Gartenbauwissenschaft, **65** (2). S. 52–64, 2000, ISSN 0016–478X. © Verlag Eugen Ulmer GmbH & Co., Stuttgart

Influence of Pre-Harvest Nitrogen Supply on Post-Harvest Behaviour of Ornamentals: Importance of Carbohydrate Status, Photosynthesis and Plant Hormones

Einfluß der Stickstoffversorgung während der Kultur auf das Nachernteverhalten von Zierpflanzen: Bedeutung von Kohlenhydratstatus, Photosynthese und Phytohormonen

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Summary

In this review, the potential role of carbohydrates, photosynthesis and the plant hormones ethylene, abscisic acid and cytokinins in nitrogen-affected post-harvest behaviour of ornamentals is discussed, differentiating between pre-harvest influences of nitrogen amount, nitrogen form and a secondary salt stress. The increasingly proposed function of the root as a sensor continuously monitoring root zone stress conditions is emphasized. Recently found interactions between sugars, cytokinins and light and between ammonium and ethylene in leaf senescence are considered as well as signal effects of nitrate on carbon allocation. Excessive nitrogen supply during cultivation, which also causes secondary salt stress, leads to an unfavourable physiological condition for post-harvest behaviour. Decreased carbohydrate reserves coinciding with a low photosynthetic capacity may cause post-production carbohydrate deficiency. Increased fluxes of abscisic acid via the xylem and higher concentrations in plant tissues coinciding with opposite reactions of cytokinins and high ethylene production increase the risk of growth inhibition and post-harvest senescence. Whereas a balanced ammonium:nitrate ratio potentially favours post-harvest behaviour via higher cytokinin delivery by the root system, pure ammonium fertilization can cause ammonium toxicity, carbohydrate deprivation and high ethylene production. The relevance of these internal changes to post-harvest life is estimated distinguishing between different ornamental products. Changed hormonal situation and carbohydrate deficiency are probably important factors impairing post-harvest life of potted plants after excessive nitrogen supply. An apparently lower sensitivity of cut flowers can be explained by the disconnection from the stressed root system. The variable response of leafy cuttings to high nitrogen supply is additionally proposed to be attributed to the different swiftness of rooting resulting in hormonal changes and to different contribution of photosynthesis to carbohydrate pools in dependence from plant species and light conditions.

Zusammenfassung

In diesem Sammelreferat wird die mögliche Bedeutung der Kohlenhydratreserven, der Photosynthese und der Phytohormone Ethylen, Abscisinsäure und Cytokinine für das Nachernteverhalten von Zierpflanzen unter dem Einfluß der Stickstoffversorgung während der Kultur diskutiert. Hierbei wird zwischen Einflüssen der Stickstoffmenge, der Stickstofform und eines sekundären Salzstresses unterschieden. Die zunehmend diskutierte Funktion der Wurzel als kontinuierlich die Streßsituation im Wurzelraum erfassender Sensor findet besondere Beachtung. Neue Erkenntnisse bezüglich der Wechselwirkung zwischen Zuckern, Cytokininen und Licht sowie zwischen Ethylen und Ammonium bei der Blattseneszenz werden ebenso berücksichtigt wie die kürzlich entdeckte Signalfunktion des Nitrates bei der Assimilatverteilung. Eine übermäßige Stickstoffversorgung, die zusätzlich zu sekundärem Salzstreß führt, resultiert in einer ungünstigen physiologischen Ausgangssituation für das Nachernteverhalten. Verminderte Kohlenhydratreserven und eine geringere photosynthetische Leistungsfähigkeit können einen Kohlenhydratmangel verursachen. Ein erhöhter Antransport von Abscisinsäure über das Xylem und höhere Gehalte im Pflanzengewebe, die mit einer gegenläufigen Reaktion der Cytokinine zusammentreffen, sowie eine gesteigerte Ethylenproduktion erhöhen das Risiko einer nachfolgenden Wachstumsbeeinträchtigung und beschleunigten Seneszenz. Während ein ausgewogenes Ammonium:Nitrat Verhältnis das Nachernteverhalten über eine erhöhte Cytokininnachlieferung des Wurzelsystems potentiell begünstigt, kann reine Ammoniumernährung zu Ammoniumtoxizität, Kohlenhydratmangel und erhöhter Ethylenproduktion führen. Die Bedeutung des veränderten physiologischen Status wird für verschiedene Zierpflanzenprodukte unterschiedlich bewertet. Der beeinflußte Hormonhaushalt und die Verarmung an Kohlenhydraten sind wahrscheinlich wesentliche Faktoren, die das Nachernteverhalten von Topfpflanzen nach einer hohen Stickstoffversorgung beeinträchtigen. Eine sich andeutende geringere Empfindlichkeit von Schnittblumen kann durch die Abtrennung vom gestreßten Wurzelsystem erklärt werden. Die sehr variable Reaktion von Stecklingen auf ein hohes Stickstoffangebot wird zusätzlich auf eine unterschiedliche Bewurzelungsgeschwindigkeit und deren Einfluß auf den Phytohormonhaushalt sowie auf einen je nach Pflanzenart und Lichtbedingungen unterschiedlichen Beitrag der Photosynthese zu den Kohlenhydratreserven zurückgeführt.

Introduction

Post-harvest behaviour is becoming more and more an important aspect in ornamental plant production. On the one hand, there is high predatory competition on the Central European market and high quality of products is an increasingly significant prerequisite for economic success. On the other hand, the different products are produced worldwide and stored or transported for longer periods so that resulting unfavourable environmental conditions potentially decrease quality and impaire post-harvest life.

Regarding optimal post-harvest behaviour of different ornamental products, different requirements can be expressed. Considering cutted plant parts like flowers, the major requirement is for high longevity or low senescence. Flower buds are expected to open but subsequent senescence and relatively short-termed decay of flowers are delayable but unescapable events. While these aspects are also true for particular organs of potted plants, for example flower buds, potted plants as a whole need a certain grade of vigor so that they can establish themselves under the interior conditions at the consumer and survive for a longer time. The expected life-time can be shorter, for example a few weeks, in the case of some special flowering potted plants and can be very high, for example many years, in the case of foliage plants. The requirement for high vigor or viability is even more important, if starting materials for propagation, for example cuttings or plantlets, are regarded. In this case, high potential for regeneration or growth is an essential prerequisite for practical value.

