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Review Article

Thiourea: A Molecule with Immense Biological Significance for Plants

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Abstract

Thiourea, also chemically named as *Thiocarbamide*, is a nitrogen and sulfur containing compound. It has three functional groups, amino, imino and thiol, each with important biological roles. Thiourea is being increasingly used to improve plant growth and productivity under normal and stressful conditions. Use of thiourea as seed priming agent, foliar spray or medium supplementation is more effective under environmental stress than under normal conditions. When used as seed pretreatment, thiourea increased the seed germination; while application as foliar spray improved the gas exchange properties and when used as medium supplementation, it improved the root growth and its proliferation. This indicates that thiourea is more effective in the tissues where it is applied. Although to a differential extent, thiourea is effective in improving plant growth and development under drought, salinity, heat stress and heavy metal toxicity. At physiological level, it improves the leaf gas exchange, nutrient acquisition by the root and assimilation thereafter. At biochemical level, exogenously applied thiourea improves the sugar metabolism and enhances the proteins biosynthesis. At molecular level, thiourea application modulates the pattern of gene expression regardless of the stress applied. Signaling of gene expression is a likely mechanism induced by thiourea. In a nutshell, even though considerable advancement has been made in understanding the biological roles of thiourea in modulating different mechanisms in plants, thiourea needs to be explored further for its biological roles in plants than the relevant information available thus far. © 2017 Friends Science Publishers

Keywords: Dormancy; Stress tolerance; Functional groups; Gene expression; Pigments; Plant Biomass; Sugar metabolism; Grain yield

Introduction

Plant development is a complex phenomenon and requires integration of an array of cellular pathways. Sustained cellular division is a fundamental driver in plant life starting from activation of embryo in a germinating seed to the resumption of meristematic activities in the growth apices and in the regions intercalating in the mature tissues (Srivastava, 2002; Taiz *et al.*, 2015). In addition to acquisition of nutrients from the soil and carbon fixation, the growth is strongly dependent upon the growth hormones. Produced in micro quantities, the hormones regulate the normal plant growth. However, under less than optimum conditions, production of growth promoting hormones in requisite amounts is jeopardized; the expression of negative regulators of growth is increased through the deployment of signaling mechanisms (Verma *et al.*, 2016). Under such conditions, the exogenous supply of plant growth promoting substances becomes imperative.

Traditionally, there are five classes of naturally occurring plant growth hormones. Auxins, gibberellins and cytokinins are growth promoters while ethylene and abscisic acid are growth inhibitors. In addition, the synthesis of jasmonates, vitamins, phenolics, isoprenoids, alkaloids, steroidal compounds and polyamines also play their specific roles in the plant growth regulation (Srivastava, 2002; Buchanan *et al.*, 2015; Taiz *et al.*, 2015). Lack of synthesis of natural growth regulators due to certain reasons leads to visual decline in plant growth and under such circumstances provokes the exogenous supply of growth promoting substances.

In addition to naturally occurring plant growth regulators, an array of synthetic compounds has been tested for their growth-regulatory properties with great success. For instance, synthetic auxins (e.g., 2, 4-dichlorophenoxyactic acid, nephthalene actic acid etc.), cytokinins (e.g., indole butyric acid), thiourea, hydrogen peroxide etc., have been successfully used to improve plant growth under normal or subversive conditions (Gianfagna, 1987; Wahid *et al.*, 2007; Pandey *et al.*, 2013). There are quite a few nitrogen containing growth regulating substances, such as thiourea, that have specifically proven worthwhile in improving crop growth and productivity (Farooq *et al.*, 2009; Perveen *et al.*, 2016). This is attributed to the fact that, in addition to growth-regulatory roles, these compounds are metabolized and provide as a source of nitrogen nutrition (Perveen *et al.*, 2015).

