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Drought Stress Effects on Medicinal and Aromatic Plants and the Possible Stress Amelioration by Mineral Nutrition

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ABSTRACT

Limited water supply is one of the major abiotic factors that adversely affects agricultural crop production worldwide. Drought stress disturbs the balance between the production of reactive oxygen species (ROS) and the antioxidant defense, causing the accumulation of ROS that induce oxidative stress to proteins, membrane lipids and other cellular components. Drought stress hampers photosynthesis harshly owing to interference with stomatal functioning and causing serious damage to photosynthetic apparatus through ROS production. Hence, water-stressed plants exhibit disturbance in metabolism, particularly that of carbon, nitrogen and oxygen. As a result of water stress, growth parameters associated with root and above-ground parts, e.g. leaf area, height, and fresh and dry matter of plants, are severely reduced, leading to drastic reductions in growth, yield and quality of plants. Mineral elements have numerous functions in plants including charge balance, electron carriers, structural components, and enzyme activation. Besides, these elements behave as osmotica for maintenance of turgor and growth under drought stress. However, their uptake is reduced to a great extent under water deficit. Hence, their additional supplementation under water deficit results in improvement in their uptake and mitigation of deleterious effects of drought stress. A wide range of studies on the effect of drought stress on growth, yield and quality of field crops have been conducted; however, such studies related to medicinal and aromatic plants (MAPs) are few. In this review, in addition to describing the adverse effects of water stress on the growth, yield and quality attributes of MAPs, the ameliorative role of some of the macronutrients (nitrogen, phosphorus, potassium, and calcium) is discussed.

Keywords: Nitrate reductase, praline, secondary metabolites

CONTENTS

INTRODUCTION

Water stress is a major environmental stress that affects plant morphology, physiology and biochemistry, causing a significant reduction in agricultural production (Hsiao 1973; Tyree and Karamanos 1981). It renders 25% of the world's land unproductive (Delfine *et al*. 2005). Although the effects of drought on many plants have been widely investigated, a good deal of scientific literature regarding the effect of water stress on medicinal and aromatic plants (MAPs) is, however, lacking (Sangwan *et al*. 1993; Sangwan *et al*. 2001; Farahani *et al*. 2009a). Drought-stress, imposed during vegetative period, resulted in shorter plants and smaller leaf area of mint (*Mentha arvensis*) (Abbaszadeh *et al*. 2006), yarrow (*Achillea millefolium*) (Ashoorabadi *et al*. 2006) and chicory (*Cichorium intybus*) (Taheri *et al*. 2008). There was reported short stature of plants in calendula (*Calendula officinalis*) (Rahmani *et al*. 2008) and reduction in vegetative dry matter of balm (*Melissa officinalis*) (Farahani *et al*. 2009b) due to reduced water use by plants under water stress applied during vegetative period. Water stress significantly reduced the dry matter and relative growth rate of thyme (*Thymus vulgaris*) (Letchamo *et al*. 1995). In lemongrass species, water deficit reduced plant height, leaf length, leaf area, fresh and dry weight, moisture content and the percent essential oil (EO) content (Sangwan *et al*. 1994). In contrast, oregano (*Origanum majorana*) was reported to have a higher EO content and leaf dry weight with increasing moisture deficit (Rhizopoulou and Diamantoglou 1991). The percent EO content and the main constituents of EO of sweet basil (*Ocimum basilicum* L.) and American basil (*Ocimum americanum* L.) increased under

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Invited Review

water stress (Khalid 2006). The assumed increase in percent concentration of EO of the water stressed MAPs compared to the unstressed ones was mostly ascribed to reduced growth and biomass of plants under stress because the total amount of secondary metabolites per plant was more or less the same both in stressed and unstressed plants.

The improvement in plant nutrition can contribute to increased resistance and production of the MAPs under water stress (Kleiner *et al*. 1992; Graciano *et al*. 2005; Ram *et al*. 2006; Waraich *et al*. 2011). Most of the results show that N, P and Ca nutrition ameliorated the deleterious effects of water stress in the MAPs. For example, in *Atropa belladonna* L., the maximal content of alkaloids under water stress was achieved when plants were fertilized with nitrogen (Baricevic *et al*. 1999). Application of N fertilizer significantly increased the EO percentage and yield along with significant increase in seed yield, head diameter, 1000-seed weight and number of seeds in heads per plants of calendula (*Calendula officinalis* L.) under water stress conditions. The application of N fertilizer under water deficit resulted in enhanced photosynthesis and improved chlorophyll production together with higher number of roots per plants (Rahmani *et al*. 2009). Nitrogen supplementation increased the canavanine synthesis in *Sutherlandia frutescens*, in normal conditions as well as under water and salinity stress, suggesting that mineral nutrition is more important for increasing canavanine than water and salinity stress (Colling *et al*. 2010). The ameliorative effects of P on plant growth under drought stress have been attributed to an increase in stomatal conductance (Brück *et al*. 2000), photosynthesis (Ackerson 1985), higher cell-membrane stability and improved plant water relation parameters (Sawwan *et al*. 2000). By maintaining the elevated leaf water potential, P maintains the cell turgor which in turn increases the stomatal conductance and photosynthetic rate under drought stress (Waraich *et al*. 2011). N and P fertilizer increased the growth of *Eucalyptus grandis* (Graciano *et al*. 2005) and *Mentha arvensis* L. (Ram *et al*. 2006) under water-stress conditions. *Grindelia camporum* plants supplied with high rate of NPK fertilizers exhibited significant increase in plant height, dry mass and yield of flower heads along with high levels of crude resin and resin acid (Mahmoud 2002). There was significant interaction between the water stress and fertilizer treatments; the negative effect of water-stress on total saikosaponin content and saikosaponin yield could partly be mitigated through the application of N and P fertilizers in *Bupleurum chinense* (Zhu *et al*. 2009). Li *et al*. (2003) concluded that extracellular Ca might improve the adaptation of liquorice (*Glycyrrhiza uralensis* Fisch) cells to drought stress, mitigating the oxidative stress thereof. Application of Ca also increased the drought tolerance of *Catharanthus roseus*, generating favorable changes relative to oxidative stress, osmoregulation and indole alkaloid accumulation. Water-stressed *C. roseus* plants treated with $CaCl_2$ showed an increase in total indole alkaloid content and improvement in growth of shoots and roots when compared to unstressed plants (Jaleel *et al*. 2007). Thus, it seems that yield and quality of the MAPs could be improved under water stress by supplying the plants with sufficient mineral nutrients. Drought-stress effects on MAPs and the possible amelioration of these effects by mineral nutrients has been discussed in the following review with specific reference to N, P, K, and Ca.