Nitrogen nutrition, which is one of the most important factors influencing the yield of ornamentals, additionally has a strong effect on post-harvest life. As it applies to yield, post-harvest response to pre-harvest nitrogen supply depends on nitrogen level and on nitrogen source. Effects observed on different ornamental products are summarized in Table 1, also presenting the maximum nitrogen levels applied in the respective studies. Supply of high amounts of nitrogen during cultivation impaired the post-harvest life of various potted plants. In some studies it was tried to differentiate specific nitrogen effects from secondary salt effects. The influence of high levels of nitrogen fertilizers on floral keeping quality *of Campanula* (Table 1) was less strong than of high levels of complete fertilizer with similiar electrical conductivities of the nutrient solution (SEREK 1990). On the other hand, TERHELL and HENDRIKS (1995) and TERHELL and GRANTZAU (1997) supposed that the responses of *Euphorbia pulcherrima* and *Cyclamen* to high nitrogen supply (Table 1) were caused by a specific nitrogen effect rather than by osmotic stress, because raising the salt concentrations in the substrate above those measured for the highest nitrogen supply by application of a potassium salt had no negative effect. In addition to nitrogen level, also nitrogen form influenced post-harvest behaviour of potted plants (Table 1). Symptoms of senescence observed on different organs were more pronounced in the case of high or pure ammonium supply as compared to higher proportions of nitrate.

Even though effects of the different nitrogen levels, which are hard to compare between the different studies, cannot be excluded, the negative influence of high pre-harvest nitrogen supply on post-harvest behaviour of cutted plant parts appears to be less strong than on that of potted plants (Table 1). So post-harvest life of *Cyclamen* cut flowers and *Cyrtomium* cut leaves was not impaired, though nitrogen supply for maximum yield was exceeded by 100% (Table 1). The longevity of *Pteris* was even increased with increasing nitrogen supply. Regarding ornamental cuttings, for the same species *Dendranthema grandiflorum* conflicting relationships were found in different studies (Table 1). However, subsequent rooting of chrysanthemum cuttings under greenhouse conditions during spring and summer was promoted by highest nitrogen supply to stock plants (Table 1), though the yield optimum was exceeded by 100% (KADNER and ZERCHE 1997) and a high accumulation of nitrate was observed in the root zone of stock plants (ZERCHE et al. 1999).

In summary, the different studies reveal a negative influence of high nitrogen supply on post-harvest behaviour of potted plants. But the results also point towards a relatively lower sensitivity of cutted ornamental products. It is well-known that nitrogen alters plant composition far beyond the concentration of nitrogen-containing compounds and much more than any other mineral nutrient (MARSCHNER 1995). Regarding post-harvest behaviour, nitrogen fertilization influences also for example dry matter concentration and partitioning between shoots and roots, pH in the root zone and cytoplasm of root cells and uptake and availability of other nutrients. As a result, proton toxicity and physiological calcium deficiency may impair post-harvest life following high supply of ammonium as discussed by TERHELL and HENDRIKS (1995) and STARKEY and PEDERSEN (1997). However, particularly carbohydrates and plant hormones are crucial interal factors for post-harvest behaviour and are also strongly influenced by nitrogen nutrition. Therefore the intention of this review is to elucidate the possible relationships between nitrogen supply, carbohydrate status, photosynthetic capacity, the plant hormones ethylene, abscisic acid (ABA) and cytokinins, and post-harvest behaviour of ornamentals. After outlining the potential role of the particular internal factor in post-harvest life, the influences of nitrogen amount, nitrogen form, and a possible secondary salt effect are described. In conclusion, the different aspects are summarized and integrated into an estimation of the relevance of the respective internal factor to the nitrogen-affected post-harvest behaviour of different ornamental products.

Carbohydrates as factors of nitrogen-affected post-harvest behaviour

While structural carbohydrates are the essential prerequisite for the stability of plant tissues, two major functions of non-structural carbohydrates are to provide energy for catabolic processes like respiration and to provide carbon skeletons for the formation of other compounds. In addition, certain carbohydrates like sucrose are osmotically active and so are important factors for the maintainance of turgor pressure for example in cut flowers. Furthermore they are decisive in transport processes and growth. In this connection sucrose is discussed to be a cytokinin-affected key

Table 1. Influence of pre-harvest nitrogen supply on post-harvest behaviour of ornamental products.

Einfluß der Stickstoffversorgung während der Kultur auf das Nachernteverhalten von Zierpflanzenprodukten.

Plant	Cultivation as	Influence of high nitrogen level: Effect	Maximum level[1]; level for maximum yield[1]	Symptoms	Reference
Dendranthema-Grandiflorum-hybrids	potted plant			decreased flower longevity	ROUDE et al. 1991
Euphorbia pulcherrima	potted plant	↓	21.4 mmol N l^{-1}	leaf drop, root damage	TER HELL and HENDRIKS 1995
Impatiens New-Guinea-hybrids	potted plant	↓	10.7 mmol N l^{-1}	bud drop, root damage	TER HELL and HENDRIKS 1995
Rosa-hybrids	potted plant	↓	14.3 mmol N l^{-1}	bud drop, root damage	TER HELL andHENDRIKS 1995
Campanula carpatica	potted plant	↓	14.6 mmol N l^{-1}	decreased flower longevity	SEREK 1990
Cyclamen persicum	potted plant	↓ ↓	maximum concentration in substrate: 38.7 mmol N l^{-1}; concentration for maximum growth: 8.9 mmol N l^{-1}	bud drop, leaf senescence	TER HELL und Grantzau 1997
Rosa-hybrids	cut flowers	↓	21.4 mmol N l^{-1}; maximum yield at 10.7 mmol N l^{-1}	decreased vase life	MENARD et al. 1995
Cyclamen persicum	cut flowers	NE	11.4 mmol N l^{-1}; maximum yield at 5 mmol N l^{-1}		WARTENBERG 1998
Cyrtomium	cut folige	NE	321 mmol N per plant per year; maximum yield at 179 mmol N per plant per year		AMBERGER-OCHSENBAUER 1995
Pteris sp.	cut folige	↑	321 mmol N per plant per year	increased longevity	AMBERGER-OCHSENBAUER 1995
Dendranthema-Grandiflorum-hybrids	cuttings	↑	14.3 mmol N l^{-1}, positive effect of increased nitrogen supply until yield maximum of 8.6 mmol N l^{-1} (5 % N_t)	higher root number	RÖBER 1978
	cuttings	↓	12 mmol N l^{-1}; maximum yield at 8 mmol N l^{-1} for nutrition with nitrate and ammonium+nitrate	root number and mass negatively correlated with N_t in cuttings	RÖBER and REUTHER 1982
	cuttings	NE	14.3 mmol N l^{-1}; maximum yield at 7.1 mmol N l^{-1}	NE on storage ability	KADNER and ZERCHE 1997
		↑	14.3 mmol N l^{-1}; maximum yield at 7.1 mmol N l^{-1}	root number, length and fresh mass positively	DRÜGE et al. 1998a
		↑	286 mmol N per m^2 per week; maximum yield at 143 mmol N per m^2 per week	correlated with N_t (up to 6.8 %) in cuttings	DRÜGE et al. 1998b ZERCHE et al. 1999