Thiourea is a nitrogen and sulfur containing compound

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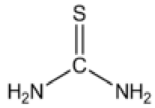
and is being increasing explored for its growth promotion role in plant biology under different environmental perturbations. Ever since thiourea has been known as stimulator of germination by reliever of seed and buds from dormancy (Mayer, 1956; Liacos and Nord, 1961; Esashi and Katoh, 1977). Although at a slower pace, research on exploring the possible morphological, physiological and molecular mechanisms of thiourea remained of interest to the plant biologists. More recent studies have explored the involvement of thiourea in the modulation of gene expression and induction of signaling mechanisms both under normal or stressful conditions (Srivastava *et al.*, 2010a, b). Despite all that no comprehensive review is thus far available in literature on the possible role of this very important organic compound in plant biology. This review covers an account of available data on the physiological and molecular roles of thiourea in improving plant grown under normal and stressful conditions.

Molecular Properties of Thiourea

According to International Union of Pure and Applied Chemistry (IUPAC), *Thiocarbamide* is the alternate name of *Thiourea*. With a molecular weight of 76.12 g/mol, thiourea molecule is made of four elements carbon (15.77%), hydrogen (5.31%), nitrogen (36.81%) and sulfur (42.11%). Oxygen in the urea molecule is replaced with sulfur to make thiourea molecule. This replacement makes the properties of thiourea substantially different from urea. It is sparingly soluble in water with a solubility of 142 g/L at 25ºC.



Two main functional groups in thiourea are thiol (–SH) and amino (–NH_2) groups, which make it a physiologically more important molecule (Jocelyn, 1972; Sahu *et al.*, 2005). The thiol group helps in the stabilization of chemistry of group proteins (Torchinskii, 1974). Moreover, thiol group can scavenge the reactive oxygen species in living systems (Robak and Marcinkiewicz, 1995). The amino (–NH_2) group acts as a base because it has a lone pair of electrons. It gives specific properties to the compounds possessing it (Nelson and Cox, 2012). As far as the mode of action of thiourea is concerned, in animal system it inhibits the peroxidase activity in thyroid gland and inhibits the thyroid production. However, most of the intake amount is excreted unchanged via the kidneys (Gupta, 2012). However, in *Chlorella* the saturation of the thiourea occurred at 5 µM, and there is very limited metabolism of thiourea in the alga (Syrett and Bekheet, 1977). Recent studies tend to unfold the possibility of biochemical and molecular mechanisms triggered by thiourea in plants under control of growth limiting environments (Srivastava *et al.*, 2011, 2017; Seif El-Yazal and Rady, 2013).

Role of Thiourea in Plant Biology

In plant biological pursuits, the effects of thiourea have been implicated on many aspects. Thiourea enhances growth in many plant species irrespective of the growth stage at which it is applied (Table 1). Thiourea has long been known to break innate or environmentally imposed seed and bud dormancy (Chang and Sung, 2000; El-Keblawy, 2013). It has been used as seed pretreatment, foliar spray and medium supplementation, although there are great differences in the levels of exogenous application in different application modes (Aldasoro *et al.*, 1981; Sahu and Singh, 1995; Burman *et al.*, 2004; Nadeem *et al.*, 2012; Perveen *et al.*, 2016). Nonetheless, irrespective of mode of application, thiourea enhanced the growth of a wide range of plant species (Table 1). However, the application of thiourea to environmentally stressed plants is more effective than its application to plants grown under normal conditions (Table 2).

Initially considered as growth stimulant in breaking bud dormancy and increasing crop yields, the thiourea is now known to have great roles in oxidative stress tolerance and modulation of gene expression and regulation and induction of signaling mechanisms (Ratnakumar *et al.*, 2016). In dormant seeds of cocklebur, the primary influence of thiourea was on the axial growth (increase in fresh weight and ethylene production) when applied at 100 mM concentration rather than cotyledonary growth (Esashi and Katoh, 1977). The dormancy breaking effect of thiourea is related to its growth enhancing property *in vivo* (Germchi *et al.*, 2010, 2011) or *in vitro* (Ikram *et al.*, 2014). There are a range of cellular mechanisms induced by thiourea under normal or adverse conditions (Table 3).

