soil mineral N assimilation by roots or atmospheric N₂ symbiotic fixation within nodules, but also from other catabolic processes, export of

previously stored soluble compounds, or recycling from phloem to xylem in the roots. These latter processes however represent only about 15% of the N exported by the roots.

2.3.2 Composition of saps

Xylem sap pH is mildly acidic (between 6 and 6.5) and is characterized by a low osmolarity. Among the few organic and inorganic solutes, xylem sap is mainly composed of N compounds (amino acids, amides, ureides), organic acids and nitrate ions content being much lower. The C skeletons of N compounds originate from C transported by shoots to roots *via* the phloem. Carbon (C) xylem sap originates mainly from amino compounds although sugars may accumulate in xylem sap to concentrations up to 50 mol m⁻³. The main solutes in xylem sap are highly specific to the species, the source of N in soil or the stages of development. In legumes, aminotransferases form the main N compounds exported from the nodules. These compounds are glutamine and asparagine for temperate legumes and ureides (allantoin and allantoic acid) for tropical legumes (Parsons & Sunley, 2001). The N compound spectrum found in xylem also depends upon the N nutrition regime: temperate legumes supplied with large amounts of nitrate in the nutrient solution will shift from asparagine export to glutamine export from roots to xylem following nitrate assimilation. Similarly, tropical legumes will export amides instead of ureides following nitrate supplementation. In non legume plants such as maize supplied with nitrate, the xylem sap has higher glutamine concentration while maize fed with ammonium has higher asparagine concentration in xylem (Murphy & Lewis, 1987). Glutamine and asparagine are also the predominant amino compounds in oilseed rape (Balint & Rengel, 2011) or barley (Lewis et al., 1982).

Phloem sap has an alkaline pH (7 to 8.5) and transports mostly sucrose, in some species fructanes, raffinose-family oligosaccharides (raffinose, stachyose, verbascose), and a tiny amount of hexoses (glucose and fructose) except in wounded tissues, alcohol sugars and amino acids. Nitrogenous compounds in phloem are similar to those in xylem but more concentrated (5 to 40-fold, Pate et al., 1975). Their concentration varies among plant species, from around 0.1 mol m⁻³ (Hunt et al., 2010), to over 1.2 mol m⁻³ (Faria et al., 2007). Aspartate and glutamate and their corresponding amides, asparagine and glutamine often predominates (Girousse et al., 1996; Hunt et al., 2010; Sanders et al., 2009). The relative concentrations of threonine, histidine, tryptophane, and valine vary between plant species. Sulfur amino acids are less concentrated in phloem sap, cysteine is present as a trace in phloem sap, glutathione is usually also found in the sap (Fisher & Macnicol, 1986; Jongebloed et al., 2004), S-methylmethionine (Bourgis et al., 1999). Phloem never contains either ammonium (Riens et al., 1991) or nitrate (Fan et al., 2009; Hayashi & Chino 1986; Lohaus et al., 2000; Patrick et al., 2001). The precise composition of phloem sap is influenced by abiotic factors, such as temperature, N and water availability (Balint & Rengel, 2011; Mitchell & Madore, 1992; Tilsner et al., 2005). It has been also reported that amino acid composition of phloem sap changed as function of genotype performance in term of NUE. For instance, the phloem sap of oilseed rape genotypes more efficient in remobilising N were proposed to contain greater amounts and/or proportions of asparagine, which is the most efficient N transporter (N : C ratio equal to 0.5, compared with 0.4 for glutamine) (Seiffert et al., 1999).

2.3.3 Carbon transport associated with N compounds

Nitrogenous compounds are exported by roots to shoots *via* the xylem but the transfer from xylem to phloem thereafter varies according to the electrical charge of the compounds.

Xylem to phloem transfers occur mostly in the higher part of the plant and allow N from the transpiration stream to be directed to low transpiring organs such as apices, young leaves, fruits. Amino acids such as arginine are in xylem sap under the cationic form and bounded on the negatively-charged cell wall of xylem vessels. Vascular tissues of stems, petioles and major veins of the leaves are then able to attract them (McNeil et al., 1979; Pate et al., 1979a) while neutral amino acids and amides (such asparagine, valine, glutamine, allantoin) can be delivered according to the selectivity of cell uptake in stems or be transferred from xylem to phloem (Pate & Layzell, 1981). The amino acids under anionic forms in xylem sap (allantoic acid, aspartate and glutamate) and nitrate can be transported to transpiring organs such as leaves. The presence in xylem sap of compounds not easily transferred to phloem (arginine, asparagine and glutamine) ensures that N compounds arising from root assimilation are retained by mature parts of aerial organs, in particular cell mesophyll, for synthesis of leaf proteins needed for C assimilation. Compounds easily exchanged between xylem and phloem (asparagine, glutamine and valine) have a major importance for loading upward flow (mostly asparagine) or downward flow (mostly glutamine) of translocated compounds with N, hence providing N to meristematic tissues during their growth, and developing fruits (Pate et al., 1981). Amides (asparagine and glutamine) which are the main compounds concerned with xylem to phloem transfer are therefore beneficial for the N nutrition of such tissues because their low C/N ratio (2 and 2.5, respectively) enriches the phloem in N.

2.3.4 Source – sink relationships for N

In legumes, there is a preferential N transfer toward apices as compared to roots and 40% of this N is issued from the xylem transpiration stream, the remaining coming from phloem (Layzell et al., 1981). Young developing leaves import most of their C and N needs from phloem up to the point where they transpire actively. Thereafter xylem furnishes up to 80% of the total N necessary for leaf growth while leaves behave as a source for C. Minor veins of source leaves are the main sites of exported sugars and amino compounds in phloem companion cells or xylem transfer cells which then supply sieve elements with carbohydrates, amino compounds, proteins or RNAs which are involved in long distance signalling in response to developmental or stress triggers (Lough & Lucas, 2006; Turgeon & Wolf, 2009). Sucrose synthesised within photosynthetic organs attracts xylem water by osmosis. Amino compounds may additionally be loaded *via* the apoplast from xylem in phloem. Control of symplasmic loading may occur through either plasmodesmata density or conductance. Apoplastic loading in turn is supposed to be regulated by sucrose pool size or phytohormones (arising from roots *via* the transpiration stream or in phloem imported water from recycled xylem) responding to the sink/source ratios: an increase in this ratio would enhance membrane protein levels of sucrose transporter. Phloem loaded compounds further flow through the phloem by osmotic pressure differences (Minchin & Lacomte, 2005; Thompson, 2006) either following symplastic or apoplastic pathway toward sinks which maintain an osmotic gradient by either 1) respiring sucrose, 2) storing it in vacuoles, or 3) converting it to osmotically inactive forms (starch, cellulose, proteins etc.) (van Bel, 2003). This allows elaborated phloem sap to be delivered to sink organs having low transpiration rates such as growing organs, fruits, apices.

