Potential of salt and drought stress to increase pharmaceutical significant secondary compounds in plants

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Abstract

It is well known that spices derived from plants grown under mediterranean or semi-arid climate conditions, respectively, are much more pronounced in taste and are more aroma intensive than those obtained from equivalent plants, but cultivated in moderate climate, e.g. in Central Europe. Analogous quality differences are observed with regard to medicinal plants, i.e. the content of the relevant secondary plant products in general is less in plants grown in a moderate Atlantic climate than in those derived from semi-arid regions. Based on plant physiological considerations, this phenomenon can be explained easily: in semi arid regions - due to limited water supply and much higher light intensities - the plants are exposed to a significant higher drought stress than the plants grown in Central Europe.

Unfortunately, in the literature only very limited data on these obvious coherences are available. This review is aimed to compile the corresponding data published so far. In most cases, comparative analyses revealed that the content of secondary plant products indeed is higher in plants that suffer drought stress than in those cultivated under optimal conditions.

Under stress, a strong oversupply of reduction equivalents is generated. In order to prevent damage by oxygen radicals, NADPH + H^+ is reoxidized by photorespiration or violaxanthine cycle. Yet, the high concentration of reduction equivalents also leads to a stronger rate of synthesis of highly reduced compounds, i.e. isoprenoids, phenols or alkaloids.

Unfortunately, these coherences have not been considered adequately neither in general plant physiology nor in reflection of medicinal or spice plants. In this review, a basis for further considerations of the physiology and biochemistry of secondary plant metabolism is presented. Special emphasis is put on aspects of quality improvement by increasing the concentration of secondary compounds in spices and medicinal plants by deliberately applying drought stress.

Keywords: drought stress, salt stress, secondary plant products, medicinal plants, spice plants, quality improvement

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Zusammenfassung

Steigerung des Gehaltes an Sekundärstoffwechselprodukten in Gewürz- und Arzneipflanzen durch Salz- und Trockenstress

Gewürze aus Pflanzen, die in Südeuropa oder in semiariden Gebieten angebaut wurden, sind stets aromatischer als Produkte, die von Pflanzen stammen, die in gemäßigten Klimaten gewachsen sind. Ähnliche Qualitätsunterschiede finden sich auch bei Medizinalpflanzen, bei denen die Gehalte an relevanten Naturstoffen deutlich niedriger sind, wenn die Pflanzen in moderatem Klima kultiviert wurden. Aus pflanzenbiologischer Sicht lässt sich dieses Phänomen leicht erklären: in trockenen Gebieten sind die Pflanzen aufgrund der begrenzten Wasserversorgung und den höheren Lichtintensitäten meist einem größeren Trockenstress ausgesetzt als in Mitteleuropa.

Leider wurde dieser Bezug in der wissenschaftlichen Literatur bislang kaum beachtet, und es gibt nur wenige Arbeiten, die diese Thematik berücksichtigen. Die Sichtung der bislang publizierten Daten zeigt, dass die Sekundärstoff-Gehalte in den meisten Pflanzen tatsächlich höher sind, wenn sie Trockenstress ausgesetzt waren.

Stress führt zu einem Überangebot an NADPH + H^+; dieses wird - um eine Schädigung durch Sauerstoff-Radikale zu vermeiden - durch Photorespiration oder den Violaxanthin-Zyklus effektiv re-oxidiert; dennoch führt das hohe Reduktionspotential zur vermehrten Synthese reduzierter Verbindungen wie Isoprenoiden, Phenolen oder Alkaloiden.

Leider wurden diese Zusammenhänge bislang noch nicht adäquat bei wissenschaftlichen Arbeiten zum Sekundärstoffwechsel oder über Arzneipflanzen berücksichtigt. In diesem Review wird, aufbauend auf einer Literaturübersicht, die Basis für eine weiterführende pflanzenphysiologische Bearbeitung des pflanzlichen Sekundärstoffwechsels vorgestellt. Eine besondere Aufmerksamkeit kommt dabei der Qualitätsverbesserung pflanzlicher Produkte durch gezielte Steigerung der Sekundärstoff-Konzentrationen in Gewürz- und Arzneipflanzen durch bewussten Einsatz von Trockenstress zu.