EFFECT OF DROUGHT STRESS ON GROWTH ATTRIBUTES OF MAPs

Studies on the effect of water stress on growth and development of the MAPs are inadequate. As per studies conducted so far, there has been found significant reduction in vegetative growth of the MAPs under water deficit. During the vegetative period, drought stress resulted in shorter plants and smaller leaf areas of mint (*Mentha arvensis*) (Abbaszadeh *et al*. 2006), yarrow (*Achillea millefolium*) (Ashoorabadi *et al*. 2006) and chicory (*Cichorium intybus*) (Taheri *et al*. 2008). Likewise, the reduction in plant height of calendula (*Calendula officinalis*) (Rahmani *et al*. 2008) and vegetative dry matter of balm (*Melissa officinalis*) (Farahani *et al*. 2009b) was ascribed to reduced water use by the plants under water deficit. Growth and EO content of fennel (*Foeniculum vulgare*) plants was also adversely affected by unfavorable irrigation schedules (Patel *et al*. 2000). Letchamo *et al*. (1995) found a significant reduction in dry matter and relative growth rate of thyme (*Thymus vulgaris*) grown under drought stress. Similarly, Alishah *et al*. (2006) demonstrated significant decrease in plant height, stem diameter, number and area of leaves and leaf area index as a consequence of soil moisture stress in purple basil (*Ocimum basilicum*). Khorasaninejad *et al*. (2011) also observed significant reduction in growth parameters of peppermint (*Mentha piperita* L.) under water stress. Water deficit reduced plant height, leaf length, leaf area, fresh and dry weight, moisture content and the percent EO content of lemongrass species, namely, *Cymbopogon nardus* and C. *pendulus* (Sangwan *et al*. 1994). In contrast, oregano (*Origanum majorana*) was reported to have a higher EO content and leaf dry weight with increasing moisture deficit (Rhizopoulou and Diamantoglou 1991). Jaleel *et al*. (2008) found significant reduction in root length, shoot length, total leaf area, and fresh and dry weights of plants together with reduced contents of leaf photosynthetic pigment under water stress treatments in *Catharanthus roseus*. Drought stress decreased the root length in *Abelmoschus esculentum* (Sankar *et al*. 2007), *Albizia* seedlings (Valli *et al*. 2005), *Eucalyptus microthea* seedlings (Berninger *et al*. 2000). Drought stress decreased the plant biomass in *Asteriscus maritimus* (Rodríguez *et al*. 2005) and in *Albizia* seedlings (Valli *et al*. 2005). Decrease in total dry weight was ascribed to significant decrease in plant growth, photosynthesis and canopy structure during drought stress in *Abelmoschus esculentum* (Sankar *et al*. 2007). The leaf chlorophyll content in *Allium schoenoprasum* was also decreased due to desiccation treatments (Egert and Tevini 2002). Jaleel *et al*. (2008) reported drought-stress mediated decrease in leaf area duration, cumulative water transpired, net assimilation rate, mean transpiration rate, harvest index, and biomass yield in *Catharanthus roseus*; while, water use efficiency was significantly increased under water stress. Koocheki *et al*. (2008) evaluated the effect of water stress on growth of four medicinal plants, *viz*. Shiraz thyme (*Zataria multiflora*), kakooti (*Ziziphora clinopodioides*), garden thyme (*Thymus vulgaris*), and cat thyme (*Teucrium polium*) in greenhouse conditions. Results indicated that drought stress increased chlorophyll content in kakooti, specific leaf weight in Shiraz thyme and kakooti, and canopy temperature in Shiraz thyme and cat thyme as compared with controls. A significant positive correlation was observed between the root-to-top ratio and drought levels. Kakooti was the most drought-resistant, while garden thyme had the lowest resistance to drought. Petropoulos *et al*. (2008) observed that growth parameters *viz*. foliage weight, root weight, and leaf number of three cultivars of parsley (*Petroselinum crispum* Mill.), designated as plain-leafed, curly-leafed and turnip-rooted types, were significantly reduced both under mild and severe water stress conditions. In *Salvia officinalis*, a depressive effect of drought was noted on leaf water potential (-1.2 to -4.8 MPa) and plant growth. The detrimental effect of drought was more pronounced with the intensity of water stress. Plants subjected to severe water deficit produced thinner stems with fewer, dry and smaller leaves than the control ones. Water stress reduced plant height, with the severe stress being more deleterious than mild stress. Drought stress also decreased the fresh and dry matter weights significantly (Bettaieb *et al*. 2008). Khalil *et al*. (2010) noticed a significant increase in plant height, number of branches, number of leaves, leaf area, and fresh and dry weight of basil (*Ocimum basilicum*) under 50% soil moisture level, while further increase in water stress level resulted in significant decrease in these growth parameters. Aziz *et al*. (2008) recorded significant increase in plant height and fresh and dry weight of thyme (*Thymus vulgaris*) plants that received irrigation every 3 days compared to those irrigated every 5, 7 and 10 days. Plant growth attributes (height, fresh and dry matter weights) as well as yield components of cumin (*Cuminum cyminum*) were significantly increased under moderate water deficit, while these parameters were adversely affected under severe water stress (Bettaieb *et al.* 2011). Thus, though water stress adversely affects the growth of MAPs in general, it seems that growth of MAPs may be increased using moderate water deficit; similar results may possibly be obtained regarding EO and other secondary metabolites of MAPs under a low intensity of water stress.

EFFECT OF DROUGHT STRESS ON CONTENT AND COMPOSITION OF ESSENTIAL OIL OF MAPs

The content of EO and its composition is affected by different factors, including genetic makeup (Muzik *et al.* 1989) and cultivation conditions, such as climate, habitat, harvesting time, environmental stresses, and the use of mineral nutrients (Min *et al.* 2005; Stutte 2006). Water deficit in plants may lead to physiological disorders, such as a reduction in photosynthesis and transpiration that may cause changes in the yield and composition of EO in aromatic plants (Sarker *et al.* 2005). Although the effects of water stress on many plants have been widely investigated, not much is known about the biosynthesis and accumulation of EO in aromatic plants under water deficit conditions (Sangwan *et al.* 1993). The effect of water stress on EO was previously studied in excised leaves of palmarosa (*Cymbopogon martinii* var. Motia) and citronella java (*C. winterianus*) (Sangwan *et al.* 1994). Sangwan *et al.* (1993, 1994) conducted short- as well as long-term, experiments regarding the effect of moisture stress on different species of *Cymbopogon*. Short-term water stress substantially affected the essential oil biosynthesis, with the response being different in different *Cymbopogon* species. It was suggested that the reduction in leaf area due to water stress might result in a higher density of the leaf oil glands, leading to an elevated amount of oil accumulation (Coronel *et al.* 1984; Charles *et al.* 1990; Simon *et al.* 1992). However, experiments with *Cymbopogons* revealed that water stress could alter the oil biogenetic capacity of plant that occurred without any change in the number of oil glands in the leaves as a result of short term stress conditions. Similarly, the changes in any other morphological parameter might be unlikely (Sangwan *et al.* 1993). In another set of experiments, these workers studied long term effects of water deficit on two lemon grass species, *viz*. *C. nardus* var. confertiflorus and *C. pendulus*. The amount of essential oil produced under drought conditions was either maintained or enhanced, depending on the species and magnitude of the stress. The major oil constituents, geraniol and citral, were increased in both the species. The activity of the enzyme geraniol dehydrogenase was also modulated under moisture stress. Based on the data regarding physiological parameters and EO content, Sangwan *et al.* (1993, 1994) demonstrated that the growth of relatively drought resistant *Cymbopogon* species was reduced under water stress with a significant enhancement in the percent EO content. Compositional alterations in EO content, occurring due to water stress, have also been elucidated in mint (Chattopadhyay and Subramanyam 1993) and sweet basil (*Ocimum basilicum*) (Simon *et al.* 1992). In lemongrasses, the stress-mediated changes in oil composition were more prominently reflected in the major constituents of EO, *viz*. citral and geraniol (Sangwan *et al.* 1994). It suggested that closer planting of aromatic grasses in drought-affected areas might be a way of maintaining oil production. Farooqi *et al.* (1998) reported the increase in oil biogenesis of citronella java (*Cymbopogon winterianus*) under water stress that was due to either an increase or decrease or no change in the EO yield, depending on the genotypes (Shabih *et al.* 1999). In contrast, water-stress had a negative impact on herbage and EO yield of geranium as the interval between stress applications increased (Putievsky *et al.* 1990). The citronellol to geraniol ratio was also increased as the interval between final irrigation and harvest was extended. Razmjoo *et al* (2008); however, recorded severe reductions in flower yield and EO content of chamomile (*Matricaria chamomila*) due to water stress and salinity; whereas, Radacsi *et al.* (2010) found only a slight increase in EO concentration in response to drought stress in basil (*Ocimum basilicum* L.), noticing a significant decrease in the proportion of linalool content in the EO. Chalchat *et al.* (1994) observed a strong depression in the EO yield in *Artemisia annua*, while a plentiful irrigation raised it. Weiss (1997) registered that the long dry spells of drought severely retarded the plant growth, reduced the EO content, and changed the EO characteristics of drought tolerant species of geranium. Likewise, water deficit decreased the EO yield of rosemary (*Rosmarinus officinalis* L.) (Singh and Ramesh 2000) and anise (*Pimpinella anisum* L.) (Zehtab-Salmasi *et al.* 2001). Contrarily, Ozturk *et al.* (2004) noticed a significant increase (from 0.12 to 0.16%) in EO content of lemon balm (*Melissa officinalis* L.) as a consequence of water stress. Water stress also caused an increase in the EO production of thyme (Aziz *et al.* 2008) and citronella grass (*Cymbopogen winterianus* Jowitt.) (Fatima *et al* 2006) expressed on fresh weight basis. The accumulation of EO in Iranian *Satureja hortensis* L increased significantly under severe water stress at the flowering stage, when the mean leaf water potential (LWP) decreased from -0.5 to -1.6 MPa. The severe water stress treatment affected the quantity of EO more than moderate water stress during the vegetative and flowering stages. The main EO constituents were carvacrol and γ-terpinene. The amount of carvacrol increased under moderate stress, while γ-terpinene content decreased under moderate as well as severe water stress conditions (Baher *et al.* 2002). Khazaie *et al.* (2008) observed no change in total harvested herbage biomass and EO production in thyme (*Thymus vulgaris*) as a result of irrigation frequency, suggesting the possibility of saving water through longer interval irrigations. Abbaszadeh *et al.* (2009) observed an increase in EO percentage and yield as a result of water stress, recommending the moderate water stress to increase EO production in balm (*Melissa officinalis* L.). Percent EO content of geranium (*Pelargonium capitatum*), calculated on fresh weight basis, increased significantly on account of increasing the irrigation frequency; however, a short duration (one week) water stress just before harvesting significantly increased total EO yield as well as oil content in the fresh herbage (Eiasu *et al.* 2008).