2.4 Nitrogen remobilization and storage are crucial for plant N management

2.4.1 Remobilization

Optimization of N remobilization efficiency (NRE) in crop plants is probably one of the main lever to improve NUE. Indeed, increasing N remobilisation from senescent organs or

damaged tissues represents an important adaptative trait allowing plants (1) to recycle N resources from the vegetative parts, (2) to limit N loss in the dry remains and (3) to reduce N fertilizer inputs (Masclaux-Daubresse et al., 2010). In legumes or non-legume plants, leaves usually represent the main source organ for N, even during sequential senescence (which occurs leaf rank per leaf rank at vegetative stage) or monocarpic senescence (characterized by a general senescence of leaves and other vegetative tissues) where N content of phloem sap increases because of enhanced mobilisation of N.

Proteolysis is one of the most important processes of N remobilization (Hörtensteiner & Feller, 2002; Zimmerman and Zentgraf, 2005). Moreover, the effective recycling of the N compounds from source leaves to sink growing tissues requires a fine coordination between sink demand and the processes of proteolysis. This is particularly important when plants are confronted by stresses that could lead to strong modifications of the source/sink relationships (see §3). Based on a study of N flux using ¹⁵N tracing methods, the physiological events and proteomic changes involved in the remobilisation of N associated with sequential senescence were recently investigated in leaves of oilseed rape at vegetative stage (Desclos et al., 2009). This work reveals that four proteases were specifically involved in N remobilisation: FtsH, a chloroplastic protease, is induced transiently during early stages of N remobilisation and could be involved in the earlier degradation of chloroplastic proteins such as Rubisco; an Aspartic protease that increases at the beginning of senescence and is maintained at a high level until the abscission, would be implied in proteolysis in vacuolar and chloroplastic compartments during the course of leaf senescence; Proteasome β subunit A1 and SAG12 (cysteine protease), are strongly induced during the later phase of senescence, suggesting that these proteases are more specifically involved in the proteolysis processes occurring at the final stages of leaf senescence.

During the reproductive stage, N compounds provided *via* the recycling and remobilization associated to leaf senescence are largely requisitioned for optimum flowering and grain filling (Brouquisse et al., 2001; Gallais et al., 2006; Guiboileau et al., 2010; Malagoli et al., 2005; Masclaux-Daubresse et al., 2008). Indeed, at this stage, N assimilation usually decreases, mostly due to abiotic stress and as such, leaves are solicited for supplying amino acids to the reproductive organs, between 50 to 80% of their N needs, for legumes (Salon et al., 2001, Schiltz et al., 2005), oilseed rape (Malagoli et al., 2005), wheat (Kichey et al., 2007), maize (Masclaux et al., 2001) or rice (Tabuchi et al., 2007). Mobilised amino acids are issued from a) proteolysis of chloroplastic proteins (70 to 80% of total leaf - Liu et al., 2008 - mostly consisting of Rubisco, Mae et al., 1993), b) exo/endopeptidases attack of cytosolic proteins *via* sequestration within double membrane vesicles called autophagosomes (Ishida et al., 2008; Wada et al., 2009) pathway and senescence-associated vesicle (SAV that contains cysteine protease SAG12; Otegui et al., 2005) trafficking, c) removal of short lived proteins through the ubiquitin-26S proteasome for regular cell maintenance. The photosynthetic activity is then progressively reduced by N remobilisation. During N mobilisation from senescent leaves to filling seeds in pea (Schiltz et al., 2005), a proteomic approach has also reported the induction of chloroplastic proteases such as ATP-dependent Clp protease and ATP-dependent Zn-activated protease (FtsH) which were concomitant with the decline of leaf proteins. During leaf senescence, proteolysis of chloroplast proteins would release glutamate that serves as a substrate of the glutamate dehydrogenase (GDH, Purnell & Botella, 1997). GDH would, in turn, provide 2-oxoglutarate to support respiration and ammonium reassimilated by cytosolic GS1 for export and remobilization (Masclaux-Daubresse et al., 2006). Therefore, several evidences have reported the induction of the

activity of cytosolic GS1 during leaf senescence and supports the role of cytosolic GS1 in the efficient remobilization of amino acids for senescing leaves towards grain-filling (for a review see Masclaux-Daubresse et al., 2010). For instance, the role of GS1 in N management, growth rate, yield, and grain-filling has been suggested by the finding of co-localizations between QTLs (quantitative trait loci) for agronomic traits and GS activity (Hirel et al., 2001; Obara et al., 2004).

Following proteolysis, the resulting amino acids are distributed towards sink tissues by phloem loading that is ensured by amino acids transporters and permeases. In mature leaf of oilseed rape, Tilsner et al. (2005) have reported that remobilization of amino acids in mature leaf of oilseed rape was concomitant with the up-regulation of AAP1 gene expression, suggesting that this permease has a pivotal role in amino acid exportation. Phloem sap supplies around 90% of the fruits' N needs, while xylem sap the rest. During fruit development, phloem amino acid content increases (Pate et al., 1977; Peoples et al., 1985).

2.4.2 Storage

When N acquisition and assimilation is superior to N demand for growth or in case of asynchronism between remobilization of N in sources organs and N requirement for growth of sink tissues, numerous plants are capable of modifying their N fluxes in order to transiently store N in their organs (Millard, 1988; Staswick, 1994; Volenec et al., 1996). The predominant N reserves are usually amino acids and soluble proteins that are accumulated in specific sub-cellular compartments (vacuole, chloroplast) of various storage organs: tuber, root, taproot, stolon, stem as well as leaf. Deposition of N as soluble protein form in storage organs may have several advantages for plants. First, the storage of N as proteins in cell vacuoles might avoid potential osmotic problems that accompany the accumulation of N as nitrate. Second, this makes it possible to sequester N for extended periods without major consequences for cellular metabolism (Millard, 1988). Additionally, specific proteins called vegetative storage proteins (VSPs) have been characterized for their preferential function as a temporary N reserve in many herbaceous and woody species (Avicé et al., 2003; Bewley, 2002; Ourry et al., 2001). These VSPs may represent between 5 and 40% of total soluble proteins and are strongly remobilized to sustain shoot or fruit growth. For instance, in perennial forage legumes such as alfalfa and white clover, studies performed under environmentally controlled or field conditions have shown that N reserve availability, and particularly VSPs concentration, are closely related to shoot regrowth after defoliation or to the spring shoot growth (Avicé et al., 1997; Justes et al., 2002; Simon et al., 2004). In addition to their role in N storage, converging evidences suggest that VSPs possess alternatives roles including defence against pathogen attack and tolerance to various abiotic stresses such as cold, elevated temperature or drought (Avicé et al., 2003; Dhont et al., 2006; Erice-Soreasu et al., 2007).