Seed Dormancy Break and Promotion of Germination

Seed dormancy is mainly due to inability of embryonic tissues to emerge out through the seed coat. This may be due to either hardness of the seed coat, presence of germination inhibitors (seed coat-enhanced or physiological dormancy) or dead embryo (embryo-enhanced dormancy). In the latter case, the seed is unable to germinate at all, while the seed coat related dormancy, whether innate or environmentally induced, can be broken by various means (Baskin and Baskin, 1998; Table 1). Nitrogenous compounds, like nitrate and thiourea, and growth promoters have been successfully implicated in breaking both the innate and environmentally imposed seed dormancy and promotion of seed germination (Aldasoro *et al.*, 1981; El-Keblawy and Gairola, 2017).

In addition to breaking innate dormancy (El-Keblawy and Gairola, 2017), the seed treatment with thiourea accelerates the seed germination in non-dormant seeds. Such a tendency of thiourea to enhance germination has been well established in glycophytes, halophytes and desert annuals (Table 1) under optimal and less than optimal conditions (Table 2). For instance, in sunflower 10 mg/L thiourea

Table 1: Role of exogenous application of thiourea in improving various attributes in different plant species applied under different application modes

Mode of application	Growth stage	Effective level of thiourea used	Plant species	Parameter studied	Extent of improvement (over control)	Reference
Seed priming	Seed germination	10 mg/L	Sunflower	Days to germination; Final germination percentage	2.41 days earlier start of germination; 60.46% increase in final germination	Wahid *et al.*, 2008
Seed priming	Seed germination	400 mg/L	Wheat	Days to 50% emergence	Reduced by 2.22 days	Chattha *et al.*, 2017
Seed pretreatment	Seed germination	1000 mg/L for 4 h	*Coriandrum sativum*	Days to germination	20.90%	Shanu *et al.*, 2013
Seed soaking	Seed germination	20 µM for 72 h	*Berberis jaeschkeana*	Germination percentage; germination rate; mean germination time	64.28%; 71.90%; 2.67%	Belwal *et al.*, 2015
Seed soaking	Seed germination	5 mM	Dormant seeds of 16 desert annuals	Final germination percentage	96.3% in *Anastatica hierochuntica* (Brassicaceae)	El-Keblawy and Gairola, 2017
Minituber treatment	Bud sprouting	1% thiourea for 1 h	Potato	Reduction in no. of days till sprouting; reduction in days to sprout emergence; Increase in tuber weight	Reduced 14 days; Reduced by 9 days; ~48%	Germchi *et al.*, 2011
Tuber dipping	Tuber bud sprouting	500–750 mM	Potato	Tuber yield	20%	Mani *et al.*, 2012
Seed soaking	Vegetative and flowering stages	500 ppm	Cowpea	Grain yield	26%	Anitha *et al.*, 2004
Foliar spray	Five weeks before anticipated bud break	2–5% aqueous solution	Grape vines	Bud break; Fruitful shoot	6.81–11.41%; 4.88–8.33%	Hopping, 1977
Foliar spray	Two times prior to bud formation	10%	Pear tree	Days to bud break; Final fruit set; Fruit yield/plant	8 days earlier; 62.15% 86.92%	Jana and Das, 2014
Foliar spray	Advanced growth stages	500 mg/L at pre-flowering and flower initiation stage	Lentil	Grain yield	20%	Singh and Singh, 2017
Foliar spray	Flower initiation	0.05%	Mustard	Grain yield	8.9%	Sardana *et al.*, 2008
Foliar spray	Vegetative and flowering stages	1000 mg/L	Coriander	Nitrogen; Potassium; Seed yield; Straw yield	~26%; ~26%; ~25%; ~26%	Balai and Keshwa, 2011
Foliar spray	Tillering + flowering stages	0.5 + 0.5 kg/ha	Wheat	Grain yield	23.9%	Sahu and Singh, 1995
Foliar spray	Silky and Milky stages	1500 mg/L	Maize	Chlorophyll a; Chlorophyll b; Carotenoids	18.60 and 11.17%; 38.59 and 36.74%; 27.11 and 30.55%	Amin *et al.*, 2013
Medium supplemented	At harvest	10 kg/ha	Wheat	Grain yield	17.3%	Sahu and Singh, 1995
Medium supplemented	*In vitro* culture	0.1 mg/dm^3; 0.5 mg/dm^3	*Lilium* sp.	No. of bulblet per explant; bulblet fresh weight	47.62%; 52.01%	Kumar *et al.*, 2007
Medium supplementation	*In vitro* culture	400 µM	Maize	Callusing induction; direct shooting; direct rooting	18; 22%; 36%;	Sanaullah *et al.*, 2016