Schlüsselwörter: Trockenstress, Salzstress, sekundäre Pflanzenstoffe, Medizinalpflanzen, Gewürzpflanzen, Qualitätssteigerung

1 Introduction

It is well known that spices that are derived from plants grown under mediterranean or semi-arid climate conditions are much more pronounced in taste and more aroma-intensive than those obtained from equivalent plants, but cultivated in a moderate climate, i.e. in Central Europe. Analogous quality differences could be observed with regard to medicinal plants: the content of the corresponding relevant secondary plant products in general is less in plants grown in a moderate Atlantic climate than in those derived from semi-arid regions. Obviously, the different growth condition must have a significant impact on the synthesis and accumulation of secondary plant products. In this context, there are various hints that stress reactions, especially corresponding responses to salt and drought stress might be responsible for the increase or decrease in the content of relevant natural products. However, despite this obvious conjuncture, corresponding research with respect to the scientific background is rare or even still lacking. This article gives an overview on the various effects of drought and salt stress, presents various aspects of the biochemical and plant physiological background of this phenomenon and tries to give a solid explanation for it.

2 Drought and salt stress - general aspects

In general, the atmospheric CO_2-concentration is limiting photosynthesis. Yet, when this maximum photosynthetic rate should be achieved, CO_2 influx must be maximal, i.e. by opening the stomata. This however - due to the corresponding high evaporation rates - results in a severe loss of water, which - at least in all water limiting habitats - would lead to desiccation processes. Consequently, plants react with partial stomata closure. As result of this compromise between maximization of photosynthesis and minimization of water loss, the imbalance between the delivery of reductions equivalents (NADPH + H^+) by photosynthetic electron chain and their consumption by CO_2-fixation via Calvin cycle is even higher than under “normal” CO_2-limiting conditions. The consequence of such over-reducing status is the production of various oxygen radicals that are formed via pseudo-cyclic electron transport (Figure 1), known as Mehler reaction (e.g. Hideg et al., 1995; Chen et al., 2004). Yet, at ambient, standard conditions, general protective mechanisms i.e. photorespiration (Smirnoff, 1993; Wingler et al., 2000) and the xanthophyll cycle (Lin et al., 2002; Latowski et al., 2004) are able to re-oxidize the NADPH + H^+ which is overproduced by the electron transport chain and thus suppressing the generation oxygen radicals. Under stress condition, however, over-reduction of the electron transport chain reaches the level, where electron flow to oxygen is inevitable (Smirnoff, 1993; Chen et al., 2004). Consequently, superoxide radicals are produced which easily react subsequently to further various toxic oxygen species, i.e. hydroxyl radicals (Jakob & Heber, 1996). In order to detoxify these toxic oxygen species, during evolution, plants have acquired an effective detoxification system. Radicals are scavenged by the action of superoxide dismutase (SOD) that produces hydrogen peroxide which subsequently is reduced by ascorbate to water, catalyzed by the ascorbate peroxidase (e.g. Smirnoff, 1993; Shalata et al. 2001).

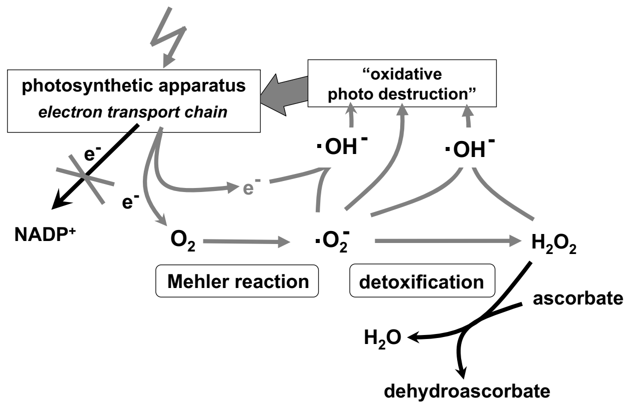

Figure 1:

Scheme of oxidative photodestruction by reactive oxygen species (Mehler reaction). In a highly over-reduced status, the entire pool of $NADP^+$ is reduced to NADP + H^+ and is not available as electron acceptor. As result, the electrons driven by photosynthetic electron chain, are transferred to molecular oxygen (Mehler-reaction or pseudocyclic electron transport) to yield superoxide, which might react with further electrons to hydroxyl radicals. Generally, superoxide is disproportionized by the action of superoxide dismutase to molecular oxygen and hydrogen peroxide, which subsequently is detoxified by ascorbate peroxidase.