3. Impact of N limitation, heat stress and drought on plant N fluxes

3.1 Impact of N limitation on plant N fluxes

In non legumes, all the components of NUE are affected by low mineral N availability. To cope with this, plants have evolved a suite of adaptive responses to successfully finish their life cycles to produce offspring, rather than die early and barren due to insufficient N nutrient (Kant et al., 2008; Peng et al., 2007). Several physiological and biochemical changes occur in plants as adaptive responses to N limitation, including an increase in N uptake by high-affinity transporters, remobilization of N from older to younger leaves and

reproductive parts, a delay of growth and development, a decrease of photosynthesis capacity, and increased anthocyanin accumulation (Peng et al., 2007). For legumes, soil mineral N availability is the main environmental factor affecting symbiotic N₂ fixation, and consequently the relative contributions of soil mineral N assimilation by the root and symbiotic N₂ fixation to overall plant N uptake (i.e. the N source) (Moreau et al., 2008; Streeter & Wong, 1988; Voisin et al., 2002b).

3.1.1 N limitation affects the morphology of root system

Root architecture is a major determinant of the size of the root-soil interface and of the resulting water and nutrients acquisition by the plants. A low N supply generally leads to decreased root growth, suppression of lateral root initiation, increase in the C/N ratio (ie sucrose-to-nitrate ratio) within the plant, reduction in photosynthesis, and early leaf senescence (Kant et al., 2008; Malamy, 2005; Malamy & Ryan, 2001; Martin et al., 2002; Paul & Driscoll, 1997; Wingler et al., 2006; Zhang, 2007). Several genes of *Arabidopsis thaliana* involved in root development through hormonal signals and/or nutrient perception were reviewed by Casson & Lindsey (2003). But much less is known concerning legume root development. The root system of legumes is less extended than that of cereals (Greenwood et al., 1982; Hamblin & Tennant, 1987). Actually, in legumes, root growth competes for C with nodule formation (Voisin et al., 2003b). As such, when symbiotic N₂ fixation occurs, root growth is limited due to C competition within the plant. Both in field and greenhouse conditions, lower root growth was observed for pea plants grown in conditions of low nitrate availability compared to plants fertilised with nitrate (Voisin et al., 2002a; Voisin et al., 2010). It is also known that nitrate locally stimulates root proliferation, which results in increase of soil-root interface. For pea plants, in the field local nitrate-stimulated root proliferation was essentially observed in the ploughed layer (the upper 20 cm) but nitrate did impact neither root repartition within the profile nor maximal rooting depth (Voisin et al., 2002a). Thus, the root system of pea remains shallow (around 80 cm deep) whatever the N source.

3.1.2 Adaptative response to N limitation

Plants have developed adaptive responses, allowing them to modulate the efficiency of root N acquisition as a function of both external N availability and their own nutritional status (for review, Forde, 2002; von Wiren et al., 2000).

N Limitation and soil mineral N uptake: In non leguminous species, plant response to low nitrate availability triggers increased activity and affinity of nitrate uptake systems of the roots (Crawford & Glass, 1998; Gazzarrini et al., 1999; Lejay et al., 1999; Rawat et al., 1999), together with enhanced lateral root growth promoting root branching, and thus, soil exploration (Forde & Lorenzo, 2001). This regulation involves local NO₃⁻ signalling and the systemic action of long distance signals of the plant N status. Nitrate transporters (NRT2.1; NAR2; NRT1.1) and N assimilation genes (nitrate reductase, glutamine synthetase) are induced by either a fall in the plant N status or the availability of another N source (ie ammonium). Among signals putatively involved, translocation of glutamine from shoot to root by the phloem has been shown to regulate N uptake by decreasing the expression of NRT2.1 (Gansel et al., 2001). Limitation of nitrate may also influence the activity of NRT1.1, considered as a nitrate sensor (Ho et al., 2009). Indeed, both high and low affinity nitrate transport of NRT1.1 depend upon phosphorylation / dephosphorylation by the CBL-interacting protein kinase CIPK23 (Liu & Tsay, 2003) and are mediated by low nitrate

conditions (Ho et al., 2009). Ammonium uptake is known to be repressed by high external N and to be induced under N deficiency, by mechanisms that may act at both the transcriptional and post-transcriptional levels (Gazzarrini et al., 1999; Lanquar et al., 2009; Rawat et al., 1999; Yuan et al., 2007). It was reported that some AMT genes (ammonium transporter gene family) showed increased expression during early N limitation, whereas the expression of other transporters increased only after prolonged starvation (Loqué & von Wirén 2004). In legumes, the adaptive response to local N limitation was investigated using split root systems (Jeudy et al., 2010; Ruffel et al., 2008). As for non leguminous plants, it was shown that *Medicago truncatula* plants have the ability to rapidly compensate local nitrate limitation through the increase of nitrate uptake activity of the roots still exposed to nitrate, thus maintaining N uptake by the plant. However, for plants grown with NH_4^+ , the short term increase of NH_4^+ uptake in response to local limitation is insufficient to sustain N uptake and growth (Ruffel et al., 2008), presumably due to overall limitation of the NH_4^+ capacity of plant roots (Salon et al., 2009). The short-term response to local nitrate limitation is associated to a long term developmental response, with root proliferation of the roots in the nitrate exposed roots, at the expense of the N-limited roots that stop growing (Jeudy et al., 2010). Quantitative studies have shown that the sensitivity to soil mineral N or the N_2 fixation capacity could differ among species or genotypes within a species (Harper & Gibson, 1984; Streeter & Wong, 1988; Ewing & Robson, 1990; Sulieman & Schulze, 2010). In the field, plant N requirement can generally be sustained with or without fertiliser N application, i.e. whatever the N source (in pea: Sagan et al., 1993; Voisin et al., 2002a). Nonetheless, for some legume species, plant N requirements may not be fulfilled when symbiotic N_2 fixation is the main source. For example, in soybean, N nutrition can be limiting is case where no N fertiliser is supplied at sowing (Croizat et al., 1994; Gan et al., 2002). As another example, the symbiotic association between *Medicago truncatula* cv Jemalong and *Rhizobium meliloti* strain 2011 (Moreau et al., 2008) or Sm 1021 (Terpolilli et al., 2008), which are most frequently used in genomic studies, lead to N stressed plants when N_2 fixation is the main N source for plant growth.