Taheri *et al.* (2008) noticed a significant increase in the EO percentage and the content of compounds such as kaempferol in water-stressed plants of chicory (*Cichorium intybus*), while the unstressed plants showed significant increase in EO yield. The experimental results obtained by Farahani *et al.* (2009b) revealed a significant drop in EO yield of balm (*Melissa officinalis* L.), but the percentage of EO was increased under water deficit stress; on the other hand, both EO percentage and the main constituents of EO increased in sweet basil (*Ocimum basilicum* L.) and American basil (*Ocimum americanum* L.) under water stress. A soil water status equivalent to 75% of the field water capacity resulted in the highest yield of herbage and EO in two basil species (Khalid 2006). Three parsley (*Petroselinum crispum* Mill.) cultivars (plain-leaf, curly-leaf and turnip-root types) were grown under water deficit conditions (35–40% and 45–60% available soil water) in order to evaluate the effect of water stress on the yield and composition of EO. Water stress increased the yield of EO (on fresh weight basis) in plain-leaf and curly-leaf cultivars, but not in the turnip-root ones. However, on per meter square basis, the foliage EO yield increased significantly in curly-leaf cultivar only. Water stress also caused changes in the relative contribution of certain aroma constituents of the essential oils (principally 1, 3, 8-*p*-menthatriene, myristicin, terpinolene + *p*-cymenene), but these changes varied between cultivars. The EO yield of roots was low and the water stress had relatively slight effect on the composition of root oil. It was concluded that because the biomass of plants subjected to water deficit was reduced, it was possible to increase the plant density of plain-leaf or curly-leaf parsley cultivars, thereby, further increasing the EO yield per meter square. It was suggested that while using water deficit stress to enhance EO production of parsley, the likely changes in oil composition must also be taken into account, which in turn may relate to the cultivar (Petropoulos *et al*. 2008). Through the aforementioned discussion, it appears that drought stress increases the EO percentage but not the absolute EO content of the MAPs. This is evident by the water stress effects on EO content/yield and EO percentage registered recorded in several MAPs. For example, Fatima *et al*. (2006) showed that water stress increased the EO percentage but simultaneously decreased the EO content in the excised leaves of palmarosa (*Cymbopogon martinii* var. motia) and citronella (*C. winterianus*). Farahani *et al*. (2009a) argued that as the shoot yield of balm was decreased due to water stress, the EO percentage on shoot weight basis was obviously increased. Similarly, Rahmani *et al*. (2009) showed the highest EO yield under no stress condition and the highest EO percentage under water stress condition in calendula. Bettaieb *et al*. (2008) investigated the effect of water deficit on fatty acid contents, EO yield and the composition of EO and fatty acids in the aerial parts of *Salvia officinalis*. Moderate water deficit increased the EO yield significantly. The main EO constituents (camphor, β-thujone and 1,8-cineole) were also increased significantly under moderate water deficit. Thus, a range of water deficit could, presumably, be employed to increase the EO yield in the MAPs, using various cultivars and plant density rates.

EFFECT OF DROUGHT STRESS ON SECONDARY METABOLITES OF MAPs

The influence of environmental conditions is regarded as important, as these factors directly affect the chemical constituents of medicinal plants, often leading to unpredictable changes at metabolic level and causing alterations in plant growth and development, in general (Colling *et al*. 2010). There are indications that water stress might be responsible for the increase (**Table 1A, 1B**) or decrease (Eiasu *et al*. 2008; Szabó *et al*. 2008; Khalil *et al*. 2010; Radacsi *et al*. 2010; Gutbrodt *et al*. 2011; Osuagwu *et al*. 2011) in the content of secondary plant products. In addition, all the secondary metabolites may not increase in the same proportion in response to water stress of certain intensity. In this regard, Zhang *et al*. (2011) reported that the level of ergonovine was higher than that of ergine (ergot alkaloids) in the leaves of drunken horse grass (*Achnatherum inebrians*) at the same water stress level. Furthermore, water stress may not increase the amount of secondary metabolites in all the MAPs. Accordingly, Manukyan (2011) noted that the influence of drought stress of the same intensity was significantly positive for the content of polyphenols in lemon balm (*Melissa officinalis* L.) and sage (*Salvia officinalis* L.), but not in lemon catmint (*Nepeta cataria* L.). Besides, plants show variable response to drought stress of different intensity for different secondary metabolites. For example, a medium-intensity water stress was more influential to increase the accumulation of secondary metabolites (flavonoids, tannins, chlorogenic acids and anthraquinones) in the leaves of *Myrica rubra* than a light-intensity water stress (Yang and Li 2011). In peppermint (*Mentha piperita* L.), the highest content of mentone and menthofuran were obtained under 100% field capacity (no water stress), while the highest values of menthol were obtained under the water stress of 70% field capacity (Khorasaninejad *et al*. 2011). Leaf-content of citronellol and citronellyl formate in geranium (*Pelargonium capitatum*) tended to increase with an increase in the stress level, but the reverse was true for geraniol and geranyl formate; while, other major essential oil components were unaffected by water stress (Eiasu *et al*. 2008). In Grapevine (*vitis vinifera* L.), flavonoid to hydroxycinnamate ratio was markedly increased in drought-stressed plants compared to that in well-watered ones, while the quercetin to kaempferol ratio was only slightly increased because of drought stress (Scalabrelli *et al*. 2007). Water stress has a strong impact on the metabolic pathways responsible for the accumulation of the related natural products. However, in many such studies, the corresponding results are not conclusive and a thorough review of the literature may help to reach the decisive conclusions regarding the effects of drought stress on the accumulation of secondary plant products. In a wide array of experiments it could be shown that plants which are exposed to water stress 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 (**Tables 1A, 1B**).

There is no doubt that the application of drought stress enhances the concentration of secondary plant products. However, it is difficult to conclude whether the assumed increase in concentration of secondary plant products in comparison to non-stressed plants is due to stress or just because of corresponding reduction in plant biomass under stress as the total amount of secondary metabolites per plant is more or less the same both in stressed and unstressed plants, whereas the plant biomass is significantly lower in the stressed plants. For example, Khalil *et al*. (2010) observed significant increase in growth parameters and photosynthetic pigments (chlorophyll *a*, chlorophyll *b*, total chlorophyll and carotenoids) in basil (*Ocimum basilicum*) plants at 50% soil moisture; however, further moisture-stress reduced the growth parameters as well as photosynthetic pigments significantly. Marchese *et al*. (2010) found that a moderate water deficit prior to harvesting induced artemisinin accumulation in wormwood (*Artemisia annua* L.) with no detrimental effect on plant biomass production. Zhu *et al*. (2009) reported significant increase in the contents of saikosaponin a and d due to a mild water stress in *Bupleurum chinense* DC roots that was accompanied by the decrease in root biomass. Similarly, thyme (*Thymus vulgare*) plants subjected to water stress gave the highest relative percentage of thymol together with significant reduction in growth parameters (Aziz *et al*. 2008). In purple basil (*Ocimum basilicum*), water stress resulted in decreased contents of leaf anthocyanin and proline, which was accompanied with a concomitant decrease in growth parameters (Alishah *et al*. 2006). There was recorded a strong negative correlation between growth and total phenolic glycoside concentration in black poplar (*Populus nigra*), with the former being decreased and the latter being increased (Hale *et al*. 2005). Further, de Abreu and Mazzafera (2005) reported that the content of various phenols and betulinic acid was drastically higher in plants grown under drought stress in *Hypericum brasiliense*. Total amount of secondary products per plant was also significantly higher in plants grown under drought stress than in plants cultivated under normal conditions. Although stressed plants were quite short in stature, the yield of phenolic compounds was 10% higher in stressed plants compared to that in unstressed plants, while the total content of betulinic acid was nearly the same in stressed as well as unstressed plants. In addition, Nogués *et al*. (1998) found a significant increase in phenolic compounds in water stressed pea (*Pisum sativum*) plants. Though the total biomass of drought stressed pea plants was just about one third of those of unstressed plants, the overall anthocyanin yield was about 25% higher in the stressed than in unstressed plants. Contrarily, the overall yield of total flavanoids was nearly the same in plants grown under drought stress or normal conditions. Thus, in most cases, it is not clear if a higher metabolite concentration present in the stressed plants is due to the accumulation of higher amount of metabolites or as a result of putative increase in concentration owing to the reduced plant biomass. The latter effect was monitored by Brachet and Cosson (1986) who revealed a strong increase in the concentration of tropane alkaloids in salt stressed plants. When calculated on

Table 1A Positive effect of drought stress on concentration of various secondary plant products.