When plants are growing on soils, where the negative water potential is caused by high salinity, they are severely affected by the corresponding high osmotic pressure. In addition to the water limiting effects resulting from drought stress, the cells have also to deal with the high osmotic pressure. Apart from soils with original or genuine salinity, many soils in arid regions of the world are oversalted due to excessive irrigation. Current estimates indicate that 10 - 35 % of the world’s agricultural land is now affected, with very significant areas becoming unusable each year (for review see e.g. Yokoi et al., 2002; Parida & Das, 2005). As pointed out for the drought stress response, also the plants suffering from salt stress have to cope with the production of toxic oxygen species. Thus, the free radical scavenging and detoxification reactions are typical metabolic events for these plants. Moreover, they have to adjust the osmotic potential, which generally is achieved by accumulation of compatible osmolytes and osmoprotectants (for review see e.g. Hasegawa et al., 2000; Bohnert et al., 1995).

3 Production of secondary plant products under stress conditions

As outlined above, the concentrations of various secondary plant products are strongly depending on the growing conditions and it is obvious that especially stress situations have a strong impact on the metabolic pathways responsible for the accumulation of the related natural products. Yet, corresponding comparative analyses have to cope with the fact that mostly more than one environmental factor are different in corresponding traits, e.g. increase in light intensity mostly is entailed with elevated temperatures or a lower water availability, and drought conditions often are correlated with higher salt concentrations in the soil. Indeed, in many studies the corresponding results are not conclusive; nevertheless - when thoroughly reviewing the literature - decisive deductions for the effects of drought and salt stress on the accumulation of secondary plant products can be made. In a whole array of experiments it could be shown that plants which are exposed to drought stress indeed produce higher amounts of secondary metabolites. This counts for phenols and terpenes as well as for nitrogen containing substances, such as alkaloids, cyanogenic glucosides, or glucosinolates respectively (Table 1a and 1b). There is no doubt that the application of drought stress enhances the concentration of secondary plant products. However, it has to be taken into consideration that especially drought stress also reduces the growth of most plants. Consequently, it could not be excluded that the putative increase in concentration of secondary plant products in comparison to non-stressed plants just results from the fact that the total amount of secondary metabolites per plant is more or less the same in both traits whereas the biomass is significantly lower in the stressed plants.

Unfortunately, in most of the studies, no data on the overall biomasses of the plants analysed are given. Indeed, in most cases this lack of information is not due to incomplete analyses or superficiality, but it could be ascribed to the fact that only some special plant parts - i.e. roots,

Table 1a:
Drought stress entails a concentration increase of various secondary plant products: phenols and terpenes

chlorogenic acid	*Helianthus annuus*	massive increase (tenfold)	Del Moral, 1972
total phenols	*Echinacea purpurea*	strong increase (67 %)	Gray et al., 2003
total phenols	*Prunus persica*	higher content in stressed plants	Kubota et al., 1988
phenolic compounds	*Thymus capitatus*	higher content in stressed plants	Delitala et al., 1986
total phenols	*Hypericum brasiliense*	strong increase (over 80 %)	deAbreu & Mazzafera, 2005
rutine	*Hypericum brasiliense*	massive increase (about fivefold)	deAbreu & Mazzafera, 2005
flavonoids	*Pisum sativum*	strong increase (45 %)	Nogués et al., 1998
anthocyanins	*Pisum sativum*	strong increase (over 80 %)	Nogués et al., 1998
epicatechins	*Camellia sinensis*	massive increase	Hernandez et al.,2006
dihydroxy-xanthone	*Hypericum brasiliense*	strong increase (over 300 %)	deAbreu & Mazzafera, 2005
betulinic acid	*Hypericum brasiliense*	strong increase (about 60 %)	deAbreu & Mazzafera, 2005