Symbiotic N_2 Fixation is an original adaptive feature of legumes to low mineral N supply. In situations of low mineral N availability, legume plants have the ability to sustain the plant N requirement through a symbiotic association with soil bacteria enabling atmospheric N_2 fixation. Quantitative studies have shown a correlative negative relationship between soil nitrate availability and symbiotic N_2 fixation (Voisin et al., 2002b). In legumes, numerous studies have shown that nitrate ions can affect symbiotic N_2 fixation (Streeter, 1985a; 1985b). However, the mechanisms by which nitrate limits symbiotic N_2 fixation remain a matter of debate. This limitation could involve changes in the N composition of the phloem sap (Neo & Layzell, 1997; Sulieman et al., 2010). Moreover, a long term effect may also play a major role in the limitation of symbiotic N_2 fixation by nitrate, through a limitation of the photosynthate flow from shoots to roots (Francisco & Akao, 1993), resulting first in a limitation of C supply to nodules (Jeudy et al., 2010) and finally to senescence of nodules exposed to high levels of nitrate (Naudin et al., 2011).

The finely-tuned regulation of nodule number is the main component of the adaptive response of legumes to N limitation. Actually, an internal regulation of nodule number occurs through a systemic feedback-regulated inhibition of nodule formation on young root segments by nodules pre-existing in the root system (Bhuvaneshvari et al., 1980; Kosslak & Bolhool, 1984; Pierce & Bauer, 1983). This leads to an “autoregulation of nodulation” (called AON) and the

control of nodule number by the host plant (Caetano-Anollès & Greshoff, 1990) through reciprocal shoot-root signalling (see Kinkema et al., 2006; Oka-kira & Kawaguchi, 2006 for review). Although the nature of the signals involved in the AON regulation has not been unambiguously elucidated, potential candidate compounds include either phytohormones, like ethylene (Schmidt et al., 1999), auxin (van Noorden et al., 2006) or brassinosteroids, jasmonic and abscisic acids (Oka-kira & Kawaguchi, 2006), or long distance signals involving the whole plant N status (Ruffel et al., 2008). Hypernodulating mutants, which are defective in AON, display excessive nodule numbers compared to wild type (Bourion et al., 2007) and maintain nodulation even when roots are exposed to nitrate. It was observed in pea that nodule number can vary in a wide range for a given wild type genotype, not only depending on nitrate but also on light conditions (Voisin et al., 2010). In this study, it was shown that nodulation was initiated after the exhaustion of seed reserves, in situations of N limiting conditions, and that nodule numbers were adjusted to plant N requirement for growth, that varied with climatic conditions. Nodule biomass was shown to be co-regulated with nodule number (Voisin et al., 2010), which is in accordance the co-localisation of QTLs of nodule number and nodule biomass in pea (Bourion et al., 2010). Finally, a positive relationship was observed between nodule growth and C availability within the plant (Voisin et al., 2010), in accordance with authors who have shown that nodule biomass is increased together with photosynthesis level when it is modulated by light intensity (Bethenfalway et al., 1978; Kosslak & Bohlool, 1984) or CO₂ concentration (Hardy & Havelka, 1976; Murphy, 1986). Jeudy et al (2010) showed in *Medicago truncatula* that, unlike NO₃⁻ fed plants, N₂-fixing plants lack the ability to compensate rapidly for a localised N limitation (induced by replacement of N₂ by argon in the below-ground atmosphere) by up-regulating the N₂-fixation activity of roots supplied elsewhere with N. However, they display a long-term response *via* a growth stimulation of pre-existing nodules, and the generation of new nodules. Nonetheless, due to the delay between N stress perception and the effectiveness of the adaptive response through N₂ fixation by new nodules, N₂-fixing stressed plants experience a temporary N deficiency that reduces growth. Even if the mechanisms may be different when nodule functioning is disturbed by other abiotic or biotic stresses, the adaptive response for SNF recovery consecutive to stress removal may be similar. As such, following short term exposure to nitrate, nitrate removal induced an extra-wave of nodulation (Naudin et al, 2011).

3.1.3 The nutrient contents of xylem and phloem saps are modified by abiotic stress

N limitation caused impaired N assimilation in soybean and a few non-legumes species (tomato, maize, and sunflower), leading to specific changes in the amino acid composition of the xylem sap with an elevated aspartate/asparagine ratio and a decrease of glutamine concentration compared with plants grown at adequate N supply (Amarante et al., 2006). In spring oilseed rape, Balint & Rengel (2011) reported that xylem sap had higher concentrations of aspartate than asparagine under both limited and ample N supplies, indicating that this ratio might be a specific trait and may differ for legumes and non-legumes species. The composition of phloem sap is also influenced by N availability. Proline synthesis and its accumulation are enhanced. The modes of N nutrition influence the N content (amino acids and amides) of the xylem and phloem saps.

3.1.4 N partitioning among organs and mobilization of N compounds

In Arabidopsis, N limitation increases both N remobilization and translocation of the N absorbed post-flowering to the seeds (Masclaux-Daubresse & Chardon, 2011). Under low

mineral N availability, leaf senescence can occur prematurely (Gombert et al., 2006). For instance, in oilseed rape at vegetative stage, N deficiency accelerates senescence in older leaves, enabling the foliar N compounds to be recycled and remobilized towards the developing tissues (Gombert et al., 2006, 2010; Tilsner et al., 2005). N starvation resulted in a significant lower residual N in fallen leaves of oilseed rape than in the control that is due to the reduction of period corresponding from maturity to the initiation of senescence and to the extension of the duration of phase of recycling (from initiation of senescence to leaf abscission). This better recycling and remobilization of N-containing compounds during N starvation-induced senescence is also related to the induction of proteolysis and amino acids exportation with a specific up-regulation of amino acid permease AAP1 (Avice et al., unpublished data). Recently, transcriptome analysis has shown that most of the autophagy genes are up-regulated in response to N limitation (Thompson & Vierstra, 2005; Wingler et al., 2009) and suggesting that autophagy play a role in N management during leaf ageing.

3.1.5 N limitation effect on seed quality

In planta, the seed N concentration pattern during the seed filling is the result of two processes which are not controlled similarly: seed dry matter accumulation and seed N accumulation. In both legumes and non legumes plants, the rate of seed dry matter accumulation is not significantly responsive to changes in plant N availability because it is determined before the beginning of the seed filling by the seed cell number (in maize: Jones & Simmons, 1983; in wheat: Jenner et al., 1991; in soybean and pea: Munier-Jolain & Ney, 1998). In contrast, the rate of seed N accumulation can vary during the seed filling upon N availability in plant (in wheat: Jenner et al., 1991; in soybean: Hayati et al., 1996; in pea: Lhuillier-Soundélé et al., 1999a; 1999b). N limitation can affect negatively plant N availability during the seed period and consequently decrease the rate of seed N accumulation and seed N concentration (in wheat: Debaeke et al., 1996; in soybean: Streeter, 1978; Hayati et al., 1996; in pea: Lhuillier-Soundélé et al., 1999a).