[1] in the respective study, concentration in nutrient solution if not indicated otherwise ↑ positive effect ↓ negative effect NE no effect

factor mediating carbon allocation to shoots and roots in relation to nitrogen supply (VAN DER WERF and NAGEL 1996). Osmotically active carbohydrates can substantially contribute to the tolerance of plants against certain types of stresses like drought, frost and salt stress by osmotical adjustment and by protection of proteins and biomembrans from the detrimental effects of high ionic concentrations (Larcher 1995). Far above osmotical effects, sugars modulate gene expression in plants which has been reviewed in detail by KOCH (1996). Carbohydrate depletion upregulates genes for photosynthesis, remobilisation, and export, while decreasing mRNAs for storage and utilization. Abundant sugar levels exert opposite effects through a combination of gene repression and induction. Significant interactions between sugars and cytokinins in senescence of leaves have recently been discovered by WINGLER et al. (1998). They found that sugars can promote leaf senescence and counteract the senecence-inhibiting influence of cytokinins particularly under low light conditions. These interactions will be described in detail on page 6.

Influence of nitrogen amount and source on carbohydrate status

With increasing nitrogen supply, more carbon is directed into amino acid and protein synthesis and less into carbohydrates, and consequently sugar and starch contents were often found to decrease drastically, while the total amount of structural carbohydrates usually remains constant (KAISER 1997). As it can be seen from Figure 1 illustrating these relationships for chrysanthemum cuttings (DRÜGE et al. 1998a), the negative relationship between nitrogen and carbohydrates becomes stronger with increasing nitrogen concentrations. This is based on the fact, that starting from suboptimal levels with increasing nitrogen supply an increase in photosynthesis (see page 4) can initially cover the increasing requirement for carbon skeletons for nitrogen assimilation, whereas increased carbon demand exceeds increased carbon fixation at very high nitrogen supply (MARSCHNER 1995).

Nitrogen supply not only influences amount of carbohydrates in plants but also allocation of carbon within the plant. So a high ratio of shoot to root biomass is a typical characteristic of nitrogen-rich plants. SCHEIBLE et al. (1997) recently could demonstrate by using mutants and transformants of tobacco with decreased expression of nitrate reductase, that nitrate concentration in the shoot per se is a strong signal regulating the shoot:root ratio independently from protein, amino acid and glutamine levels. The authors found a highly significant correlation between leaf nitrate content and the shoot:root ratio for eight genotypes growing at a wide range of nitrate supply. Accumulation of nitrate in shoots was proven to inhibit root growth in split-root experiments and lead to a strong inhibition of starch synthesis and turnover in leaves and to decreased sugar levels in roots.

Specific effects of ammonium versus nitrate nutrition on plant physiology has recently been discussed by WIESLER (1997), GERENDAS et al. (1997) and KANDLBINDER et al. (1997). The following energetic aspects can be summarized from their papers. At first, assimilation of nitrate needs more energy than assimilation of ammonium. However, whereas ammonium, once taken up, has to be detoxified rapidly in the roots by assimilation into organic compounds, nitrate may be translocated in high quantities to the shoot, where it can be reduced and then undergo the same fate as ammonium. Alternatively, excess nitrate can be stored at low energetic costs in the vacuoles of roots and shoots. Regarding these differences, particularly a high supply of ammonium causes a high demand of carbon skeletons in roots as compared to nitrate, which may result in a deprivation of nonstructural carbohydrates especially in roots. However, effects of different nitrogen forms on carbohydrate concentrations in roots and shoots were found to be variable showing slightly increased concentrations with mixed nitrogen nutrition or sometimes even higher concentrations for ammonium supply as compared to nitrate supply (GERENDAS et al. 1997) also depending from pH (KANDLBINDER et al. 1997). These variable effects may be based on the fact, that carbohydrate concentrations provide no information about carbon fluxes from shoot to roots (WIESLER 1997). But also the signal effect of nitrate mentioned above may influence carbon fluxes independently from energy requirement for assimilation.

Secondary salt stress and carbohydrate status

Above specific nitrogen effects, high nitrogen supply may affect carbohydrate condition of plants by secondary osmotic stress resulting from the high salt concentrations. Besides negative effects on photosynthesis (see p. 5), salt-stressed roots have a higher carbohydrate requirement for maintainance of respiration (MARSCHNER 1995). However, concentrations of different sugars and starch in leaves of different plants either decreased or increased in response to salt stress. The different effects are thought to be attributed to different reactions of source activities (photosynthesis) as related to sink activities (POLJAKOFF-MAYBER and LERNER 1994).

Photosynthesis as factor of nitrogen-affected post-harvest behaviour

The capability of photosynthesis is then of high importance, if the carbohydrate reserves in the ornamental product or the post-harvest carbohydrate supply will not meet the carbohydrate demand during post-harvest life. But ornamental products can only benefit from a higher photosynthetic capacity if the post-harvest environmental conditions (mainly photosynthetic photon flux density) allow photosynthetic activity.