Table 1b:
Drought stress entails a concentration increase of various secondary plant products: nitrogen containing secondary plant products

morphine alkaloids	*Papaver somniferum*	strong increase	Szabo et al., 2003
chinolizidin alkaloids	*Lupinus angustifolius*	strong increase	Christiansen al.,1997
pyrrolizidine alkaloids	*Senecio longilobus*	strong increase	Briske & Camp, 1982
trigonelline	*Glycine max*	strong increase	Cho et al., 2003
cyanogenic glucosides	*Manihot esculenta*	strong increase	DeBruijn, 1973
cyanogenic glucosides	*Manihot esculenta*	strong increase	Okogbenin et al., 2003
cyanogenic glucosides	*Triglochin maritima*	strong increase	Clawson & Moran, 1937
cyanogenic glucosides	*Eucalyptus cladocalyx*	strong increase	Woodrow et al., 2002
glucosinolates	*Brassica napus*	massive increase	Jensen et al., 1996
glucosinolates	*Brassica napus*	significant increase	Bouchereau et al., 1996

leaves, or seeds - had been of special interest. Consequently, the entire content of natural products on a whole plant basis was not in the centre of focus. Nevertheless, in some studies the information on the total content could be calculated. In the case of *Hypericum brasiliense* - where the content of various phenols and betulinic acid is drastically higher in plants grown under drought stress (Table 1a) - the data from de Abreu and Mazzafera (2005) showed that also the total amount of some secondary plant products per plant indeed is significantly higher in plants grown under drought stress than in those cultivated under normal conditions. Although stressed plants had been quite smaller, the product of biomass and substance concentration yields in a 10 % higher amount of phenolic compounds; however, the total content of betulinic acid was nearly the same in plants when grown under drought stress or under standard conditions. Also the studies published by Nogués et al. (1998), who found a massive increase of phenolic compounds in stressed peas (Table 1a), allow calculating the overall yield of the related substances. Despite the fact that the total biomass of pea plants grown under drought stress is just about one third of those cultivated under standard condition, the overall amount of anthocyanins (product of biomass and anthocyanin concentration) is about 25 % higher in the stressed plants. Apart from that, the overall yield of total flavanoids was nearly the same in *Pisum sativum* plants grown under drought stress or under non-stress conditions.

As outlined for plants suffering drought stress, also in those exposed to salt stress, the concentration of active compounds is higher than in the control plants cultivated under standard conditions. The corresponding data are given in Table 2. As mentioned for the drought stress experiments, also the related salt-stress grown plants reveal a significant smaller biomass than the control plants. Consequently, only from those literature data, where in addition to the concentration of natural products also solid data on the different biomass gains are mentioned, reliable statement on the causales for the higher metabolite concentrations under salt stress condition can be drawn. Thus, in most cases, it is not decidable, if the higher concentrations detected for the stressed plants indeed result from a higher overall amount of metabolites or might be due to a putative increase in concentration that could be ascribed to the reduced biomass. The latter effect obviously was monitored by Brachet & Cosson (1986) who determined a strong increase in the concentration of tropane alkaloids in salt stressed plants. When calculated on the total biomass of the corresponding plants, the reputed increase is compensated fully by the decrease of entire biomass. Also for *Hordeum vulgare*, the significant higher concentration of flavanoids observed in salt stressed plants (Ali & Abbas, 2003)indeed is due to a very pronounced reduction of biomass (40 %). Therefore - despite an significant enhancement of the flavanoids concentration in stressed plants - the overall amount of flavanoids in these stressed plants is quite lower than in the control plants. Unfortunately, no further data with respect to the total biomass gains in salt stressed and unstressed plants are available, and thus no statement with respect of a real biomass enhancement can be drawn. Yet, in contrast to drought stress, the situation seems to be much more unclear.