3.2 Impact of heat stress on plant N fluxes

Temperature is one of the main environmental factors explaining the variations of yield and quality in crop plants (Wheeler et al., 2000 in different annual crops; Karjalainen & Kortet, 1987 in pea; Sidlauskas & Bernotas, 2003 in oilseed rape ; Peng et al., 2004 in rice ; Schlenker & Roberts, 2009 in corn, soybean and cotton; Peltonen-Sainio et al., 2010 in barley, wheat and oilseed rape ; Asseng et al., 2011 in wheat). Temperature changes are not necessary deleterious to plants: air or soil temperature regulates the rate of many growth and development processes of plants. A threshold high temperature refers to a value of daily mean temperature at which a detectable reduction in growth begins (Wahid et al., 2007). Such heat stress can have damaging impacts on both vegetative and reproductive tissues by causing proteins to unfold, affecting membrane fluidity, metabolism and cytoskeleton rearrangements (Ruelland & Zachowsky, 2010). Although, it is difficult to define a limiting temperature for an integrative process like growth, it is known that heat stress threshold temperatures vary in plant species with the origin of their habitats. For the temperate legume crop pea (*Pisum sativum* L.), a temperate above 25°C can be considered as limiting (Guilioni et al., 2003). Regarding the differing effects of temperature on the plant physiology in each range, stress-inducing temperature has been defined as severe when temperature exceeds 35°C for a few hours a day for a few days (Guilioni & Jeuffroy, 2010). The threshold

temperature during flowering, which results in seed yield losses, was 29.5 °C for three *Brassica* species (*B. napus*, *B. napa* and *B. juncea* L.) (Morrison & Stewart, 2002). In temperate cereals as wheat, two heat ranges may produce distinct negative reactions: a moderate high temperature range between 15 and 32°C, and a severe heat stress above 32°C (Wardlaw & Wrigley, 1994). Schlenker & Roberts (2009) found that temperature above a threshold is harmful to yields of tropical crops (close to 30°C for corn, soybean and cotton). Although photosynthesis and C metabolism are considered as the physiological processes most sensitive to high temperature (Wahid et al., 2007) and were widely studied, N fluxes in crops plants can be significantly affected by this environmental factor and progress are currently made on this subject.

3.2.1 N acquisition and assimilation

3.2.1.1 Root morphology

Soils in the field show temperature gradients and diurnal oscillations that can strongly affect root growth (Walter et al. 2009). However, depending on soil depth, changes in soil temperature are delayed and display lower amplitude than those encountered for the atmospheric temperature. At moderate temperature, the length of main and lateral roots increases almost linearly with temperature in oilseed rape (Nagel et al., 2009) and various plant species, such as cereals, cotton, sunflowers and forage legumes (Al-Ani & Hay, 1983; McMichael & Quisenberry, 1993). The temperature effect seems to be more pronounced on root branching than on tap root lateral growth, thus root branching increases with higher temperature up to the optimal temperature of a plant (McMichael & Quisenberry, 1993; Nagel et al., 2009). Wahid et al. (2007) suggested that heat stress can cause root growth inhibition. Moreover root viability decreases at high soil temperature (Rachmilevitch et al., 2006).

3.2.1.2 Nitrate uptake and assimilation

In non legume plants, N accumulation relies on nitrate and ammonium assimilation. Rates of N assimilation usually decrease at high temperature (Rachmilevitch et al., 2006). Moreover N allocation to root growth increases at high temperature (Rachmilevitch et al., 2006), thus the translocation of N from roots to shoots may be modified by high temperatures (DeLucia et al., 1992). In legumes, nitrate assimilation is also affected by high temperature, with decreased levels and activities of nitrate reductase, glutamine synthetase and glutamate synthase and lowered synthesis of ureides (Sahulka & Lisa, 1979 in pea ; Hungria & Vargas, 2000).

3.2.1.3 Symbiotic N₂ fixation

The responses of legume-Rhizobium symbiosis to a wide range of elevated temperatures were observed in temperate and tropical legumes. The optimum temperatures for N₂ fixation vary widely between legumes species and reflect their environmental adaptation (Chalk et al., 2010). For temperate legumes the optimum temperature for N₂ fixation is between 15 and 25°C (Sprent et al., 1988), while for tropical legumes, upper limits for N₂ fixation range between 27 and 40°C (Hungria & Vargas, 2000). High temperatures decrease significantly the survival of rhizobia (Chalk et al., 2010; Hungria & Vargas, 2000) and affect the competitive ability of Rhizobium strains (Bordeleau & Prévost, 1994; Chalk et al., 2010). Rhizobium is most vulnerable to stress when it is free-living outside the symbiotic relationship (Chalk et al., 2010). So, repeated inoculation and higher rates of inoculation of

grain legumes may be needed to guaranty optimum N₂ fixation in tropical soils (even when the strain is already present in the soil) (Hungria & Vargas, 2000). High temperatures can also inhibit all steps of nodule establishment by affecting the exchange of molecular signals between host plants and rhizobia, the root-infection process being probably the most affected (Hungria & Vargas, 2000). If nodules are formed, high temperatures may either decrease N₂ fixation efficiency by affecting nitrogenase activity or nodule longevity by accelerating nodule senescence (Bordeleau & Prévost, 1994 ; Hungria & Vargas, 2000).

3.2.2 N partitioning among organs and mobilization of N compounds

Assimilate partitioning can be affected by high temperature (Wahid et al., 2007). Increased remobilisation efficiency of reserves from leaves, stems or other plant parts has been suggested as potential strategy to improve grain filling and yield in wheat under heat stress (Wahid et al., 2007). This suggestion is mostly based on C assimilate movements : heat stress in wheat significantly increased total non-structural carbohydrates (TNC) remobilization efficiency with significant differences observed among genotypes (Blum et al., 1994 ; Tahir & Nakata, 2005). Some results have suggested that the acceleration of senescence by temperature was due to an increase in N assimilate remobilization to seeds (Spiertz, 1977 in wheat). However, for a moderate temperature range, this hypothesis was not verified in pea or soybean as the rate of apparent N remobilization was similar among temperatures (Grangirard et al., 2001; Larmure et al., 2005). Moreover, more recent results in wheat suggest on the contrary that heat stress reduced N remobilization (Ercoli et al., 2010; Tahir & Nakata 2005); in agreement with the results of ¹⁵N assimilate labeling experiments in rice, suggesting that high temperatures induce a decrease in N transport from shoots to the ears *via* the phloem (Ito et al., 2009). Further investigations may improve the understanding of the effect of high temperature on N assimilate partitioning and their physiological basis.