primed achenes germinated 2.41 days earlier while final germination percentage was 60.46% greater than the non-primed achenes (Wahid *et al.*, 2008). Soaking of *Berberis jaeschkeana* seed in 20 µM thiourea for 72 h substantially improved the germination characteristics such as rate, final percentage and mean germination time (Belwal *et al.*, 2015). Likewise, soaking of wheat seeds in 400 mg/L thiourea solution reduced the time to 50% emergence by 2.22 days (Chattha *et al.*, 2017).

The efficiency of thiourea in improving seed germination under stress conditions was even more impressive. Quite a few studies show that thiourea breaks the environmentally-imposed seed dormancy in plants (Table 2). It breaks the dormancy and overcomes the negative effects of high temperature on seed germination and other developmental cascades both in halophyte (Khan *et al.*, 2002; 2003a, b) and glycophyte (Aldasoro *et al*., 1981; Nadeem *et al.*, 2012). The extent of reduction would, however, depend upon the effective or optimized level of thiourea used and the method of seed treatment. For instance, pretreatment of *Carthimum maritinum* seeds in 10 mM thiourea and germinating in 100 mM NaCl solution increased the final germination percentage and velocity of germination by 61 and 69%, respectively as compared to unpretreated control seeds (Atia *et al.*, 2006). Thiourea seed treatment also showed the potential to overcome salinity-induced dormancy even at lower concentrations in seeds of *Allenrolfea occidentalis* (Gul and Weber, 1998) and under relatively higher salt levels in *Atriplex prostrata* (Khan *et al.*, 2003a) and *Salicorania rubra* (Khan *et al.*, 2003b) seeds. Exposure to 1.3 mM thiourea quite effectively (up to 85%) improved the rate of germination under salt and cold stresses in capsicum seed, while the control seeds could hardly germinate (Yadav *et al.*, 2011).

Table 2: Role of exogenous application of thiourea in improving stress tolerance in different plant species applied under different application modes