Influence of nitrogen amount and source on photosynthetic capacity

In green leaf cells, up to 75 % of the total organic nitrogen is located in the chloroplasts, mainly as enzyme protein (MARSCHNER 1995), from which ribulose 1,5-bisphosphate carboxylase and proteins of the thylakoid membranes build the main constituent part (EVANS 1989). As a result, the photosynthetic capacity usually rises with increasing nitrogen content in linear propor-

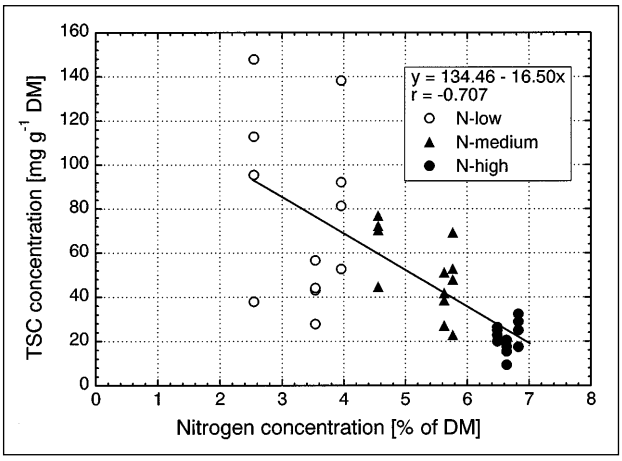


Fig. 1. Regression between nitrogen and total soluble carbohydrate concentrations (TSC) in chrysanthemum cuttings at harvest and after 1, 2, 3 and 4 weeks of cool-storage at 0.5 °C (DRÜGE et al. 1998).
Regression zwischen den Konzentrationen an Stickstoff und gesamt-löslichen Kohlenhydraten (TSC) in Chrysanthemenstecklingen zum Erntetermin und nach 1, 2, 3 und 4 Wochen Kühllagerung bei 0.5 °C (DRÜGE et al. 1998).

tion, until limitation by other factors evokes saturation characteristic (EVANS 1989, LARCHER 1995). The increase in leaf photosynthetic rate with increased leaf nitrogen was generally found to be greater at high actual photosynthetic photon flux densities (PPFD) as compared to lower PPFD (CIOMPI et al. 1996, REDDY et al. 1996, ALLISON et al. 1997). In conclusion, plants containing high levels of leaf N on the one hand are capable for utilizing more PPFD than plants with low leaf N. But on the other hand, the increase in photosynthesis by higher nitrogen levels will be smaller at lower PPFD. Regarding these relationships and the usually low PPFD under the interior conditions at the consumer, the post-harvest benefit for example of potted plants from higher nitrogen-contents via a higher photosynthetic activity might be small.

A high proportion of ammonium as related to nitrate may slightly increase photosynthetic rate per leaf area. But resulting from the usually lower leaf area the photosynthetic rate per plant is usually lower for ammonium fertilized plants as compared to nitrate nutrition (WIESLER 1997).

Secondary salt stress and photosynthesis

Increasing salinity can decrease photosynthetic rate of leaves for example by decreasing stomatal conductance whereas respiration increases, which can result in a drastic reduction in net CO_2 assimilation (MARSCHNER 1995). Abscisic acid and cytokinins are assumed to be involved in these reactions. Salinity was discussed by URBAN et al. (1995) to be the main factor inducing the observed decrease in photosynthesis and transpiration rate of potted roses in response to high levels of nitrate (Table 2). Regarding the basically positive relationship between leaf nitrogen contents and photosynthesis mentioned above, this interpretation appears to be conclusive, but specific nitrogen or nitrate effects were not excluded in this study.

Table 2. Influence of nitrogen nutrition on transpiration and photosynthesis of Rosa-hybrids cv. „Vivaldi" (adapted from URBAN et al. 1995).
Einfluß der Stickstoffversorgung auf die Transpiration und Photosynthese von Rosa-Hybriden cv. „Vivaldi" (nach URBAN et al. 1995).

Nitrogen concentration in nutrient solution [mmol NO_3-N l^{-1}]	Transpiration[1)] [mmol H_2O m^{-2} s^{-1}]	Photosynthesis[1)] [μmol CO_2 m^{-2} s^{-1}]
3.5	6.8 a[2)]	12 a
7	5.3 b	9.4 b
14	4.5 c	7.6 c

[1)] measurements at PAR of 861–890 μmol m^{-2} s^{-1}
[2)] a,b,c significantly different at $p \leq 0.05$

Ethylene as factor of nitrogen-affected post-harvest behaviour

The production of the gaseous plant hormone ethylene by various plant parts and organs on the one hand is increased by many different stress conditions, which has been reviewed by HYODO (1991) and recently by MORGAN and DREW (1997). On the other hand ethylene is a senescence promoting agent triggering premature senescence of different plant organs, if plants are sensitive to this hormone (MATTOO and AHARONI 1988). Sensitivity of different organs varies among plant species resulting in different dose response curves and different reactions like for example leaf yellowing for *Pelargonium* and *Epipremnum,* abscission of leaves for *Schefflera* and *Hibiscus*, abscission of flowers for *Begonia*, *Fuchsia,* and *Hibiscus*, and bud blasting and flower wilting in the case of *Campanula* (WOLTERING 1987). In this connection, the sensitivity of plant tissues to ethylene is discussed to be a function of the concentrations of other hormones (REID 1995). Ethylene production can be triggered by ethylene via an autocatalytic effect, which has been found in senescing tissues, but also can be autoinhibited by its own biosynthesis which has been recognized in a number of vegetative tissues (MATTOO and WHITE 1991).

Influence of nitrogen amount and source on ethylene

Nitrogen starvation of plants may decrease ethylene production, but at the same time the sensitivity of certain tissues to ethylene can be increased so that also the ethylene response of plants may be stronger after nitrogen starvation (LYNCH and BROWN 1997).