Seed N accumulation comes from daily N accumulation by the plant and from N remobilised from vegetative parts in both legumes and non-legumes plants (in wheat: Jeuffroy et al., 2000; in pea : Pate, 1985; Schiltz et al., 2005). The rate of seed N accumulation is mostly determined by plant N availability from these two sources (in pea: Lhuillier-Soundélé et al., 1999b; in soybean: Hayati et al., 1996; in wheat : Jenner et al., 1991), consequently any effect of temperature on plant N available for seeds should also affect the rate of seed N accumulation. Indeed, in wheat, the influence of high temperatures on seed N accumulation was modified when N supply to plants was modulated (Zahedi et al., 2004). In pea, a higher N availability for the seed at a higher temperature (in a moderate range of 13-23°C) resulted in an increase in the rate of seed N accumulation (Larmure et al., 2005). Moreover, high temperatures affect seed N accumulation because elevated temperature during the reproductive phase causes earlier cessation of total dry matter accumulation in seeds (in wheat: Spiertz, 1977; Hunt et al., 1991; Blum et al., 1994; in soybean: Egli & Wardlaw, 1980).

3.2.3 High temperatures affect both seed N concentration and composition

Literature generally indicates that seed N concentration progressively increases when temperatures rise during the reproductive period in both legumes and non-legumes plants. This increased seed N concentration seems to result from differing susceptibilities of starch and N accumulation in seed to high temperature. In pea, when high temperature occurs either during or after flowering seed N concentration is increased (Karjalainen & Kortet,

1987; Larmure et al., 2005). In wheat and barley, when temperature is increased in a moderate range of 15-32°C during post anthesis, grain N concentration is increased (Bhullar & Jenner, 1985; Jenner et al., 1991; Passarella et al., 2002; Wardlaw & Wrigley, 1994). In rice after heading, kernel N concentration increases when temperature is raised from day/night values of 27/22°C to 33/28°C but remains thereafter steady when temperature is subsequently increased up to 39/34°C (Tashiro & Wardlaw, 1991). Similarly, in soybean, in the range of temperature encountered by the plants during the reproductive period seed N concentration increases with temperature up to a day/night temperature of 40/30°C (Piper & Boote, 1999; Thomas et al., 2003).

Several authors suggest that the earlier arrest of seed filling due to heat stress interferes with the accumulation and processing of the latest proteins accumulated. In wheat, high temperatures increase the level of globulin protein storage causing a reduction of the albumin/globulin content in mature seeds (Hurkman et al., 2009; Stone & Nicolas, 1996). In pea, the final level of vicilin storage proteins was higher under heat stress (Bourgeois et al., 2009). High temperature during seed filling also affects the accumulation level of stress/defense proteins, like heat shock proteins (Bourgeois et al., 2009; Hurkman et al., 2009; Majoul et al., 2003). The magnitude in which a heat stress during seed filling period affects seed quality depends on the heat tolerance of the genotype, the intensity and the timing of heat stress (Stone & Nicolas, 1996; Passarella et al., 2002; Spiertz et al., 2006). These modifications in final protein composition may have an impact on the digestibility of proteins allergenic potential and seed germination.

3.2.4 Impact of heat stress on N rhizodeposition

Root exudation increases at elevated temperature, suggesting that root exudation of organic substances (Uselman et al., 2000 in *Robinia pseudoacacia* L.; Arai-Sanoh et al., 2010 in rice). Moreover, symbiotically N₂-fixing plants continue to exude organic substances, even under extreme N limitation (Uselman et al., 2000). Roots longevity could also be decreased as soil temperature increases, because maintenance respiration of the roots is probably increased (Pritchard, 2011). Fine root, along with their symbionts, are responsible for a significant input of organic C and N to soil, where much of its is eventually made available to other soils organisms (Pritchard, 2011). These additional organic inputs into the soil at elevated temperature may stimulate the microbial community. Moreover, an interspecific transfer of N between legumes and non legumes crops can take place within a short period (20 days) in legume-based grassland even at relatively low temperature (13°C), suggesting that legumes could lead to a substantial contribution of soil N (Gylfadottir et al., 2007 with white clover *Trifolium repens* and smooth meadow grass *Poa pratensis*).

3.3 Impact of water deficit on plant N fluxes

Water stress is one of the most important factors limiting crop yields world-wide (Kramer & Boyer, 1997), especially in arid and semi-arid areas, although its occurrence fluctuates at different temporal and spatial levels (Bai et al., 2004; Knapp et al., 2001; Xu et al., 2009). In addition, with climate change, plants will be subjected to increased variability of water availability, including increased frequency and intensity of extreme droughts (Gutschick and BassiriRad, 2003; Pereira et al., 2006). It thus appears essential to decipher the impact of water stress on plant N fluxes.

3.3.1 Characterization of a water deficit

A water stress can be defined as the situation when the plant cannot cope anymore with a soil water deficit, leading to a decrease of water content in the tissues, and thus importantly modifying its metabolism. Plant responses to water stress can be studied *in situ* but also under controlled conditions, by water withholding or by using osmotica such as polyethylene glycol, mannitol or melibiose. Benefits and drawbacks of each of these experimental methods are presented in Verslues et al. (2006). In order to characterize the plant water status, different variables are used: either variables reflecting *stricto sensu* the plant water status (e.g. leaf water potential (Ψ), relative water content (RWC)) (Hsiao, 1973) or a variable reflecting water fluxes within the plant (e.g. fraction of transpirable soil water, FTSW) (Sarr et al., 2004). For example, in pea, a water stress is reached when $\Psi \sim -1.2$ MPa, and FTSW $\sim 0.1-0.2$ (Lecoer & Guilioni, 1998), although these values depend both on the species and on the genotype (Ladrera et al., 2007; Serraj & Sinclair, 1997).

The most obvious plant response to a water stress is a decrease in total plant biomass, which is the consequence of a reduced stomatal conductance, leading to a decrease of leaf expansion, and causing a lesser C assimilation *via* photosynthesis (Bradford & Hsiao, 1982). The impact of a water stress depends on its intensity, on its length but also on the period when it occurs during plant life cycle (Bradford & Hsiao, 1982). However, the most marked effects in term of yield losses are reached when water stress occurs during flowering or grain filling (Meckel et al., 1984; Thomas et al., 2004), which can explain the abundance of studies during these developmental stages. Even if water stress has been the subject of extensive research from the gene to the canopy levels, it still remains difficult to predict the effect of water deficit on plant N status (Gonzalez-Dugo et al., 2010).