Secondary metabolites	**Plant species**	**Level of enhancement**	**Reference**
Chlorogenic acid (polyphenolics)	*Helianthus annuus*	Massive increase (10-fold)	Del Moral 1972
Phenolic compounds	*Thymus capitatus*	Significant increase	Delitala *et al.* 1986
Total phenols	*Prunus persica*	Significant increase	Kubota *et al.* 1988
Phenolic compounds	*Pseudotsuga menziesii*	Significant increase	Horner 1990
Total terpene and monoterpenes (tricyclene, α-pinene, and camphene)	*Picea abies*	Significant increase	Kainulainen *et al.* 1992
Phenolics and terpenoids	*Cyperus rotundas*	Significant increase	Tang *et al.* 1995
Flavonoids	*Pisum sativum*	Strong increase (45%)	Nogués *et al.* 1998
Anthocyanin	*Pisum sativum*	Strong increase (over 80%)	Nogués *et al.* 1998
Total phenols	*Echinacea purpurea*	Strong increase (67%)	Gray *et al.* 2003
Rosmarinic acid (phenolics)	*Melissa officinalis*	Significant increase	Toth *et al.* 2003
Chlorogenic acid, catechin and epicatechin (polyphenolics)	*Crataegus laevigata* and *Crataegus monogyna*	Significant increase	Kirakosyan *et al.* 2004
Total phenols	*Hypericum rasiliense*	Strong increase (over 80%)	de Abreu and Mazzafera 2005
Rutine	*Hypericum brasiliense*	Massive increase (about 5-fold)	de Abreu and Mazzafera 2005
Dihydroxy-xanthone and betulinic acid	*Hypericum brasiliense*	Strong increase (over 300%)	de Abreu and Mazzafera 2005
Phenolic glycosides	*Populus nigra*	Significant increase	Hale *et al.* 2005
Anthocyanin	*Ocimum basilicum*	Significant increase	Alishah *et al.* 2006
Epicatechins (polyphenolics)	*Camellia sinensis*	Massive increase	Hernández *et al.* 2006
Ascorbic acid, α-tocopherol	*Catharanthus roseus*	Significant increase	Jalil *et al.* 2007
Favonoids	*Vitis vinifera*	Significant increase	Scalabrelli *et al.* 2007
Hyperforin	*Hypericum perforatum*	10–12 fold higher	Zobayed *et al.* 2007
Thymol	*Thymus vulgaris*	Significant increase	Aziz *et al.* 2008
Myoinositol	*Pisum sativum*	Significant increase	Charlton *et al.* 2008
Ascorbic acid, α-tocopherol and reduced glutathione	*Withania somnifera*	Significant increase	Jalil 2009
Saikosaponin	*Bupleurum chinense*	Significant increase	Zhu *et al.* 2009
Artemisinin	*Artemisia annua*	Artemisinin content (29%)	Marchese *et al.* 2010
Malondialdehyde	*Ocimum basilicum*	Significant increase	Radacsi *et al.* 2010
Polyphenols	*Melissa officinalis* and *Salvia officinalis*	Significant increase	Manukyan 2011
Menthol	*Mentha piperita*	Significant increase	Khorasaninejad *et al.* 2011
Glycyrrhizic acid	*Glycyrrhiza uralensis*	Strong increase (89%)	Li *et al.* 2011
Liquiritin	*Glycyrrhiza uralensis*	Strong increase (125%)	Li *et al.* 2011
Flavonoids	*Myrica rubra*	Significant increase	Yang and Li 2011

Table 1B Positive effect of drought stress on various nitrogen containing secondary plant products.

Secondary metabolites	**Plant species**	**Level of enhancement**	**Reference**
Cyanogenic glucosides	*Triglochin maritima*	Strong increase	Clawson and Moran 1937
Cyanogenic glucosides	*Manihot esculenta*	Strong increase	DeBruijn 1973
Pyrrolizidine alkaloids	*Senecio longilobus*	Strong increase	Briske and Camp 1982
Glucosinolates	*Brassica napus*	Significant increase	Bouchereau *et al.* 1996
Glucosinolates	*Brassica napus*	Massive increase	Jensen *et al.* 1996
Chinolizidin alkaloids	*Lupinus angustifolius*	Strong increase	Christiansenal. 1997
Cyanogenic glucosides	*Eucalyptus cladocalyx*	Strong increase	Woodrow *et al.* 2002
Trigonelline	*Glycine max*	Strong increase	Cho *et al.* 2003
Cyanogenic glucosides	*Manihot esculenta*	Strong increase	Okogbenin *et al.* 2003
Morphine alkaloids	*Papaver somniferum*	Strong increase	Szabó *et al.* 2003
Ajmalicine alkalod	*Catharanthus roseus*	Significant increase	Jalil *et al.* 2007
c-Aminobutyrate (GABA) and trigonelline	*Pisum sativum*	Significant increase	Charlton *et al.* 2008
Ajmalicine alkalod	*Catharanthus roseus*	Significant increase	Jalil *et al.* 2008
(Ergot alkaloids) ergonovine and ergine	*Achnatherum inebrians*	Significant increase	Zhang *et al.* 2011

the basis of total biomass of the plants, the apparent increase in tropane alkaloids was fully compensated with the decrease of plant biomass. According to de Abreu and Mazzafera (2005), water stress resulted in a reallocation of carbon in order to increase the levels of total amounts of secondary products in the leaves that led to reduction in growth of water-stressed plants of *Hypericum brasiliense*. According to Tang *et al.* (1995), the reallocation of photosynthates to secondary plant products under stress must be a part of the evolutionary adaptation.

Plants that suffer from drought stress generate a high amount of reducing power (NADPH + H^+) that seems to enhance the synthesis of highly reduced compounds, like isoprenoids, phenols or alkaloids. Consequently, the synthesis and accumulation of highly reduced secondary metabolites, thus produced, prevents too massive generation of oxygen radicals and the consequent damage of chloroplast by photoinhibition in the MAPs under water stress (Selmar 1992; Radacsi *et al.* 2010). Besides, the secondary compounds have capacity to scavenge reactive oxygen species (ROS) (Dixion and Paiva 1995). In fact, the secondary compounds e.g. phenylpropanoid derived phenols, flavanoids, tannins, and hydroxycinnamate esters, produced by environmental stresses, are important radical scavengers. Accordingly, Zobayed *et al.* (2007) found that the leaf tissues of St. John's wort (*Hypericum perforatum*) plants under water stress condition had a significantly higher capacity to detoxify oxygen radicals with an about 2.5-fold increase over the antioxidant potential of the leaves of non-treated (control) or recovered plants. Besides, the spices derived from plants grown under Mediterranean or semi-arid climate conditions are much more pronounced in taste and aroma than those obtained from the same plants, but cultivated in a moderate climate, advocating the accumulation of enhanced secondary plant products under water deficit. However, significant reduction in plant biomass must be taken into consideration while using a moderate water deficit for quality improvement of spice and medicinal plants. 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 (**Tables 1A, 1B**).

EFFECT OF DROUGHT STRESS ON NITRATE REDUCTASE ACTIVITY OF MAPs

In situations of water deprivation, maximal foliar extractable nitrate reductase (NR) activity has been found to decrease in various plants (Bardzik *et al.* 1971; Shaner and Boyer 1976; Heuer *et al.* 1979; Khanna-Chopra *et al.* 1980; Aparicio-Tejo and Sánchez-Díaz 1982; Smirnoff *et al.* 1985; Pandey and Agarwal 1998; da Silveira *et al.* 2001; Azedo-Silva *et al.* 2004; Krečk *et al.* 2005; Bertamini *et al.* 2006; Sivaramakrishnan *et al.* 2006; Krček *et al.* 2008). However, the references concerning the MAPs are almost nil in this regard. Post-translational regulation of NR activity is superimposed on the regulation of NR transcript accumulation (Melzer and O'Leary 1987). Imposing water stress on seedlings of maize (*Zea mays*), Bardzik *et al.* (1971) observed that the level of NR activity was a consequence of equilibrium between the rates of synthesis and degradation of the enzyme. Progressive tissue dehydration reduced both, the enzyme synthesis and the enzyme-inactivating systems. Inhibition of NR activity in wheat (*Triticum aestivum*) was ascribed to unavailability of substrate of the enzyme (nitrate) or to reduced rate of enzyme synthesis under water stress (Heuer *et al.* 1979). According to Correia *et al.* (2005), NR activity in the leaves and roots of sunflower was linearly correlated with the depletion of nitrate, while in white lupin the enzyme activity was independent of tissue nitrate concentration. Azedo-Silva *et al.* (2004) noticed that the concentration of nitrate in roots, xylem and leaves decreased in water-stressed plants of *Helianthus annus* and drought-induced decrease in NR activity was correlated with the observed changes in nitrate concentration in roots. However, a higher decrease in foliar NR activity was ascribed to the decline in nitrate flux to the leaves and not to the decreased leaf nitrate content. Diouf *et al.* (2004) observed an increase in tissue nitrate concentration in pearl millet (*Pennisetum typhoides*) under water deficit conditions and, hence, argued that the reduction in NR activity was probably not due to limited nitrate content. According to Shaner and John Boyer (1976), regulation of NR activity under water stress was due to nitrate flux and not due to nitrate content in the leaves of *Zea mays*. In seedlings that were desiccated slowly, the nitrate flux, leaf nitrate content, and NR activity decreased as the LWP decreased. The decrease in nitrate flux was ascribed to a decrease in the rate of transpiration as well as to the rate of nitrate delivery into the transpiration stream. They argued that the synthesis of NR could be increased at low LWP when seedlings were desiccated in the presence of additional nitrate, which increased the nitrate flux to the leaves. Krček *et al.* (2008) investigated the effect of drought stress and N fertilization on barley (*Hordeum vulgare* L.). Activity of NR was significantly higher when plants were grown under optimum water regime than under drought stress conditions. There was a similar situation when plants were fertilized with nitrogen compared to unfertilized control both under optimum water regime and drought stress. In an experiment conducted on barley (*Hordeum vulgare* L.) by Krečk *et al.* (2005), NR activity was significantly higher under optimal water regime than in drought stress treatments. Higher rates of applied nitrogen fertilization alleviated the adverse effect of drought stress, including the changes in NR activity. The most drought stress sensitive growth stage appeared to be shooting where N-fertilization could not stimulate NR activity significantly. Correia *et al.* (2005) investigated that foliar NR activity was negatively affected by soil drying as well as by decreased supply of nutrients in sunflower (*Helianthus annuus* L) and white lupin (*Lupinus albus* L.). Smirnoff *et al.* (1985) observed in field-grown barley (*Hordeum vulgare*) and durum wheat (*Triticum durum*) that NR activity was the highest in the plants growing with an ample N supply irrespective of level of water stress. Khanna-Chopra *et al.* (1980) emphasized the role of K nutrition under water stress, reporting a significant K-mediated increase in NR activity and other physiological parameters in *Zea mays.* Thus, applied nitrogen fertilization, particularly higher rate of N application, could alleviate the adverse effect of applied drought stress, including the changes in NR activity.