Mode of application	Growth stage	Effective level of thiourea used	Stress applied	Plant species	Parameter studied	Maximum improvement under no-stress	Maximum improvement under stress	Reference
Seed treatment	Seed germination	1% for 4 h	Mould incidence (natural growth)	*Cercocarpus* spp.	Germination percentage	60%	Reduction in the spread of mould on the germinating seed	Liacos and Nord, 1961
Seed treatment	Seed germination	0.3%	Seed storage (12 months)	*Ochradenus arabicus*	Seed germination	39.39% (0 months stored)	76.43% (12 months storage)	Nadeem *et al.*, 2012
Seed pretreatment	Seed germination	10 mM	Salt stress (100 mM)	*Crithmum maritimum*	Final germination; velocity of germination	4.11%; -6.23%	~60.5%; ~68.8%	Atia *et al.*, 2006
Seed soaking	Seed germination	500 µg/g for 4 h	Water stress (by withholding water supply)	*Cyamopsis tetragonoloba*	Leaf water potential; net photosynthesis; seed yield	0%; 8.90%; 16.82%	12.68%; 21.55%; 19.21%	Burman *et al.*, 2007
Seed dipping	Seed germination	6.6 mM	Terminal heat stress	Wheat	Chlorophyll; Membrane injury	2.37%; -3.91%	8.43%; -15.69%	Asthir *et al.*, 2013
Seed soaking	Seedling	7 mM	Heat stress	Wheat	Activities of invertases in the shoot and root	~22% (shoot) ~23% (root)	~28% (shoot) ~32% (root)	Asthir *et al.*, 2015
Foliar spray	At anthesis	10 mM	120 mM NaCl	Wheat	Flag leaf net photosynthesis; grain yield per plant	12.08%; 5.65	16.31%; 14.02%	Anjum *et al.*, 2008
Foliar spray	At anthesis	10 mM	Heat stress (7–10ºC above ambient)	Wheat	Flag leaf net photosynthesis; grain yield per plant	12.08%; 5.65	33.08%; 6.50	Anjum *et al.*, 2008
Foliar spray	Seedling (S); Pre-athesis (Pa); Maturity (M)	10 mM	120 mM NaCl	Wheat varieties	Improvement in salinity tolerance threshold	6.85–8.55 dS/m (S); 6.63–9.66 dS/m (Pa); 7.84–9.28 dS/m (M)	7.42–9.62% (S); 7.32–11.16% (Pa); 5.89–10.82% (M)	Anjum, 2008
Foliar spray	Seedling (S); Pre-athesis (Pa); Maturity (M)	10 mM	Heat stress (7–10ºC above ambient)	Wheat varieties	Improvement in heat tolerance (expressed as % decrease over control with 10 mM thiourea)	5.72–9.03% (S); 5.08–12.30% (Pa); 3.69–15.12% (M)	4.73–6.19% (S); 5.12–9.48% (Pa); 5.78–8.41% (M)	Anjum, 2008
Foliar spray at anthesis	Anthesis stage	6.6 mM	Terminal heat stress	Wheat	Plant height; 1000 grain weight	5.37%; 1.91%	8.43%; 5.99%	Asthir *et al.*, 2013
Foliar spray	Vegetative stage	2.5–5.0 mM	Drought stress	Wheat	Antioxidant defense	32%	47.8%	Hassanein *et al.*, 2015
Foliar spray	At vegetative stage (40 and 60 days after sowing)	1000 ppm	Late sowing date	Clusterbean	Seed yield; gum percentage	21.80%; 1.46%	10.58%; 12.08%	Meena and Meena, 2017
Medium supplementation	Seed germination	10 mM for 20 days	400 mM NaCl stress	*Allenrolfea occidentalis*	Germination percentage; Velocity of germination	2.0%; 4.15%	50%; 55%	Gul and Weber, 1998
Medium supplementation	Seed germination	10 mM for 20 days in germination medium	300 mM NaCl stress in germination medium	*Atriplex prostrata*	Germination percentage; Velocity of germination	18%; 10%	60%; 55%	Khan *et al.*, 2003a
Medium supplementation	Seedling stage	0.25 mM	Cd contamination	Maize	Shoot dry weight; root dry weight; net photosynthesis; carotenoids contents	11.78%; 15.23%; 6.93%; 11.11%	13.61%; 15.65%; 15.68%; 14.88%	Perveen *et al.*, 2015
Medium supplementation (*in vitro*)	Seedling stage	10 mM	500 µM Cd stress	Barley	Plant biomass yield	4.63%	20.45%	Ikram and Javed, 2015
Medium supplementation	Seedling stage	400 µM	120 mM NaCl stress	Maize	Shoot dry weight; root dry weight; leaf area	39.26%; 46.77%; 38.64%	28.57%; 36.0%; 52.63%	Sanaullah *et al.*, 2016

The advantage of seed treatment with thiourea was not only confined to germination attributes rather it was carried to advanced growth stages. For example, seeds of *Cyamopsis tetragonoloba* soaked in 500 µg/g thiourea and plants exposed to drought exhibited improvement in leaf water potential (-12.68%), net photosynthesis (21.55%) and seed yield (19.21%) compared to non-soaked plants (Burman *et al.*, 2007). Dipping wheat seeds in 6.6 mM solution of thiourea and exposing the plants to heat stress enhanced the chlorophyll content (2.37%) whilst reducing the membrane injury (3.91%) compared to non-dipped seeds (Asthir *et al.*, 2013). Soaking of wheat seeds in 7 mM thiourea solution and growing the seedlings under heat stress enhanced the activities of invertases in shoot (~22%) and root (23%) as compared to non-stressed plants (Asthir *et al.*, 2015).

In crux, thiourea is an effective chemical agent in releasing the seed mainly from physiological dormancy and promotes the seed germination, but the amount of thiourea application depends upon plant species under study.