3.3.2 Impact of water deficit on N supply, acquisition and assimilation

3.3.2.1 Soil N transformation, as affected by water deficit

Water stress conditions lead to decrease soil microbe biomass (Schimel et al., 1999), certainly by the indirect decrease of the soil available O_2 needed by aerobic micro-organisms (Smolander et al., 2005). As a consequence, the mineralization process, converting soil organic matter into NH_4^+ , as well as the nitrification process, converting NH_4^+ into NO_3^- , which are both achieved by micro-organisms, are reduced (Fierer & Schimel, 2002; Vale et al., 2007). Moreover, after a water stress, the longevity of the root system is reduced, which leads to an increase of the organic matter pool in the soil (Huang & Gao, 2000). When water stress is followed by a rewatering, then mineralization is re-activated and amplified by the high quantity of organic matter (Austin et al., 2004). Finally, soil nutrient status can influence root radial resistance to water movement as, for an example, decreased soil N availability reduces root hydraulic conductivity (Clarkson et al., 2000).

3.3.2.2 Plant N acquisition and assimilation under water deficit

The absorption of N by roots as NO_3^- or NH_4^+ requires the presence of water in the soil and especially in a close area around the roots, as these minerals are water mobile (Garwood & Williams, 1967). Hence, in a water stressed environment plant N uptake is reduced due (1) to the lower availability of the ions in the soil, (2) to the reduced water flow resulting from the reduced plant transpiration and (3) to an effect on the active transport mechanism, and on the membrane permeability (Hsiao, 1973). Yet studies showed contradictory results (Gonzalez-Dugo et al., 2010). Indeed, numerous authors concluded that N uptake was

independent from plant transpiration in various crops (Bhat, 1982; Gastal & Saugier, 1989; Schulze & Bloom, 1984) while others observed that N uptake decreased under water stress (Buljovic & Engels, 2001). As the latter have found an increase in soluble sugar content of the roots with increasing soil drought, they conclude that low N-uptake ability of roots was not caused by low assimilate supply of roots from shoots (Buljovic & Engels, 2001). In addition, increased abscisic acid (ABA) synthesis during water stress periods regulates aquaporins (either *via* their gene expression modifications or *via* post-transcriptional regulations), leading to a control of root conductance, and thus the absorption of nutrients (Beaudette et al., 2007; Ehler et al., 2009; Parent et al., 2009; Törnroth-Horsefield et al., 2006). In legume plants, the most striking response to water stress is the decrease of N₂ fixation, associated with a decrease in nodule formation, a reduced size of the nodules and a decrease in nodule specific activity (King & Purcell, 2001; Serraj et al., 1999; Streeter, 2003). In any case, the proportional dependence of plant N biomass on symbiotic N₂ fixation decreases with the extended duration of water stress (Kirda et al., 1989). Furthermore, irreversible cessation of symbiotic N₂ fixation has been shown to occur in case of extremely severe water stress conditions (Guerin et al., 1991; Sprent, 1971; Venkateswarlu et al., 1989; Walker & Miller, 1986). And finally, the severity of the N₂ fixation related response is also dependent from the bacteria strains, which can be more or less sensitive to soil drought (Djedidi et al., 2011).

Several mechanisms were proposed to explain the decrease of biological N₂ fixation. A first possibility concerns a decrease in nodule cortical permeability, limiting the O₂ supply to the bacteroids and thus decreasing their respiration. As a consequence, the nitrogenase activity is highly reduced (Durand et al., 1987; Hungria & Vargas, 2000; Walsh, 1995) causing oxidative damages. Moreover, it has been shown that under severe drought conditions, the nodule leghemoglobin content was negatively affected (Manavalan et al., 2009; Naya et al., 2007), impacting once more on the O₂ availability to the bacteroids (Marino et al., 2006). In parallel, a gene coding for a ferritin is largely up-regulated under water stress conditions, suggesting an important iron trafficking in stressed nodules, being the consequence of the leghemoglobin degradation (Clement et al., 2008). Another mechanism related to the inhibition of N₂ fixation involves a N feedback, mediated by various molecules depending on the plant species such as asparagine (Bacanamwo & Harper, 1997), glutamine (Neo & Layzell, 1997), proline, histidine, tryptophane (Larrainzar et al., 2009), ureides (Serraj et al., 2001) or even a combination between high rates of nodule asparagine and ureide and a transport of amino acids from the leaves (King & Purcell, 2005). Synthesis of proline and an induction of amino acid transporter in leaves in response to a water deficit (Rentsch et al., 1996; Bray, 1997.) contribute to explain the dramatic accumulation of proline observed in the growing region of the primary root in response to drought (Ober & Sharp, 1994).

According to Marino et al. (2007), it seems that, contrarily to plant responses to N deficiency, plant response to water stress is localized rather than systemic at least during the early times after applied drought. Some authors have suggested that symbiotic N₂ fixation inhibition and ureide accumulation in shoots following a water stress are concomitant, but are not necessary causally related, because they follow different kinetics (Alamillo et al., 2010). These authors consider that ureide accumulation is part of a general response to stress, in particular because ureides play a key role in cell protection under oxidative stress conditions (Brychkova et al., 2008), such as the nodule senescence induced by drought (Puppo et al., 2005; Yamaguchi et al., 2010). Finally, Planchet and co-authors suggested that the exploration of the putative central role of glutamate in water-deficit tolerance, through ABA

signaling, could lead to more information on changes of N metabolism under adverse environmental conditions (Planchet et al., 2011).

Moreover, C fluxes are considered as playing a major role in the regulation of symbiotic N₂ fixation in pea and soybean. Indeed, in these species, C supply (mainly in the form of malate) to the nodules declines (Arrese-Igor et al., 1999), which can be due to a decrease of the main enzyme responsible for the cleavage of sucrose in nodules : the sucrose synthase (at the gene expression as well as the enzyme activity levels). In the model plant *Medicago truncatula*, an accumulation of sugars, polyols and amino-acids was observed and the authors hypothesized that these compounds could play a role in osmotic regulation processes in the nodules, or could be related to the reduction of the plant transpiration rates, limiting the xylem flux and thus the transport of the compounds from the nodules to the other plant compartments (Larrainzar et al., 2009).

The effects of water-deficit on N uptake and N assimilation (quantified by ¹⁵N tracing methods) were recently investigated in white clover (*Trifolium repens* L.) by Lee et al. (2009). The water-deficit treatment significantly reduced the maximum NR activity, and also attenuated *de novo* synthesis of amino acids and proteins in the roots. The concentration of proline in the phloem exudates increased rapidly after 3 d of water deficit. Interestingly, the increase in proline concentrations in phloem exudates in response of water stress was closely related to reductions of N uptake, as well as NR activity in the roots and assimilation of newly absorbed N in amino acids. In addition, the accumulation of proline induced in roots by exogenous proline treatment was closely related to the decrease in NR activity. Based on these results, Lee et al. (2009) have suggested that increased proline transport to roots *via* phloem caused by water deficit has a significant influence on the down-regulation of plant N fluxes, particularly N uptake and assimilation of newly absorbed N.