Ethylene evolution of plants can be increased in response to an imbalanced supply of ammonium and nitrate (LYNCH and BROWN 1997). Studying these relationships on tomato plants, FENG and BARKER (1992a) found that pure ammonium fertilization resulted in higher ethylene evolution coinciding with a high ammonium accumulation in shoots whereas already 20 % of nitrogen supplied as nitrate drastically reduced ethylene evolution (Table 3). High ethylene evolution occured on the plants with relative high ammonium accumulation regardless of nitrogen forms and pH regimes and ammonium accumulation is discussed a causal factor promoting ethylene production (FENG and BARKER 1992a) possibly disturbing cytoplasmatic pH homeostasis (LYNCH and BROWN 1997). In this

connection, ammonium concentration has recently been proposed to be a senescence regulating factor in rice leaves by CHEN et al. (1997). The authors found that ammonium accumulation in leaves paralleled their senescence under dark conditions. Increasing the ammonium concentrations by applications of ammonium chloride or abscisic acid and decreasing ammonium concentrations by light or a cytokinin retarded and promoted senescence, respectively. Because application of silver thiosulfate inhibited the otherwise promoted senescence, CHEN et al. (1997) suggested that high ammonium concentrations increase tissue sensivity to ethylene. However, regarding the results of FENG and BARKER (1992a) mentioned above, also an involvement of ethylene production seems to be possible and this was not excluded by their experiments.

Secondary salt stress and ethylene

Ethylene production in plants can be increased by salt stress, as it was shown for tomato plants by application of natrium and calcium chloride (FENG and BARKER 1992b). This salt induced ethylene production is probably wound ethylene (LYNCH and BROWN 1997) which is produced by plants in response to injury of plant tissues (HYODO 1991). Even though there is no information about specific influences of nitrogen containing salts, it is very plausible that these may act in a similiar manner if they are supplied in excessive concentrations.

Abscisic acid as a factor of nitrogen-affected post-harvest behaviour

Abscisic acid (ABA) is usually considered as an inhibitor since its application in many cases resulted in reversible growth inhibition while senescence of fully developed tissues was often promoted (DÖRFFLING 1982, MATTHYSSE and SCOTT 1984). However, ABA was much less effective on senescence of attached leaves in comparison to leaf discs also revealing strong genotype dependencies and sometimes even positive effects were observed (Smart 1994). While reports on the effects of ABA on root growth are contradictory, growth of shoot tissues is decreased by ABA (DAVIES 1995a) and this could be mainly attributed to an inhibition of cell-wall loosening (ZEEVAART and CREELMAN 1988, NAQVI 1994). ABA has been considered a general inhibitor of RNA and protein synthesis, but there is increasing evidence that this hormone induces the formation of specific proteins in certain tissues also involving induction of distinct genes particularly in response to stress (ZEEVAART and CREELMAN 1988, DAVIES 1995a, LEUNG and GIRAUDAT 1998).

In addition to these effects, one rapid response (< 5 min) of plants to ABA is closure of stomata leading to decreased transpiration and photosynthetic rates. In this connection, stomatal conductance is not simply related to bulk leaf ABA concentrations but to the concentrations in the apoplast particularly near the guard cells, where the outer surface of the plasmalemma was shown to be a sensitive site of ABA action (HARTUNG and DAVIES 1994). While a high percentage of ABA is located in the symplast particularly in chloroplasts under conditions of light, a decreasing cell turgor can result in a substantial and rapid increase in the ABA concentration in the apoplast. Far above the compartmentation within leaves, ABA transport from roots via the transpiration stream is an important factor decreasing stomatal conductance and photosynthesis particularly under water deficit stress (ATKINSON et al. 1989, DAVIES and ZHANG 1991, MANSFIELD and MCAINSH 1995). Many inhibitory effects of ABA including stomatal closure are counteracted by cytokinins, which are discussed also as root signals affecting growth and development of plants under stress (see chapter 6).

While ABA is a growth inhibiting hormone also predisposing plant tissues to decline it can substantially contribute to adaptation of plants to stress conditions. So water loss is reduced by abscisic acid while water uptake into roots can be enhanced (HARTUNG and DAVIES 1994). Also freezing tolerance could be increased by application of ABA (ZEEVAART and CREELMAN 1988) and freezing resistance of different winter wheat varieties could be correlated with maximal ABA contents measured during cold hardening (DÖRFFLING et al. 1990). An accelerated adaptation of cultured cells to high salt concentrations was observed when ABA was applied (JACOBY 1994).

Table 3. Influence of different ammonium:nitrate ratios in the nutrient solution on ethylene evolution, ammonium accumulation and fresh weight of tomato shoots (Lycopersicon neglecta-1) (adapted from FENG and BARKER 1992a).
Einfluß unterschiedlicher Ammonium:Nitrat Verhältnisse in der Nährlösung auf die Ethylenproduktion, die Akkumulation von Ammonium und die Sproßfrischmasse von Tomatenpflanzen (Lycopersicon neglecta-1) (nach FENG and BARKER 1992a).

Molar ratio NH_4:NO_3	Ethylene evolution [nl g^{-1} hr^{-1}]	Ammonium in shoots [μg N g^{-1}]	Shoot fresh mass [g/pot]
0:100	5.5 b	35 b	37 a
20:80	6.0 b	43 b	44 a
40:60	5.0 b	46 b	44 a
60:40	4.8 b	53 b	45 a
80:20	4.1 b	74 b	44 a
100:0	15.5 a	372 a	24 a

means followed by different letters within columns are significantly different at $p \leq 0.05$. Ethylene evolution and ammonium concentration are expressed on a fresh mass basis.

Influence of nitrogen amount and source on abscisic acid

A typical response to nitrogen deficiency is an enhanced synthesis and higher levels of abscisic acid in roots and shoots (MARSCHNER 1995). On the other hand, MENARD et al. (1995) found that doubling the nitrate concentration in the nutrient solution, which did not increase flower yields of cut roses, resulted in higher ABA levels in leaves and petals (Table 4). Because vase life was inversely proportional to ABA levels at harvest (Table 4) and ABA levels increased along with vase life, ABA was discussed to play a role in the transduction chain between pre-harvest nitrogen conditions and flower senescence (MENARD et al. 1995). However, considering the very high nitrate concentration for the

Table 4. Influence of nitrogen nutrition on ABA contents in leaves and petals at harvest and flower longevity of cut roses (Rosa-hybrids) cv. 'Royalty' (adapted from MENARD et al. 1995).
Einfluß der Stickstoffversorgung auf den ABA Gehalt in Laub- und Blütenblättern zum Erntetermin und die Haltbarkeit von Schnittrosen (Rosa-Hybride) cv. 'Royalty' (nach MENARD et al. 1995).