As outlined above, plants that suffer drought stress generate a high oversupply of reduction equivalents. Despite the fact that massive amounts of NADPH + H^+ are reoxidized by photorespiration and the xanthophyll cycle, under such stress conditions, the corresponding strong reduction power seems to enhance the synthesis of highly reduced compounds, like isoprenoids, phenols or alkaloids. Consequently, the synthesis and accumulation of highly reduced secondary plant products reveals - apart from their ecological significance - a meaning within the metabolism to prevent too massive generation of oxygen radicals and the corresponding damage by photoinhibition (Selmar, 1992). It is not comprehensible, why these evident coherences have not been considered adequately up to now, neither in the field of general plant physiology and biochemistry nor in special reflections of secondary plant products. Dixion & Paiva (1995) proposed a further potentiality for the metabolism related impact of secondary compounds. Due to their capacity to scavenge reactive oxygen species, these authors propose that the phenylpropanoid derived

Table 2:
Salt stress entails a concentration increase of various secondary plant products

flavonoids	Hordeum vulgare	significant increase	Ali & Abbas, 2003
anthocyanins	Grevillea spec.	significant increase	Kennedy et al., 1999
tropane alkalois	Datura innoxia	strong increase	Brachet & Cosson;1986)
trigonelline	Glycine max	strong increase	Cho et al., 1999
glycinebetaine	Trifolium repens	massive increase	Varshney et al., 1988
di- and polyamines	Oryza sativa	massive increase (up to 200 %)	Krishnamurthy & Bhagwat, 1989
glycinebetaine	Triticum aestivum	massive increase	Krishnamurthy & Bhagwat, 1989

phenols, i.e. flavanoids, tannins, hydroxycinnamate esters, which are produced in the course of various stress situations, represent important radical scavengers. These aspects of the significance of secondary metabolites provide could contribute to the understanding of the high plasticity and variability of secondary metabolism. If we argue that in stressed plants *per se* a high pressure for the synthesis of highly reduced compounds arises, it is not deceptive that - in the course of ordinary mutations - a whole array of substances will occur which then are subject of selection pressure by environmental effects, i.e. herbivory, pathogen attacks, anorganic stresses.

In this context a general remark should be outlined: In most discussions related to secondary plant products, scientists try to ascribe certain functions for these natural products, e.g. a protective function against herbivores or pathogens, or an attracting role for pollinators and seed spreading animals. As outlined above, there is no doubt that secondary plant products have a great importance in the ecosystem and that the selection advantages by their corresponding attracting or repelling effects had been the basis for their manifestation by evolution. However, in many treatises and discussions, the corresponding functions are described in a Lamarckistic sense: "*the plants produce theses compounds in order to get protected or to attract pollinators*". Such teleological statements, however, imply that evolution is target oriented, which of course is not the case. Biology tries to handle this contradiction by pointing to the Darwinistic principles of mutation and selection: when the biosynthesis and accumulation of a certain secondary plant product took place, i.e. due to corresponding mutations, the optimization of its synthesis and the establishment in metabolism is the result of evolutive processes driven by the selection power of corresponding advantages by ecological function. During the course of evolution, this property is manifested, conserved, and integrated in the population. There is no doubt that the importance of the accumulated substance is determined by its ecological significance - however this should not be equated with the statement that these substances fulfill a purpose. In this paper, the terms "function" and "significance" are used in the strict natural scientific context and not in a teleological, Lamarckistic view.

4 Consequences of the stress enhanced accumulation of secondary plant products for the cultivation of spices and medicinal plants

The data compiled from the literature confirm that the concentration enhancement of secondary plant products due to an increasing drought stress provides a plausible explanation for the conjuncture that spices derived from plants grown under mediterranean or semi-arid climate conditions are much more pronounced in taste and aroma than those obtained from equivalent plants, but cultivated in a moderate climate. In contrast, the data on the influence of salt stress are not conclusive; a corresponding enhancement effect for secondary metabolites could not be stated unequivocally. Therefore, in contrast to the usage of drought stress, the application of salt stress seems not to be a suitable tool to increase the concentration of secondary metabolites.