The seed treatment of thiourea produces an array of profound physiological changes, which lead to the improved seed germination. The benefits of the release from seed

Table 3: Biochemical and molecular mechanisms of thiourea action in different plant species under normal or stress conditions

Mode of thiourea application	Level of thiourea/stress applied	Plant species	Physiological/Biochemical/molecular mechanism induced	Reference
Seed soaking	6.6 mM	Wheat	Improved Photosystem I and II function and enhanced antioxidant activities	Nathawat *et al.*, 2007
Seed treatment	6.5 mM and 0.3–1 M NaCl for 1 h	*B. juncea*	Coordinated regulation of signaling molecules and regulation of effector mechanism under salinity stress	Srivastava *et al.*, 2010a
Seed treatment	500 ppm	*B. juncea*	Improved mtATPase activity and mitochondria function under NaCl stress	Srivastava *et al.*, 2009
Seed treatment	10 mM + heat stress (10°C higher than control)	Sunflower	Improvement of heat tolerance with the induction of enzymatic and non-enzymatic antioxidants	Akladious *et al.*, 2014
Seed soaking	7 mM	Wheat	Further enhancement in the activities of invertases enzymes due to seed soaking in thiourea	Asthir *et al.*, 2015
Foliar spray	250 g/ha	*B. juncea*	Enhanced source strength, sucrose translocation to the developing seed, increased pod photosynthesis and oil biosynthesis	Pandey *et al.*, 2013
Medium supplementation	6.5 mM + 700 mM NaCl	*B. juncea*	Improved water homeostasis of root under salinity stress with the expression of isoforms of aquaporins (PIPs)	Srivastava *et al.*, 2010b
Medium supplementation	10 mM + 1500 µM Cd (*in vitro*)	Barley	Improved macro- and micronutrients contents and activities of antioxidants	Ikram *et al.*, 2014
Medium supplementation	0.25 mM + 1000 µM Cd	Maize	Possible inactivation of Cd and improved gas exchange properties and chlorophyll contents by thiourea	Perveen *et al.*, 2015
Medium supplementation	75 µM + 150 mM NaCl	Brassica	Modulation of post-transcriptional gene expression; Amelioration of salinity tolerance by coordinated regulation of hormones synthesis, especially auxins; Down-regulation of miRNA expression under salt stress	Srivastava *et al.*, 2017

dormancy under normal or adverse conditions are not only confined to seed germination rather are also carried to vegetative and even reproductive growth stages.

Bud Dormancy Break and Promotion of Sprouting

Bud dormancy, referred as temporary suspension of meristem growth, is an adaptive feature of tree species to tide over adverse environmental conditions. Bud dormancy may be innate or environmentally imposed. For instance, the potato tubers develop innate dormancy due to internal physiological change during long term storage (Turnbull and Hanke, 1985). The physiological mechanisms like flowering and senescence are the major signals regulating bud dormancy (Chao *et al.*, 2007). The tree plants regulate the timing of bud burst in order maximize growth whilst avoiding from stress injury (Häkkinen *et al.*, 1998; Yamane, 2014). But quite a few plants suffer bud dormancy due to harsh conditions. In addition to breaking seed dormancy the thiourea can also break the bud dormancy in several fruit tree species (Table 1). Hopping (1977) reported that, amongst other chemicals, thiourea solution (2–5%) applied five weeks prior to expected bud break enhanced the bud break (7–11%) and fruitful shoot (5–8%) in grape vines (*Vitis vinifera* L. cv. Palomino).

Thiourea (1% solution) alone or along with KNO_3 (2% solution) significantly broke the bud dormancy and improved fruit yield in peaches and nectarines (Kuden *et al.*, 1995). When applied at flower bud anthesis stage, foliar spray of 5% thiourea solution was most effective in breaking the bud dormancy and regulate flowering in *Rhododendron pulchrum* cv. Azalea (Chang and Sung, 2000). In apple (*Malus sylvestris* L. var. Ain Shemer) tree, application of thiourea enhanced the bud break and induced some changes such as accumulation of proline and biogenic amines (Seif El-Yazal and Rady, 2013). Likewise, twice application of 10% thiourea prior to bud formation reduced the time to bud break by at least eight days, and enhanced the final fruit set by 62% and final fruit yield by ~87% (Jana and Das, 2014). Thiourea (1–1.5% solution) inhibited the low temperature (4°C) induced tuber-rotting and bud dormancy, and speeded up the bud growth in potato (Wang *et al.*, 2017).