Nitrogen concentration in nutrient solution [mmol NO_3-N l^{-1}]	ABA concentration in leaves [ng g^{-1} FM]	ABA concentration in petals [ng g^{-1} FM]	Vase life duration [days]
10.7	3129±300	253±25	7.2±0.5
21.4	4520±450	383±38	5.2±0.3

plants grown under high pressure sodium lamps

high nitrogen supply (Table 4) also regarding the salinity aspects of nitrogen, it can be assumed that these results are attributed to salinity rather than to a specific nitrogen effect.

There is only little information available in literature about effects of nitrogen form on ABA. CHEN et al. (1998) recently found that higher ammonium:nitrate ratios in the nutrient solution supplied to wheat plants slightly decreased ABA levels in shoots and increased concentrations in roots, but this effect was not statistically significant.

Secondary salt stress and abscisic acid

In general, ABA levels in plants increase in response to salt stress (MIZRAHI 1980, MORGAN 1990, MARSCHNER 1995). In a similiar way as it was found for water-deficit stress (DAVIES and ZHANG 1991), the root seems to be a sensitive mediator continuously monitoring the changing salt conditions in the soil and transmitting the information to the shoot, and ABA is assumed to be involved in these processes together with cytokinins (POLJAKOFF-MAYBER and LERNER 1994).

Cytokinins as factors of nitrogen-affected post-harvest behaviour

Whereas abscisic acid and ethylene accelerate processes involved in shoot growth inhibition and senescence, cytokinins generally counteract these reactions and show opposite effects. One major effect of cytokinins is the delay of leaf senecence by inhibiting degradation of chlorophyll, proteins and nucleic acids, and in some cases even a regreening of leaves was observed after application (SMART 1994). In addition, cytokinins promote cell division depending on the presence of auxins, stimulate growth of leaves, promote shoot branching and delay adventitious rooting by counteracting auxins and promote chloroplast differentiation (DÖRFFLING 1982, MATTHYSE and SCOTT 1984, DAVIES 1995a). Different N^6-substituted adenine derivatives like zeatin, dihydrozeatin and isopentenyladenine have cytokinin activity, from which the first one is usually the most abundant naturally occurring free form in higher plants (KLECZKOWSKY and SCHELL 1995). Free cytokinins, which are mainly produced in root tips, can be converted into conjugates with sugars and amino acids showing lower but different biological activity (BINNS 1994).

During the last years the ability to transform plants with foreign genes has made it possible to increase selectively endogenous cytokinin levels providing direct evidence for their physiological role (SMART 1994). Because leaf senescence of transgenic tobacco plants was not totally prevented by higher levels of cytokinins, and higher hexose concentrations were found in older leaves as compared to a senescing wild-type tobacco, WINGLER et al. (1998) studied the interactions between cytokinins, sugars and light in senescence of wild-type leaves. The results are illustrated in Figure 2. Application of the cytokinin isopentenyladenosine to leaf discs inhibited senescence independently of light conditions. But at low photon flux density (20 μmol m^{-2} s^{-1}) glucose counteracted this inhibition and accelerated senescence determined by the decline in the photosynthetic enzyme hydroxypyruvate dehydrogenase. The acceleration of senescence and the blocking of cytokinin-induced inhibition by glucose was partially counteracted by high light conditions (250 μmol m^{-2} s^{-1}). It can be seen from Figure 2, that at low light conditions the promoting influence of sugars on senescence may be stronger than the inhibiting influence of cytokinins. This is a very important new aspect particularly regarding transport and storage of ornamental products.

Like abscisic acid, cytokinins influence stomatal conductance but in the opposite way. High concentrations of cytokinins in the transpiration stream can act directly on stomata to increase their aperture thereby promoting photosynthetic rate (INCOLL and JEWER 1987). The positive influence of cytokinins is usually more pronounced in the presence of closing stimuli such as CO_2 and ABA. In some experiments a positive effect of cytokinin application was not observed unless it was supplied together with abscisic acid (BLACKMANN and DAVIES 1983, DRÜGE and SCHÖNBECK 1992).

Influence of nitrogen amount and source on cytokinins

Because cytokinins are mainly synthesized in the roots (VAN STADEN and DAVEY 1979), there is a close relationship between root growth in general, the number of root meristems and cytokinin production in the root system (MARSCHNER 1995). Nitrogen has a strong influence on both root growth and export of cytokinins to the shoots. After nitrogen supply is interrupted or drastically reduced, cytokinin concentrations in roots, cytokinin export via xylem and concentrations in leaves decrease within a few days (WAGNER and MICHAEL 1971, SALAMA and WAREING 1979, HORGAN and WAREING 1980). When the nitrogen supply is restored, cytokinin export is rapidly enhanced

(MARSCHNER 1995). Although the possibility of a direct nitrogen effect on cytokinin production of individual root meristems cannot be dismissed, it was suggested that nitrogen most probably acts indirectly via root growth (MARSCHNER 1995).

Also the ammonium:nitrate ratio influences cytokinin concentrations in plants. As it can be seen from Table 5, mixed nitrogen source or pure ammonium nutrition increased cytokinin concentration and mass transfer in the xylem of hydroponically grown spring wheat as compared to pure nitrate supply (WANG and BELOW 1996). Similiar results were found for maize (SMICIKLAS and BELOW 1992) and apple plants (GAO et al. 1992). The physiological basis of this ammonium effect is not clear yet, but it may also be a consequence of stimulated lateral root growth either caused directly by ammonium or indirectly resulting from an enhanced basipetal transport of auxins (WIESLER 1997). But also contradicting results have been published. So cytokinin concentrations in roots, root exudate and leaves of sunflower plants decreased if nitrogen was supplied as ammonium or as ammonium nitrate in comparison with pure nitrate supply (SALAMA and WAREING 1979). However, the also markedly reduced growth of shoots and roots by ammonium supply in these experiments may have been the main limiting factor.

Secondary salt stress and cytokinins

In addition to higher ABA levels, a strong decrease in cytokinin levels in plant tissues and particularly in xylem exudates is a typical response of plants to salt stress (MORGAN 1990, POLJAKOFF-MAYBER and LERNER 1994, MARSCHNER 1995). So an increased ABA:cytokinin ratio is an important response to salinity conditions and this changed balance is more and more discussed to be a crucial factor altering plant behaviour under stress (POLJAKOF-MAYBER and LERNER 1994). Recent studies on the influence of salt stress on *Phalaenopsis* indicate, that in addition to decreased concentrations of cytokinins in salt stressed plants also a lower ratio of physiologically active free cytokinins to less active conjugates may impaire post-harvest longevity (RICHTER, pers. comm. 1998). It is obvious that a decreased availability of cytokinins is a predominating factor at least when high nitrogen supply already caused root injury as it was observed in the studies of different potted plants (Table 1).