With regard to MAPs, a study was carried out to determine the effect of drought stress on NR activity and to see if the maintenance of NR activity under water stress conditions might be a factor involved in the drought tolerance of *Lactuca sativa* L. Drought stress decreased the NR activity of water-stressed plants compared to control plants. It was suggested that such an effect on NR activity might be a factor in the drought tolerance of lettuce (Ruiz-Lozano and Azcón 1996). Besides, Singh *et al.* (2001) investigated the effect of 6-benzyladenine (BA) and ascorbic acid (AA) on NR activity under sufficient water supply and moisture stress employing senna (*Cassia angustifolia* Vahl.) plants at seedling, vegetative, flowering and pod formation stages. NR activation state and maximal extractable NR activity declined rapidly in response to drought stress.

EFFECT OF DROUGHT STRESS ON PROLINE ACCUMULATION IN MAPs

Drought stress results in an increase of free proline (Pro) biosynthesis rate. Water deficits might encourage dramatic increases in the Pro concentration of phloem sap of the MAPs (*Trifolium repens*), suggesting that increased deposition of Pro in water stressed plants could in part occur via phloem transport. The increase in proline concentrations in phloem exudates was closely related to reductions in NR activity in the roots, N uptake, and the assimilation of newly absorbed N, indicating that increased proline transport to roots via phloem caused by water deficit had a significant influence on the down-regulation of N uptake and the assimilation of newly absorbed N (Lee *et al.* 2009). A Pro transporter gene, ProT2, is strongly induced by water and salt stress in *Arabidopsis thaliana* (Rentsch *et al.* 1996). Ketchum *et al.* (1991) suggested that translation but not transcription is necessary for production of Pro in stressed cells. Stress-hypersensitive mutants of MAPs exhibited disturbed Pro metabolism that could contribute significantly to the elucidation of the signals to which Pro accumulation might respond. Petunias (*Petunia hybrida* cv. 'Mitchell') accumulated Pro under drought-stress conditions (Yamada *et al.* 2005). Khalid (2006) found significant increase in proline concentration in the leaves of *Ocimum* species (*Ocimum basilicum and O. americanum*) under water stress. Similarly, Alishah *et al.* (2006) also demonstrated drought-induced Pro accumulation in the leaves of basil (*O. basilicum*) During water stress, there were found alterations in the metabolism of Pro in cassava (*Manihot esculenta*), and the extent of alteration varied between drought-susceptible and tolerant cultivars (Sundaresan and Sudhakaran 2006). A study was conducted to determine the response of date palm (*Phoenix dactylifera* L. cv. 'Barhee' and 'Hillali') calli to water stress. After 2 weeks, Pro accumulation was assessed. Increasing PEG concentration was also associated with a progressive reduction in water content and increased content of endogenous Pro (Al-Khayri and Al-Bahrany 2004). A pretreatment of choline chloride (CC) accelerated the accumulation of Pro in *Rehmannia glutinosa* seedlings during drought stress and retarded the drop in Pro concentration after dewatering. The amount of 2.1 mM of CC was found suitable for promoting Pro accumulation in *R. glutinosa* seedlings under drought stress (Zhao *et al.* 2007). Seedlings of two genotypes of *Coffea arabica* (Catuai and BA10C1110-10), with different drought tolerance levels, were subjected to controlled water stress. Pro accumulation seemed to be related to injury imposed by water stress (Mazzafera and Teixeira 1989). Aliabadi *et al.* (2008) investigated the effects of arbuscular mycorrhizal fungi, different levels of phosphorus and drought stress on Pro accumulation rate of coriander (*Coriandrum sativum* L.). Their results exhibited that drought stress had significant enhancing effect on Pro accumulation rate and the highest Pro accumulation rate was achieved under stress conditions. Also, Baher *et al.* (2002) reported enhanced Pro accumulation in *Satureja hortensis* L. under drought stress. Conclusively, the above discussion demonstrates that proline accumulation increases under drought conditions in MAPs, in general.

ALLEVIATION OF WATER STRESS BY MINERAL NUTRITION IN MAPs

Water-stress can alter the oxidative balance of cells and acclimation to drought is generally correlated with keeping the level of ROS relatively low through the antioxidant system (Dat *et al.* 2000). A number of earlier investigations have suggested that oxidative stress plays an important role in the synthesis of secondary metabolites in plants (Shohael *et al.* 2006). For example, Ali *et al.* (2005) suggested that inhibition of membrane damage in ginseng (*Panax ginseng*) might be associated with the induction of ginsenoside production which might protect plants from oxidative damage. Similarly, de Abreu and Mazzafera (2005) suggested that an increase in phenolic compounds and betulinic acid in *Hypericum brasiliense* plants, stressed by drought and hypoxia, might represent an antioxidant response to ROS production. The observation that saikosaponins have the ability to eliminate ROS and prevent peroxidation of biomembranes (Yokozawa *et al.* 1997; Liu *et al.* 2005) suggests that the accumulation of saikosaponins under water-stress conditions may be an important part of the complex antioxidant system.

In spite of the fact that water deficit adversely affects the plant growth and biomass, exposure of plants to water-stress is known to increase the amount of secondary metabolites in a wide variety of plant species, including saikosaponin a, c and d in *Bupleurum falcatum* L. (Minami and Sugino 1995), Chlorogenic acid, catechin, and (-)-epicatechin in *Crataegus* spp. (Kirakosyan *et al.* 2004) and hypericin, betulinic acid, pseudohypericin, and rutin in *Hypericum* spp. (de Abreu and Mazzafera 2005; Zobayed *et al.* 2005). However, several studies have demonstrated that application of suitable fertilizers mitigated the detrimental effect of drought regading biomass yield (Graciano *et al.* 2005; Ram *et al.* 2006). In fact, good soil fertility increases the ability of plants to maintain relatively high levels of growth, stomatal conductance, and photosynthesis under drought conditions (Kleiner *et al.* 1992). Information about the effect of drought-stress and fertilization on medicinal plants is crucial for the development of crop management strategies, especially in arid and semi-arid regions. However, relatively little is known about this topic.

In general, drought stress reduces uptake of nutrients by the roots and their transport from roots to shoots because of restricted transpiration rates, impaired active transport and poor membrane permeability (Alam 1999). Hence, study of plant mineral nutrients relations is required to understand the effect of nutrients on plants under abiotic stresses. Steady supply of mineral nutrients *via* the roots is restricted under drought situations because of a negative effect of water stress on nutrient availability to plants. That plant nutrition may contribute to drought tolerance and increase in plant productivity under water stress has been suggested by Cakmak (2005). An ameliorative role of nutrient supply under water stress has clearly been demonstrated regarding faba bean (*Vicia faba*) in terms of plant growth, photosynthesis, productivity, and seed yield (Alderfasi and Alghamdi 2010). In the present review, ameliorative role of mineral nutrients (N, P, K and Ca) under water stress has been discussed in general, giving emphasis on medicinal and aromatic plants.