In any consideration to use the effects of drought for quality improvement of spice and medicinal plants grown in Central Europe, in must be taken into consideration that a concentration increase of active compounds induced by moderate drought stress in general is associated with a reduction of biomass production. Consequently, it has to be clarified if - and maybe to what extent - the putative gain in quality by increasing the secondary plant product concentration by applying deliberately drought stress would be compensated by decreasing yields in biomass. Thus, a corresponding decision must strongly be based on the question related to the nature of the desired product. It is obvious that in the case of spices and those medicinal plants which are used directly as pharmaceuticals, the quality and thus the concentration of active compounds is much more relevant than the total yield, whereas in all cases, where the desired compounds will be extracted, the overall yield has to be very high. Related approaches on quality improvement seem to be very promising, however, in each case, a corresponding appraisement it must be estimated. For this, however, the comprehensive knowledge of the conjuncture and the special situation for the particular plants and their cultivation condition is required. A successful and effective application of deliberate drought stress for quality improvement, e.g. by applying special watering regimes in combination with efficient soil draining by supplementation of sand, is an encouraging new tool for the production of spice and pharmaceutical relevant plants, but it implies solid and comprehensive research on the entire field mentioned above.

References

Ali RM, Abbas HM (2003) Response of salt stressed barley seedlings to phenylurea Plant Soil Environ 49(4):158–162

Bouchereau A, Clossais-Besnard N, Bensaoud A, Leport L, Renard M (1995) Water stress effects on rapeseed quality. European J Agron 5:19–30

Brachet J, Cosson L (1986) Changes in the total alkaloid content of datura innoxia Mill. subjected to salt stress. J Experimental Bot 37:650-656

Briske DD, Camp BJ (1982) Water stress increases alkaloid concentrations in threadleaf groundsel (*Senecio longilobus*). Weed Sci 30(1):106-108

Christiansen JL, JØrnsgard B, Buskov S, Olsen CE (1997) Effect of drought stress on content and composition of seed alkaloids in narrow-leafed lupin, *Lupinus angustifolius* L. European J Agron 7:307-314

Clawson AB, Moran EA (1937) Toxicity of arrowgrass for sheep and the remedial treatment. Technical Bulletin / USDA 580:16

Cho Y, Lightfoot DA, Wood AJ (1999) Trigonelline concentrations in salt stressed leaves of cultivated Glycine max. Phytochem 52(7):1235-1238

Cho Y, Njitiv N, Chen X, Lightfood DA, Wood AJ (2003) Trigonelline concentration in field-grown soybean in response to irrigation. Biol Plant 46(3):405-410

de Abreu IN, Mazzafera P (2005) Effect of water and temperature stress on the content of active constituents of Hypericum brasiliense Choisy. Plant Physiol Biochem 43:241–248

De Bruijn GH (1973) The cyanogenic character of cassava (*Manihot esculenta*). In: Nestel B, MacIntyre R (eds) Chronic cassava toxicity : proceedings of an interdisciplinary workshop, London, England, 29 - 30 January 1973. Ottawa : Internat Development Research Centre, pp 43-48

Del Moral R (1972) On the variability of chlorogenic acid concentration Oecologia 9:289–300

Delitala l-F, Gessa C, Solinas V (1986) Water stress and flexibility of phenolic metabolism in thymus capitatus. Fitoterapia 57(6):401–408

Biehler K, Fock H (1996) Evidence for the contribution of the Mehler-peroxidase reaction in dissipating excess electrons in drought-stressed wheat. Plant Physiol 112:265-272

Bohnert HJ, Nelson DE, Jensen RG (1995) Adaptations to environmental stresses. Plant Cell 7:1099-1111

Chen HX, Gao HY, An SZ, Li WJ (2004) Dissipation of excess energy in Mehler-peroxidase reaction in Rumex leaves during salt shock Photosynthetica. 42(1):117-122

Grace SC, Logan BA (2000) Energy dissipation and radical scavenging by the plant phenylpropanoid pathway. Philos Trans R Soc London Ser B 355:1499-1510

Gray DE, Pallardy SG, Garrett HE, Rottinghaus G (2003) Acute drought stress and plant age effects on alkamide and phenolic acid content in purple coneflower roots. Planta Med 69(1):50-55