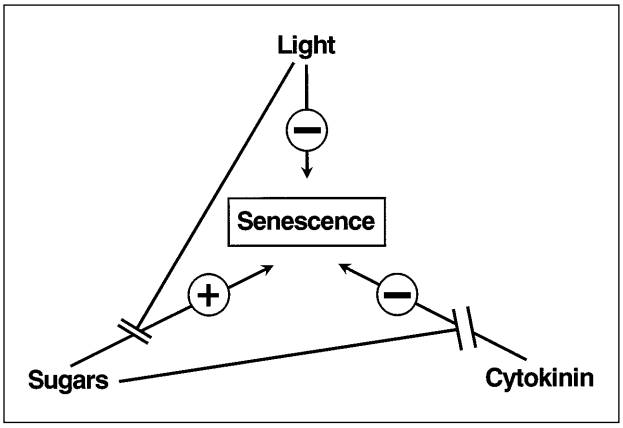


Fig. 2. Interaction of cytokinin, sugars, and light in the regulation of senescence . –, inhibition of senescence; +, acceleration of senescence; ||, partial block of the effect of sugars; | | block of the effect of cytokinin (modified after WINGLER et. al. 1998).
Wechselwirkung zwischen Cytokinin, Zuckern und Licht bei der Regulation der Seneszenz . –, Hemmung der Seneszenz; +, Beschleunigung der Seneszenz; ||, partielle Blockierung des Zuckereffektes; | | Blockierung des Cytokinineffektes (verändert nach WINGLER et. al. 1998)

Conclusions

The effects of nitrogen nutrition on the internal plant situation discussed above are summarized in Table 6. Excessive supply of nitrogen during cultivation, which also substantially increases salt concentration in the root zone, leads to an unfavourable physiological condition for post-harvest behaviour. Decreased carbohydrate reserves coinciding with a low photosynthetic capacity in the case of salt stress increases the risk of post-production carbohydrate deficiency. However, apart from energetic aspects specific sugars may promote leaf senescence (Fig. 2). In conclusion, sugars should be regarded individually in response to nitrogen supply particularly in the cases of transport, storage and other low light conditions during post-harvest life. Whereas increasing nitrogen supply from a low to an optimum level raises cytokinin and lowers ABA concentrations, excessive nitrogen supply also leading to a secondary salt stress causes opposite reactions (Table 6). Higher ABA concentrations may possibly favour post harvest behaviour due to a reduction of water loss and an increased stress tolerance, particularly if photosynthetic activity and further growth is less important. But with increasing magnitude of stress the raising ABA:cytokinin ratio and the higher ethylene production potentially impaire post-harvest behaviour by inhibition of photosynthesis and growth and by promoting post-harvest senescence. Whereas mixed nitrogen source potentially favours post-harvest behaviour via higher cytokinin delivery by the root system, pure ammonium fertilization increases the risk of ammonium toxicity, temporary carbohydrate deprivation and higher ethylene production.

As it has already been outlined in the introduction, high nitrogen fertilization does not inevitably result in impeded post-harvest performance. The post-harvest response is certainly dependent from the nitrogen level or rather from the grade of excess which is reached by the nitrogen supply. Whether a certain excess of nitrogen causes stress and impaires post-harvest life, further depends on the nitrogen sensitivity of the respective plant species or cultivar. If we look on the crucial role of plant hormones, we have to consider that not only concentrations but also sensitivity of tissues is a critical factor for phytohormone action (DAVIES 1995b) and influences of nitrogen in this aspect are almost unknown.

Considering the observations made on the different objects (Table 1) and regarding the relationships decribed above, it seems useful to distinguish additionally between different ornamental products and to regard also the varying post-harvest environmental

Table 5. Influence of ammonium:nitrate ratio in the nutrient solution on cytokinin (zeatin+zeatin-riboside) concentration and mass transfer in the xylem of two spring wheat cultivars grown hydroponically for 15 d (adapted from WANG and BELOW 1996).
Einfluß des Ammonium:Nitrat Verhältnisses in der Nährlösung auf die Konzentration und den Massenfluß von Cytokininen (Zeatin+Zeatinribosid) im Xylemsaft von zwei Sommerweizensorten nach 15 Tagen in Hydrokultur (nach WANG and BELOW 1996).

Ratio	Cytokinin concentration		Cytokinin mass transfer	
NH_4:NO_3	'Len'	'Inbar'	'Len'	'Inbar'
	[pmol ml^{-1}]		[fmol h^{-1} plant^{-1}]	
0:100	2.2	3.3	76	174
50:50	2.3	6.6	99	372
100:0	4.2	5.5	106	279
$LSD_{(0.05)}$ [1)]	0,6	0,6	20	20

[1)] significant interaction between cultivar and N source, least significant difference (LSD) at the 0.05 level for any two treatment means of a given parameter

conditions. My current thinking about these interactions is summarized in Table 7. One major difference between potted plants on the one hand and cut flowers as well as cuttings on the other hand is the fact, that potted plants will still have to tolerate the unfavourable root zone conditions during post-harvest life, whereas this is not the case if plant parts are separated. In this connection DAVIES and ZHANG (1991) already demonstrated, that retardation of leaf growth caused by a water-deficit stress of roots could be switched off by disconnecting the shoots from the stressed roots, even though the root biomass was drastically reduced. Regarding that increased ABA fluxes and decreased cytokinin fluxes via the xylem are probably main mediators of root zone stress following excessive nitrogen supply, post-harvest physiology of potted plants will continuously be affected by these signals. Disconnecting plant parts from the root system not only interrupts the actual delivery of cytokinins but also of the stress signal ABA, which can be the predominating factor influencing shoot physiology (DRÜGE and SCHÖNBECK 1992). In conclusion, the risk for impaired post-harvest behaviour by excessive nitrogen supply via hormonal mechanisms (particularly through ABA) should be higher for potted plants than for cutted plant parts like flowers and cuttings. The proposed dependency of a pre-harvest nitrogen effect on the post-harvest connection to the root system is supported by observations we made in our own experiments. Whereas a high nitrogen nutrition of chrysanthemum stock plants resulted in a lower photosynthetic activity of leaves of stock plants, it did not impaire photosynthetic activity of collected cuttings (KADNER et al., unpublished date). Apart from these relationships, production of wound ethylene may additionally force the stress situation of cutted plant parts in the case of a given ethylene sensitivity.