Nitrogen

Nitrogen (N) is an essential macronutrient for plants. It is immensely required for growth and development of MAPs (Hassan *et al.* 2009; Rahimi *et al.* 2009; Manukyan 2011). N is structural component of a number of genetic and metabolic compounds in plants (Tisdale and Nelson 1975; Hassan *et al.* 2005). N constitutes 80% of the total nutrients absorbed by plant roots (Marschner 1995). N absorption and utilization by plants under water stress is very critical for plant growth and productivity. N affects carbon partitioning and it improves accumulation of soluble sugars and starch, which, in turn, improve leaf growth (Rufty *et al.* 1988). Under a limit, N application increases antioxidative defense mechanisms in plants (Marschner 1995), resulting in reduced photooxidation of chloroplast pigments and leaf-senescence. Available N in soil is closely related to the ability of plant roots to absorb water from soil. However a number of soils are N-deficient in arid and semi arid regions (Hernández *et al.* 1997) that may render the plants more susceptible to drought stress occurring in these regions. Under water stress, closure of stomata causes a decrease in transpiration resulting in reduction in water transport through the plant; that, in turn, affects the ability of roots to absorb water and nutrients from the soil (Waraich *et al.* 2011). Drought-induced N deficiency largely inhibits plant growth under water deficit (Heckathorn *et al.* 1997) by decreasing the leaf size owing to decreased cell number and size (MacAdam *et al.* 1989). Impaired N metabolism in wheat genotypes was ascribed to increased RNAse activity and the reduction in protein and RNA contents under water stress (Martin and da Silva 1972). There have been noted changes in the enzymes associated with NO_3 assimilation in plants under water stress conditions (Larsson *et al.* 1989; Kaiser and Brendle-Behnisch 1991; Kenis *et al.* 1994; Brewitz *et al.* 1996). For example, NR, the starter enzyme of N metabolism in plants, was decreased in water-stressed leaves and of sunflower (Azedo-Silva *et al.* 2004). Water stress also adversely affected the NR activity in roots of sunflower (Azedo-Silva *et al.* 2004) and wheat (Larsson *et al.* 1989). In *Helianthus annuus* L. and *Lupinus albus* L., the soil water deficit decreased the NR activity because of decreased supply of nutrients, and the observed changes in NR activity were linearly correlated with the depletion of nitrate in the substrate (Correia *et al.* 2005). On the other hand, no effect of water stress was recorded on NR activity of maize roots (Baki *et al.* 2000). Nonetheless, increased N application to water-stressed plants exhibited improved nitrate uptake and enhanced NR activity in wheat leaves (Kathju *et al.* 1990). In fact, inorganic fertilization has been reported to mitigate the adverse effects of water stress on crop growth and development by several workers (Marschner 1995; Payne *et al.* 1995; Raun and Johnson 1999). Application of 160 kg N ha^{-1} was the best with respect to herbage yield and two components of EO (linalool and linalyl acetate) in Bergamot mint (*Mentha citrata* Ehrh) at a water deficit of 1.2 IW: CPE ratio (irrigation water: cumulative pan evaporation ratio). Higher N fertilization (240 kg N ha^{-1}) favored the synthesis of linalool, a major constituent of EO during the first harvest of the crop (Ram *et al.* 1995). Farahani *et al.* (2008a) reported that application 60 kg N ha^{-1} to calendula (*Calendula officinalis* L) plants under drought stress increased the EO percentage, but oil yield of calendula decreased in these conditions. Said-Al Ahl *et al.* (2009) recorded significant increase in the content and yield of essential oil of oregano (*Origanum majorana*) as a result of positive interaction of drought stress and N fertilization.

N nutrition has been reported to improve yield and quality of MAPs. Waraich *et al.* (2011) suggested that the detrimental effects of water stress might be minimized by improving water use efficiency in plants employing N nutrition. Patel *et al.* (2000) reported gain of potential production of fennel (*Foeniculum vulgare* Mill.) under water deficit using 90 kg N and 30 kg P_2O_5 ha^{-1}. Mahmoud (2002) observed that the plants of *Grindelia camporum*, fertilized with high amount of NPK exhibited increase in the plant height and dry mass together with yield of flower heads; however, the level of crude resin and percentage of resin acid were higher under lower levels of NPK fertilization. Zhu *et al.* (2009) reported significant increase in the root content of saikosaponin a and d of *Bupleurum chinense* with a concomitant decrease in root biomass under mild water deficit. Total yield of saikosaponin a and d were lower in the water-stressed treatment compared to the well-watered treatment. There was a significant interaction between the water and fertilizer treatments and the negative effect of water-stress on total content of saikosaponin a and d could partly be mitigated through the application of N and P fertilizers. Similarly, N and P fertilizers increased the growth of *Eucalyptus grandis* (Graciano *et al.* 2005), *Mentha arvensis* L. (Ram *et al.* 2006), and maize (*Zea mays* L.) (Moser *et al.* 2006) under water-stress conditions. Singh (1999) reported significantly enhanced herbage and EO yield of geranium (*Pelargonium graveolens*) under water stress using high N fertilizer dose (200 kg N ha^{-1}). Similarly, yield and quality of patchouli (*Pogostemon cablin*) was increased significantly under water stress by the application of high N fertilizer dose along with organic mulch by Singh *et al.* (2002). Baricevic *et al.* (1999) treated the deadly nightshade (*Atropa belladonna*) plants with different water regimes (35-95% depletion of available soil water) together with enhanced nitrogen supply (0.37-1.60 g N pot^{-1}) in a greenhouse experiment. The maximal yield of tropane alkaloids (hyoscyamine: 54 mg $plant^{-1}$ and copolamine: 7 mg $plant^{-1}$) was achieved in plants grown under an optimal irrigation regime (35% depletion of available soil water) accompanied with total nitrogen supply of 0.37 g pot^{-1}. However, the maximal content of alkaloids was achieved with 95% depletion of available soil water and a nitrogen supply of 1.60 g pot^{-1}. In contrast, Singh (1999) noticed no significant effect of irrigation regimes and nitrogen rates on the content and quality of EO of lemongrass (*Cymbopogon flexuous*). Application of N fertilizer significantly increased the EO percentage and yield, seed yield, head diameter, 1000-seed weight and number of seeds in heads per plants in calendula (*Calendula officinalis* L.) both under unstressed and water stress conditions. In addition, the application of N fertilizer resulted in enhanced photosynthesis and improved chlorophyll production together with elevated development of roots under water stress (Rahmani *et al.* 2009). According to Colling *et al.* (2010), changing the water content of the growing medium through polyethylene glycol (induced by 3%, w/v PEG 6000) had a little or no impact on the accumulation of canavanine in cultures of *Sutherlandia frutescens*. This was in contrast to the effect of water deficit induced by 3%, w/v of PEG 8000 on *in vitro Canavalia ensiformis* callus cultures (Ramírez *et al.* 1992). Such a superior capacity for canavanine production was ascribed to limited water supply, and to species-specific response (Colling *et al.* 2010). Nitrogen supplementation increased the canavanine synthesis, suggesting that mineral nutrition is more important for increasing canavanine than water and salinity stress.

N and P fertilizer increased the growth of *Eucalyptus grandis* (Graciano *et al.* 2005), *Mentha arvensis* L. (Ram *et al.* 2006), and maize (*Zea mays* L.) (Moser *et al.* 2006) under water-stress conditions. In fact good soil fertility increased the ability of plants to maintain relatively high levels of growth, stomatal conductance, and photosynthesis under drought conditions (Kleiner *et al.* 1992). From a practical point of view, these results highlight the need for appropriate amounts of N and P fertilizer in the cultivation of *B. chinense* in arid and semi-arid regions. The results are similar to those of Minami and Sugino (1995) who reported that one month of water-stress resulted in a significant increase in the saikosaponin a, c and d contents of the cork layer and surrounding tissues of *B. falcutum*. Water-stress can alter the oxidative balance of cells and acclimation to drought is generally correlated with keeping the level of ROS relatively low through the antioxidant system (Dat *et al.* 2000). A number of earlier investigations have suggested that oxidative stress plays an important role in the synthesis of secondary metabolites in plants. According to, Ali *et al.* (2005), inhibition of membrane damage in Asian ginseng and American ginseng may be associated with the induction of ginsenoside production which protects plants from oxidative damage. Similarly, an increase in phenolic compounds and betulinic acid in *Hypericum brasiliense* plants stressed by drought and hypoxia was ascribed to an antioxidant response plants to ROS production (de Abreu and Mazzafera 2005). The observation that saikosaponins have the ability to eliminate ROS and to prevent peroxidation of biomembranes (Yokozawa *et al.* 1997; Liu *et al.* 2005) suggests that the accumulation of saikosaponins under water-stress conditions may be an important part of the complex antioxidant system.