3.3.3 Impact of water deficit on N partitioning among organs, mobilization and storage of N compounds

Water stress doesn't seem to affect xylem nitrate concentration in sunflower (Schurr & Schulze, 1996), probably because of the independence of the transpiration process and the nutrient supply process (Tanner & Beevers, 2001), explained by the fact that the two transpiration independent water flows (flux of water associated with volume expansion and Münch's counterflow in the phloem) were found to ensure plant nutrient transport (Gonzalez-Dugo et al., 2010).

When drought was imposed on one month alfalfa (*Medicago sativa*) plants, N flux determined using ¹⁵N pulse-chase labelling revealed that N compounds in leaves were redistributed mainly towards roots and secondary in stems (Eric & Avice, unpublished data). This was accompanied by increase of proline, and soluble proteins (especially VSP) concentrations in roots (Eric-Soreasu et al., 2007). Interestingly, when water recovery was applied after drought, ¹⁵N analysis demonstrated that N reserves were remobilized from roots and stems to growing leaves. This was concomitant with the decrease of VSP and proline concentrations in roots of alfalfa. Additionally, it was reported that alfalfa plants treated by ABA (a phytohormone highly involved in the mechanisms of drought tolerance) (1) provoked a massive redistribution of N from leaves to the roots, (2) induced the accumulation of VSP in taproot after 6 d of treatment and (3) stimulated the steady-state 32 kDa VSP transcript within 3d of treatment (Avice et al., 2003). These last data suggest that the drought-induced accumulation of VSP may be regulated by ABA. Thus, the capacity to

remobilize N reserves from leaves and store these recycling N compounds in perennial organs under specific soluble proteins and amino-acids forms during critical phases of alfalfa development, may represent an adaptive trait with regard to plant tolerance against water stress.

In pea, N partitioning between below ground part and above ground part is not modified by water stress (around 15% of N allocated to the roots and 85% to the above ground part), when it has been applied either at the flowering stage or during seed filling stage (Mahieu et al., 2009). In soybean, it has been shown that under a continuous water stress treatment from the beginning of seed filling until physiological maturity, the decreasing rate of leaf N and chlorophyll was more intense (de Souza et al., 1997). In cereals, similar observations were made, considering that these post anthesis water deficits could result in early leaf senescence, and thus more remobilization of pre-anthesis stored assimilates to grains (Yang & Zhang, 2006). Moreover, a water stress induces a shortened seed-filling period, leading to smaller seeds and lower yields, but interestingly, oil and protein content are not modified in soybean (Dornbos & Mullen, 1992) or in pea (Croizat et al., 1992). The origin of the remobilized N for seed filling accounts for 90% from the above ground part in pea, and is significantly reduced under water stress conditions, as well as the amount of N remobilized from roots for seed filling or released into the soil (Mahieu et al., 2009).

3.3.4 Impact of water deficit on N rhizodeposition

Root exudates could play a major role in the maintenance of soil-root contact, which is especially important to the plant under drying conditions, when hydraulic continuity will be lost (McCully & Boyer, 1997; Walker et al., 2003; Wittenmayer & Merbach, 2005). In pea, the rate of N derived from rhizodeposition decreases with water stress, but the proportion of N allocated to rhizodeposition process is not modified. In other words, the amount of rhizodeposited N is directly proportional to the plant total N amount (Mahieu et al., 2009). This results was corroborated by a study carried out on *Lupinus argenteus* (Goergen et al., 2009).

4. Conclusion

A decline in the growth trends of cereal and legume yields has been witnessed over the last two decades (Brisson et al., 2010). Abiotic stresses appear to be important factors of climatic change explaining the decrease in yields (Wheeler et al., 2000; Challinor et al., 2005), especially heat stress during seed filling and drought during elongation (Schlenker & Roberts, 2009; Peng et al., 2004, Brisson et al., 2010). Thus, genetic progress made in the second half of the 20th century was partly counteracted by climate change. The 21th century will be extremely challenging to agriculture because of this global climate change. A global increase in temperature (of about 0.2°C per decade), a change in the distribution of precipitation and an intensification of drought in arid and semiarid areas are projected (Salinger, 2005; IPCC, 2007). Abiotic stresses (heat stress, water stress, and N limitation) will thus occur more frequently and in a simultaneous manner, especially high temperature and water deficit. Finally, changes in the climate variability and increase in temperature will modify the pest and disease distribution and how these need to be managed (Vadez et al., 2011).

The crop productivity is considerably more reduced by combined stresses than by a stress alone (Shah & Paulsen, 2003; Xu & Zhou, 2006). But little is known about their combined impact on plant N fluxes. Xu & Zhou (2006) suggested that high temperature, combined

with severe soil drought weaken N anabolism and strengthen protein catabolism. This emphasizes the need to further understanding of how plants react and adapt to abiotic stresses.

Undoubtedly, the future challenge relies not only on breeding new varieties well adapted to climate change, but also on the development of new cultural practices such as intercropping between non legume plants and legumes.

5. References

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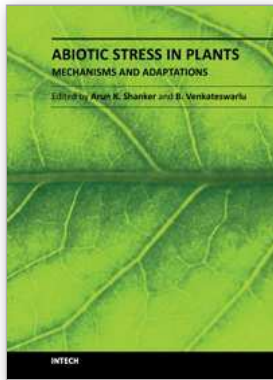
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Abiotic Stress in Plants - Mechanisms and Adaptations

Edited by Prof. Arun Shanker

ISBN 978-953-307-394-1

Hard cover, 428 pages

Publisher InTech

Published online 22, September, 2011

Published in print edition September, 2011

World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly divided into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Salon Christophe, Avice Jean-Christophe, Larmure Annabelle, Ourry Alain, Prudent Marion and Voisin Anne-Sophie (2011). Plant N Fluxes and Modulation by Nitrogen, Heat and Water Stresses: A Review Based on Comparison of Legumes and Non Legume Plants, Abiotic Stress in Plants - Mechanisms and Adaptations, Prof. Arun Shanker (Ed.), ISBN: 978-953-307-394-1, InTech, Available from:
<http://www.intechopen.com/books/abiotic-stress-in-plants-mechanisms-and-adaptations/plant-n-fluxes-and-modulation-by-nitrogen-heat-and-water-stresses-a-review-based-on-comparison-of->

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