The usually lower carbohydrate reserves resulting from excessive nitrogen supply can also be assumed an important factor impairing post-production life of potted plants. Even if the photosynthetic capacity would be increased by higher nitrogen contents in plants, particularly under the usually low light conditions at the consumer photosynthesis may not cover the post-harvest carbohydrate demand, which might be additionally increased by high nitrogen supply. If photosynthesis is additionally impaired by a secondary salt stress, this is the worst case. The importance of photosynthetic capacity as related to carbohydrate reserves depends on environmental conditions like light and temperature. But photosynthesis becomes at least increasingly predominant along with post-harvest life because carbohydrate reserves will be used up by the plants.

The general observation, that longevity of cut flowers produced in summer is higher than of those produced in winter from the first view supports the conclusion that carbohydrate reserves are also important prerequisites for vase life. However, no relations were found between vase life of cut roses of several cultivars grown at different light intensities or temperatures and the carbohydrate pools in leaves and flower buds (MARISSEN 1998, pers. comm.), which queries the importance of carbohydrates to cut flowers. Considering also that the carbohydrate sink deriving from the root system is eliminated with harvest, decreased internal carbohydrate reserves in cut flowers resulting from excessive nitrogen supply may be of lower relevance to post-harvest life as compared to those in potted plants. Regarding additionally the low light conditions at the consumer, decreased photosynthesis should be of minor relevance to vase life.

As already outlined in the first chapter, the influence of nitrogen on post-harvest behaviour of cuttings with

Table 6. Summary of effects of nitrogen nutrition on carbohydrate reserves, photosynthesis and plant hormones (references see chapters 2–6).
Zusammenfassende Darstellung der Einflüsse der Stickstoffernährung auf Kohlenhydratreserven, Photosynthese und Phytohormonhaushalt (Quellen siehe Abschnitte 2–6).

Nitrogen supply	Carbohydrate reserves	Photosynthesis	Ethylene production	ABA concentration	Cytokinin concentration
excessive amount/ salt accumulation [1)]	↓	↓	↑	↑	↓
ammonium+nitrate [2)]	↑?	?	NE	?	↑
pure ammonium [2)]	↓?	±	↑	?	↑

↑ increase, ↓ decrease, ± slight increase per leaf area, decrease per plant, NE no effect; ? unclear
[1)] as compared to optimal supply [2)] as compared to pure nitrate supply

the main requirement for a high rooting capability is very variable among different and even for same plant species (RÖBER and REUTHER 1982, HARTMANN et al. 1990, DRÜGE et al. 1998a,b). Whereas a higher ABA:cytokinin ratio and an increased ethylene production in response to excessive nitrogen supply may promote leaf senescence, lower cytokinin concentrations may increase auxin:cytokinin ratio in the cutting base potentially favouring adventitious rooting. If plant species (or even cultivars) differ in their sensitivities of various tissues (for example in leaves and stems) to these hormones, similar concentrations at harvest and also similiar hormonal changes after harvest may cause different responses. In addition, newly formed roots can change the hormonal situation very rapidly for example by production of cytokinins (FEATONBY-SMITH and VANSTADEN 1981). Therefore the varying swiftness of rooting among plant species and light conditions should result in different hormonal situations and consequently in different responses to high pre-harvest nitrogen supply. While photosynthesis of cuttings of *Pelargonium zonale* (FORSCHNER and REUTHER 1984) and *Euphorbia pulcheririma* (SVENSON and DAVIES 1990) was found to be on a low level during propagation unless first roots were formed, carbohydrate pools of leafy cuttings of other species may be substantially increased by photosynthesis (HAISSIG 1986). Results obtained from DRÜGE et. al. (1998a,b) indicated that this is particular the case for chrysanthemums rooting under favourable light conditions. Recently KADNER and DRÜGE (1999) demonstrated that chrysanthemum cuttings have a high photosynthetic activity even during the early rooting period under adequate light conditions. In conclusion, the importance of carbohydrate reserves as related to photosynthetic capacity under the influence of high nitrogen supply should vary among the different plant species and light conditions during rooting.

It can be summarized that depending on the various ornamental products and post-harvest environmental conditions different crucial metabolic processes affect post-harvest behaviour following excessive nitrogen supply. Delivery of unfavourable hormonal signals by the stressed root system and carbohydrate deficiency are proposed to be important factors impairing post-harvest life of potted plants which appear to be more sensitive to excess nitrogen than cut flowers and cuttings. Response of leafy cuttings is variable and, in addition to hormonal balance and carbohydrate reserves, photosynthesis probably plays an important role for certain plant species. The interactions among different factors and involved crucial mechanisms are only poorly understood so that future research is necessary to clarify these relationships.

Writing of this review was supported by the ministry for nutrition, agriculture and forestry of the Federal Republic of Germany, the ministry for nutrition, agriculture and forestry of the state of Brandenburg and the ministry for nutrition, agriculture and forestry of the free state of Thuringia.

Table 7. Estimated risk of impaired post-harvest behaviour of different ornamental products following excessive nitrogen supply by affecting plant hormones, carbohydrate reserves and photosynthesis. For a discussion see the text.
Bewertetes Risiko einer Beeinträchtigung des Nachernteverhaltens unterschiedlicher Zierpflanzenprodukte in Folge einer Überversorgung mit Stickstoff durch Beeinflussung des Phytohormonhaushaltes, der Kohlenhydratreserven und der Photosynthese. Diskussion siehe Text.

Product	Risk of impairement by affecting		
	plant hormones	carbohydrate reserves	photosynthesis
potted plants	+++	++	++
cut flowers	++	+?	–
cuttings	×	×	×

–, +, ++, +++ = minor, low, medium, high risk
× = risk strongly depending on other interacting factors

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Eingegangen: 17.12.1998/18.3.1999

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