Phosphorus

Phosphate (P) is the major element involved in energy metabolism of plants. The MAPs require this important nutrient for proper growth and EO production (Saharkhiz *et al.* 2011). It is important constituent of ATP (Adenosine triphosphate) that is required for energy interconversion in plant metabolism (Palta 2000). Plant phosphate levels are usually low in dry-soil conditions due to impaired P uptake by roots and, therefore, needs to be replenished under drought stress conditions (Waraich *et al.* 2011). P deficiency causes reduction in stomatal conductance and regeneration capacity of ribulose 1,5 bisphosphate (RuBP) that, in turn, results in reduced photosynthetic rate (Brooks 1986). Impaired photosynthetic rate due to P deficiency results in diminished relative leaf-growth rate (Kirschbaum and Tompkins 1990). The starch is accumulated in leaves under P limited condition because photosynthates are not utilized for plant growth (Fredeen *et al.* 1989). P deficiency also reduces nitrate uptake and its assimilation by nitrate reductase (Pilbeam *et al.* 1993). Since P is a constituent of nucleic acids, phospholipids, phosphor-proteins, dinucleotides and ATP, P limitation hinders the processes required for storage and transfer of energy, photosynthesis, regulation of enzymes and the transport of carbohydrates (Hu and Schmidhalter 2001). Uptake of P by crop plants is generally reduced in dry-soil conditions (Pinkerton and Simpson 1986). Translocation of P to the shoots is severely restricted even under relatively mild drought stress (Rasnick 1970). The application of P fertilizer can improve plant growth considerably under drought conditions (Ackerson 1985; Studer 1993; Garg *et al.* 2004). The ameliorative effects of P on plant growth under drought have been attributed to an increase in stomatal conductance (Brück *et al.* 2000), photosynthesis (Ackerson 1985), higher cell-membrane stability, improved plant water relation parameters and elevated drought tolerance (Sawwan *et al.* 2000). P uptake has been reported to be improved using mycorrhiza that enhances plant growth under water deficit by increasing the uptake of not only of P but also of micronutrients such as Zn, Cu, Mn, and Fe (Bagayoko *et al.* 2000). P improves the root growth and maintains high LWP under water deficit. In turn, the improved root growth results in improved water and nutrient uptake leading to enhanced NR activity and better assimilation of nitrate under drought condition. P has been reported to increase leaf relative water content in wheat (Basak and Dravid 1997) and cherry (Centritto *et al.* 1999) under water stress. Similarly, P treatment led to improve LWP in water stressed chickpea (Gupta *et al.* 1995). By maintaining the high leaf water potential, P maintains the cell turgor that, in turn, increases the stomatal conductance and photosynthetic rate under drought (Waraich *et al.* 2011). Future strategies for increasing P uptake might include overexpression of genes encoding for high-affinity P transporters, especially for the P-deficient soils of the semi-arid tropics (Smith 2002). As far as MAPs are concerned, reports are meager revealing the ameliorative role of P under water stress. Shubhra *et al.* (2004) reported the positive role of P in alleviation of the deleterious effects of water deficit in clusterbean (*Cyamopsis tetragonoloba* L.) in terms of relative water content, chlorophyll content, and soluble sugars content in leaves at vegetative, flowering and pod-filling stages. P application also enhanced the seed-gum content of water stressed plants recorded at harvest. Bhadoria *et al.* (1997) and Garg *et al.* (1998) also reported enhanced synthesis of polysaccharide in the seed of clusterbean under unstressed as well as water stressed conditions. According to Farahani *et al.* (2008b), application of P together with arbuscular mycorrhizal fungi (AMF) resulted in maximum level of EO yield, biological yield, shoot P content, root yield and seed yield of coriander (*Coriandrum sativum* L.) under water stress. Similar results were obtained by Saharkhiz *et al.* (2011) in basil (*Ocimum sanctum*) under irrigated conditions. An improved EO percentage in flowering shoot was achieved at 35 kg P ha^{-1}. In addition, the highest dose of P (70 kg ha^{-1}) applied with AMF improved water and P uptake from the soil and helped maintain the accumulation of dry matter in plants under water stress. Application of P (150 kg P ha^{-1}) significantly increased the EO content as well as the contents of camphor and chrysanthenyl-acetate in feverfew (*Tanacetum parthenium* L.) when applied under severe water deficit, while irrigation treatments alone did not change the EO content and/or EO components (Saharkhiz and Omidbaigi 2008). Jain and Gupta (2005) reported that application of 40 kg P_2O_5 ha^{-1} enhanced the EO and protein content in the seed of fenugreek (*Trigonella foenumgraecum*) under mild water deficit, while under severe water deficit 40 kg P_2O_5 ha^{-1} increased the EO content with a concomitant decrease in seed protein content. According to Said-Al Ahl and Abdou (2009), the yield of fresh herb and EO of dragonhead (*Dracocephalum moldavica* L.) was significantly lowered with the rise in water stress levels. However, fresh herb and EO yields increased significantly with an increase in P application at a higher dose. But, EO percentage increased with increase in moisture and P levels. The maximum value of herb fresh yield and EO content were obtained from plants irrigated with 80% available soil moisture (ASM) combined with P fertilizer applied at 1.6 g pot^{-1}. The highest content of geranial (26.73%), geraniol (45.98%) and geranyl acetate (87.45%) was obtained due to 40% ASM combined with 0.8 g pot^{-1}, 85% ASM alone and 60% ASM combined with 1.6 g pot^{-1}, respectively.

Potassium

Potassium (K) is essential for many physiological processes, such as photosynthesis, translocation of photosynthates into sink organs, maintenance of turgor, functioning of stomata and activation of several enzymes (Marschner 1995; Mengel and Kirkby 2001; Taiz and Zeiger 2006). Adequate soil moisture influences K uptake by plants by stimulating root growth and K diffusion towards the root in the soil (Kafkafi 1990). The plants suffering from environmental stresses have a larger internal requirement for K because of sufficient K being unavailable to plants under stress (Marschner 1995; Cakmak and Engels 1999; Cakmak 2005). Hence, plenty supply of K helps to reduce crop stress caused by drought, chilling, high light intensity, heat and deficiencies of other nutrients (Kant and Kafkafi 2002; Cakmak 2005). Combined effects of low temperatures and low soil moisture were alleviated by increasing the concentration of K^+ in the soil (Kafkafi 1990). Further, increased application of K has been shown to enhance photosynthetic rate, plant growth, and yield in different crops under water stress conditions (Sharma *et al.* 1996; Tiwari *et al.* 1998; Yadav *et al.* 1999; Egilla *et al.* 2001). K-fed plants maintained higher LWP, lower osmotic potential, greater turgor potential and improved relative water content as compared to the untreated plants in *Vigna radiata* (Nandwal *et al.* 1998), maize (Premachandra *et al.* 1991), and wheat (Pier and Berkowitz 1987; Sen Gupta *et al.* 1989) grown under water stress. Root nodulation, nitrogenase activity and dry matter yield increased with increment of K supply in broad bean grown at moisture level of only 1/4 of the field capacity (Abd-Alla and Wahab 1995). K is predominant osmolyte accumulated in drought-stressed tropical grasses (Ford and Wilson 1981), soybean (Itoh and Kumura 1987), maize (Premachandra *et al.* 1991), chickpea (Khanna-Chopra *et al.* 1994; Moinuddin and Imas 2007) and wheat (Damon *et al.* 2011), contributing significantly to osmotic adjustment (OA), a well known drought tolerance mechanism in plants (Morgan 1984; Moinuddin and Khanna-Chopra 2004; Moinuddin *et al.* 2005). When K^+ is deficient, the stomata cannot function properly and water losses from plant may reach damaging levels (Gething 1990). This effect of drought can be more severe when plants are grown with inadequate supply of K, as K itself is required for stomatal movement (Humble and Raschke 1971). The closure of stomata in response to water stress also reduces the carboxylation efficiency of the chloroplasts. Further, environmental stresses cause oxidative damage to cells by inducing formation of ROS during photosynthesis (Bowler *et al.* 1992; Elstner and Osswald 1994; Foyer *et al.* 1994). Formation of ROS is intensified because of inhibited CO_2 reduction by drought stress. ROS formation under severe drought stress would exert severe oxidative damage to chloroplasts. Consequently, drought-stressed plants exhibit impaired photosynthesis and disturbed carbohydrate metabolism (Seel *et al.* 1991; Quartacci *et al.* 1994; Jiang and Zhang 2002). Under low K supply, drought-induced ROS production might further be enhanced due to K-deficiency-induced disturbances in stomatal opening, plant water relations and photosynthesis (Marschner 1995; Mengel and Kirkby 2001). In addition, chloroplasts lose high amounts of K to further induce further ROS formation and depress photosynthesis under drought conditions (Sen Gupta and Berkowitz 1987; Berkowitz and Kroll 1988). Seemingly, the larger K requirement of water stressed plants might be related to the protective role of K against stress induced photo-oxidative damage (Pier and Berkowitz 1987; Sen Gupta *et al.* 1989). Increases in severity of drought stress might, therefore, result in corresponding increases in K demand to maintain photosynthesis and protect chloroplasts from oxidative damage. Application of more K than that usually applied for irrigated plants is required to maintain photosynthetic activity (Pier and Berkowitz 1987; Sen Gupta *et al.* 1989; Ashraf *et al.* 2002) and adequate amount of photosynthetic pigments in leaves (Ashraf *et al.* 2002; Tuna *et al.* 2010) under water stress. Sangakkara *et al.* (2000) reported substantial removal of harmful effects of drought on photosynthesis as a result of sufficient K supply in legumes. Similarly, decreases in grain yield resulting from restricted irrigation were greatly eliminated by increasing K supply to crops (Hadi *et al.* 1997; Singh and Kuhad 2005). Umar (2006) demonstrated that K fertilization proved helpful in mitigating the adverse effects of water stress on mustard, sorghum and groundnut. The production of above ground biomass, seed yield and relative water content were highly correlated with the tissue K concentration, showing that concentration of K in leaves played a vital role in increasing water stress resistance and stabilizing yield in the crops studied. Baque *et al.* (2006) revealed that yield and yield attributes of wheat were improved due to high level of K (greater than recommended dose) irrespective of the level of soil moisture. Increasing levels of K elevated the uptake of N, P and K in plants and improved the dry matter production in different plant parts under water stress condition. K application improved some essential nutrients in leaves of melon (*Cucumis melo* L.) plants, but the values were still not the same as those in the control. However, additional supply of K to the root zone increased the levels of K and Ca much higher than those at the control treatment, indicating the role of K in drought tolerance of plants (Tuna *et al.* 2010). Significant variation in leaf K concentration was recorded among cotton (*Gossypium hirsutum*) genotypes sampled at flowering and fruiting stages. Stomatal conductance and specific leaf weight were the physiological traits more consistently related to leaf K concentration. Boll production and seed cotton yield was also positively correlated with leaf K concentration in one of the years of experimentation. It was suggested that variation in K uptake might be exploited to improve plant K status and yield of cotton under water-limited environments (López *et al.* 2008). Thus, improvement in K nutritional status of plants might be of great importance to achieve high yields under rain-fed conditions. According to Waraich *et al.* (2011), detrimental effects of drought could be diminished via improving water use efficiency of crop plants by high K nutrition under water deficit. Under water deficit, plants supplied with high K nutrition are more tolerant to water stress than K-deficient plants, because the former may utilize the available soil moisture more efficiently than the latter. In fact, K results in improvement in LWP, relative water content, osmotic potential and turgor of the cells (Lindhauer 1995; Sangakkara *et al.* 1996; Ashraf *et al.* 2002; Tuna *et al.* 2010) and regulates the stomatal functioning (Kant and Kafkafi 2002) under water stress conditions. It enhances photosynthetic rate, plant growth and yield under water stress conditions (Sangakkara *et al.* 1996; Egilla *et al.* 2001; Ashraf *et al.* 2002; Singh and Kuhad 2005; López *et al.* 2008; El-Abady *et al.* 2009; Alderfasi and Refay 2010). Singh and Kuhad (2005) in chickpea (*Cicer arietinum* L.) and El-Abady *et al.* 2009 in wheat (*Triticum aestivum*) demonstrated the positive effect of K application on seed quality under water stress. Additionally, K has been reported to improve nitrogen fixation in leguminous plants under water stress conditions (Sangakkara *et al.* 1996). K maintains a high pH in chloroplast stroma and protects the photosynthetic machinery from the photooxidative damage under water stress (Cakmak 1997). Thus, K application to crops under water stress conditions may improve growth, photosynthesis, nitrogen metabolism, yield and quality of crops under unstressed conditions. Unfortunately, almost no record is available in scientific literature with regard alleviation of drought stress effects by K application in the MAPs. However, K along with N has been reported to increase growth parameters and herb yield of periwinkle (*Catharanthus roseus* G. Don) in irrigated conditions (Hassan *et al.* 2009).