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol 51:463–499

Hernaéndez I, Alegre L, Munné-Bosch S (2006) Enhanced oxidation of flavan-3-ols and proanthocyanidin accumulation in water-stressed tea plants. Phytochem 67:1120–1126

Hideg E, Spetea C, Vass I (1995) Superoxide radicals are not the main promoters of acceptor-side-induced photoinhibitory damage in spinach thylakoids. Photosynth Res 46:399-407

Jakob B, Heber U (1996) Photoproduction and detoxification of hydroxyl radicals in chloroplasts and leaves and relation to photoinactivation of Photosystems I and II. Plant Cell Physiol 37(5):629-635

Jensen CR, Mogensen VO, Mortensen G, Fieldsend JK, Milford GFJ, Andersen MN, Thage JH (1996) Seed glucosinolate, oil and protein contents of field-grown rape (*Brassica napus* L.) affected by soil drying and evaporative demand. Field Crops Res 47:93-105

Kennedy BF, De Filippis LF (1999) Physiological and oxidative response to NaCl of the salt tolerant Grevillea ilicifolia and the salt sensitive Grevillea arenaria. J Plant Physiol 155(6):746-754

Krishnamurthy R, Bhagwat KA (1989) Polyamines as modulators of salt tolerance in rice cultivars. Plant Physiol 91:500–504

Krishnamurthy R, Bhagwat KA (1990) Accumulation of choline and glycine-betaine in salt-stressed wheat seedlings. Curr Sci 59(2):111-112

Kubota N, Mimura H, Shimamura K (1988) The effects of drought and flooding on the phenolic compounds in peach fruits. Okayama Daigaku Nogakubu Gakujutsu 171:17-21

Latowski D, Grzyb J, Strzałka K (2004) The xanthophyll cycle - molecular mechanism and physiological significance. Acta Physiol Plant 26(2):197-212

Lin RC, Xu CC, Li LB, Kuang TY (2002) Xanthophyll cycle and its molecular mechanism in photoprotection. Acta Bot Sin 44(4):379-383

Nogueés S, Allen DJ, Morison JIL, Baker NR (1998) Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. Plant Physiol 117:173–181

Okogbenin E, Ekanayake IJ, Porto MCM (2003) Genotypic variability in adaptation responses of selected clones of cassava to drought stress in the Sudan aavanna zone of Nigeria. J Agron Crop Sci 189(6):376–389

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants : a review. Ecotoxicol Environ Safety 60:324–349

Selmar D (1992) Die Metabolisierung cyanogener Verbindungen : pflanzenphysiologische und biochemische Untersuchungen zum Metabolismus cyanogener Naturstoffe als Basis einer Betrachtung der Multifunktionalität sekundärer Pflanzenstoffe. Braunschweig : Univ, 197 p, [Habilitation]

Shalata A, Mittova V, Volokita M, Guy M, Tal M (2001) Response of the cultivated tomato and its wild salt-tolerant relative *Lycopersicon pennellii* to salt-dependent oxidative stress : the root antioxidative system Physiol Plant 112(4):487-494

Smirnoff N (1993) The role of active oxygen in the response of plants to water deficit and desiccation. New Phytol 125(1):27-58

Szabó B, Tyihák E, Szabó LG, Botz L (2003) Mycotoxin and drought stress induced change of alkaloid content of Papaver somniferum plantlets. Acta Bot Hungarica 45(3/4):409-417

Varshney KA, Gangwar LP (1988) Choline and betaine accumulation in *Trifolium alexandrinum* L. during salt stress. Egypt J Botany 31(1-3):81-86

Wingler A, Lea PJ, Quick WP, Leegood RC (2000) Photorespiration : metabolic pathways and their role in stress protection. Philos Trans R Soc London Ser B 355:1517-1529

Woodrow IE, Slocum DJ, Gleadow RM (2002) Influence of water stress on cyanogenic capacity in Eucalyptus cladocalyx. Funct Plant Biol 29(1)103–110

Yokoi S, Bressan RA, Hasegawa PM (2002) Salt stress tolerance of plants. Working Rep / Jpn Intern Res Center Agric Sci 25-33

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Physiol 53:247–273