Calcium

Calcium (Ca) has a very prominent role in the maintenance of cell structure as it is important constituent of the cell wall (Taiz and Zeiger 2006). However, with the discovery of calmodulin, it has become clear that Ca is a major controller of plant metabolism and development; it stimulates the plant growth and development under normal as well as stress conditions (Poovaiah and Reddy 2000). The effects of Ca on cell elongation, the senescence process and photosynthetic activity are dependent on its cytosolic concentration, which is governed by the activity of Ca channels in the plasma membrane (Knight 2000). It is unequivocally involved in linking stress perception and evocation of various adaptive cellular responses, as well as in regulating diverse physiological processes, including those affected by abscisic acid (Gong *et al.* 1998). Ca is considered to play important role in mediating stress responses during injury, recovery from injury, and acclimation to stress by activating the plasma membrane enzyme ATPase, which is required to pump back the nutrients lost in cell membrane damage during water stress (Palta 2000). Ca protects the integrity of cell membranes, reduces the membrane permeability and prevents ion leakage caused by environmental stress.

Plant scientists have studied the effects of calcium on growth of plants and production of secondary metabolites regarding several medicinal plants (Lee and Yang 2005; Supanjani *et al.* 2005; Karaivazoglou *et al.* 2007; Dordas 2009; Naeem *et al.* 2009). According to Jaleel *et al.* (2007), application of $CaCl_2$ increased the drought tolerance of *Catharanthus roseus* with favorable changes in oxidative stress, osmoregulation and indole alkaloid accumulation. Further, they reported that *C. roseus* plants grown under water deficit environments without $CaCl_2$ showed increased contents of lipid peroxidation (LPO), H_2O_2, glycinebetaine (GB) and PRO coupled with decreased activity of proline oxidase (PROX) and increased the activity of γ-glutamyl kinase (γ-GK). Application of $CaCl_2$ lowered the PRO concentration in drought-stressed plants while increasing the activity of PROX and decreasing that of γ-GK. Application of $CaCl_2$ appeared to confer osmoprotection to cells owing to its additive role with regard to GB accumulation under drought-stress. The drought-stressed plants of *C. roseus* treated with $CaCl_2$ showed an increase in total content of indole alkaloids in shoots and roots when compared to drought-stressed or well-watered plants with no $CaCl_2$ treatment. Chowdhury and Choudhuri (1986) observed a significant decrease in the relative water content and LWP in two species of jute (*Corchorus capsularis* L. and *C. olitorius* L.) subjected to water stress. Pre-treatment of seeds with 5 m*M* of $CaCl_2$ improved the water uptake capacity of plants without altering the stomatal movement. Further, they observed a greater decrease in the uptake of phosphate (^{32}P) in *C. olitorius* than in *C. capsularis* under water-deficit stress, with Ca application counteracting the adverse effects of drought-stress. Ca may also be involved in drought tolerance of plants because it regulates antioxidant metabolism. Application of Ca considerably increased the fresh weight and RWC of liquorice (*Glycyrrhiza glabra*) cells subjected to 10-days water stress (Li *et al.* 2003). Compared to untreated cells (control), lesser amounts of MDA and H_2O_2 were accumulated in Ca-treated cells in addition to increased activities of CAT, SOD and POD in Ca-treated cells during the water-stress period. Water stress induced oxidative stress in liquorice cells; however, application of external Ca (40 mM L^{-1}) improved it significantly. Li *et al.* (2003) concluded that extracellular Ca might improve the adaptation of liquorice cells to drought stress, mitigating the oxidative stress thereof. Ca-mediated drought tolerance in the MAPs has not yet been reported.

CONCLUSIONS AND FUTURE PROSPECTS

Drought stress is one of the major limitations to the agricultural productivity worldwide, influencing the normal physiology and growth of plants in many ways. One of the major factors responsible for hampered plant growth and productivity under drought stress is the production of ROS in the organelles including chloroplasts, mitochondria and peroxisomes, causing peroxidation of lipids of cellular membranes and degradation of enzyme proteins and nucleic acids. Drought stress inhibits photosynthesis in plants due to stomatal closure and severe damage to chloroplast and photosynthetic apparatus on account of tremendous production of ROS. Further, severe moisture deficits inhibit the activities of enzymes of carbon and nitrogen assimilation and those of ATP synthesis, resulting in severe damage to cellular metabolism and drastic reductions in plant growth.

The research work conducted on the MAPs indicates significant reductions in plant growth and productivity under water deficit. Concerning quality of the MAPs, water stress increases the EO percentage in the plant tissue significantly; however, the absolute EO yield is not increased in water-stressed plants. This is evident by the research work conducted on several MAPs, including palmarosa (*Cymbopogon martinii*), citronella (*Cymbopogon winterianus*), balm (*Melissa officinalis* L.), basil (*Ocimum basilicum* L.), thyme (*Thymus vulgaris*), calendula (*Calendula officinalis*), etc. The assumed increase in percent concentration of essential oil of the water stressed MAPs compared to the unstressed ones was mostly ascribed to reduced growth and biomass of plants under water deficit. Hence, it was suggested to increase plant density in order to increase the total EO yield per unit land area. In one of the investigations, a moderate water deficit significantly increased the EO yield as well as the main EO constituents of *Salvia officinalis*. Accordingly, it was suggested to employ a moderate water deficit level together with a high plant density to increase the total yield of EO and its constituents per unit land area in the MAPs. Similar considerations may be made to enhance the production of several useful secondary metabolites in the MAPs, because the production of the latter follows a similar trend as do the content of EO and its constituents under water deficit.

Increasing evidence suggests that mineral-nutrient status of plants plays a critical role in increasing the plant resistance to water stress. Of the mineral elements, macroelements, such as N, P, K, Ca and Mg, play very important role in this regard as they are required by the plants in large quantities. In fact, these mineral elements have frequently been reported to ameliorate the adverse effects of drought stress substantially, if not completely, with regard to a number of crop plants. As regards the MAPs, there are several reports indicating the amelioration of drought stress effects by supply of mineral nutrients in higher amounts than those required in normal conditions. Most of the references belong to N, P and Ca in this regard. Surprisingly, there is hardly any reference with respect to ameliorative effects of K (as well as of Mg) on the MAPs under water stress; whereas, there are a number of references available in the scientific literature for other crop plants in this connection, particularly regarding K. In future, the research projects need to be undertaken to explore the role of K (as well as of Mg and different micro-elements) in amelioration of drought stress effects regarding the MAPs. Besides, a pile of work is waiting to be conducted to improve the production of EO and its constituents together with that of several useful secondary plant metabolites of the MAPs, using the appropriate amounts and sources of macro- and micro-elements. A lot of agronomical researches also need to be conducted to improve the quality of the MAPs in respect with exploring the relationship between agronomic practices and absorption of mineral nutrients by the MAPs under water deficit that may also require employing various cultivars and genotypes. Apart from the effect of drying soil on the transport of mineral nutrients to plant roots, the adaptive mechanisms related to cellular and whole plant responses to water stress are of prime importance. Hence, a very important aspect of MAPs research, which requires due attention to be paid by the plant scientists, is to explore the details of morphological, physiological and molecular mechanisms with regard to ameliorative effect of the mineral elements under water deficit. The research projects may be undertaken regarding the aforementioned aspects in order to further improve growth, yield and quality of the MAPs.

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