To conclude, foliar spray of optimized concentrations of thiourea can break both innate and/or imposed bud dormancies and promote bud sprouting, but this greatly depends upon the plant species. Although limited studies are available, the effects of thiourea are related to the production of physiological changes in the buds before sprouting commences morphologically.

Modes of Exogenous Application of Thiourea

Thiourea has been quite successfully used for enhancing growth and yield of many plant species (Tables 1 and 2). Thiourea molecule has different functional groups, the biological properties of which makes it a valuable organic compound (Jocelyn, 1972). The exogenous use of thiourea has been brought in via different modes of application at early, mid and advanced growth stages. The role of thiourea applied as seed pretreatment or foliar spray to the dormant seeds or buds and promotion of seed germination and bud sprouting, respectively has been discussed in the previous sections. However, foliar spray and medium supplementation *in vivo* (in soil) or *in vitro* have been found to be of immense value in enhancing the growth and yield under normal or stressful conditions, as documented below.

Foliar Spray

In an exclusive number of studies, foliar spray has been a more preferred mode of thiourea application (Table 1). Due to having biologically important functional groups exogenous application of thiourea promoted the growth of many crops (Jocelyn, 1972). About 50% of the foliar thiourea applied is absorbed in the plant leaves while rest of it goes residual on the ground. Assuming an amount of 250 g/ha foliar applied over 100,000 plants, only about 0.25 mg would be available to leaves for producing physiological changes (Ratnakumar *et al.*, 2016).

A great number of studies provide evidence regarding efficacious role of foliar applied thiourea in modulating physiological mechanisms and improving final yield. In pearl millet, foliar spray of 1000 ppm thiourea at pre-flowering stage of pearl millet significantly enhanced the crop growth and dry matter as compared to water sprayed control plants (Parihar *et al.*, 1997). Foliar spray with 2000 ppm of thiourea increased chlorophyll content, shoot dry weight and final weight per 100 seeds by delaying senescence and improving photosynthetic capacity in soybean (Jagetiya and Kaur, 2006). According to Solanki (2002), soil and foliar application of thiourea (500 ppm) were effective in increasing dry matter distribution in leave and pods and leaf area index over control on cluster bean grown on loamy sand soils.

Foliar application of thiourea effectively improved the mineral nutrition and its metabolism in plants, together with improved nutritional quality of grains. For example, foliar spray of 0.1% thiourea at grain formation stage significantly improved the maize grain protein content over control (Sahu and Solanki, 1991). Foliar spray of thiourea (15 ppm) increased the phosphorous uptake in potato (Sud *et al*., 1991). Foliar spray of 500 ppm thiourea at capsule formation stage in the poppy crop increased the nitrogen concentration of leaf and the total uptake of nutrients by the crop (Saini, 1991). In addition to increasing seed yield and straw yield, the foliar spray of thiourea at two growth stages increased the nitrogen and potassium uptake in coriander (Balai and Keshwa, 2011). Of the two bioregulators (salicylic acid and thiourea) used as foliar spray, 1500 mg/L thiourea was more effective in enhancing the 100-grain weight, grain yield per feddan, harvest index as well as grain quality attributes like crude proteins, soluble sugars, total free amino acids and soluble phenolics (Amin *et al*., 2013).

In addition to improved tissue nutrient contents, foliar application of thiourea also improved photosynthetic pigment contents (Table 1). Foliar spray of 5 mM thiourea improved the photosystem activity along with the expression of antioxidant (both enzymatic and non-enzymatic system (Hassanein *et al*., 2015). Thiourea increased the chlorophyll content of leaves up to 3.6% over control in maize (Sahu *et al.*, 1993). Sharma and Singh (2005) found that foliar spray of 1000 ppm thiourea solution on maize significantly increased chlorophyll content over water sprayed plants. Two times (at 25 and 45 days after sowing) foliar spray of 0.1% thiourea increased net rate of photosynthesis, chlorophyll content, starch and nitrate reductase activity in cluster bean (Garg *et al*., 2006). Foliar spray of thiourea at 75 and 90 days after sowing increased the growth and photosynthetic pigments. Among the photosynthetic pigments, the increase in chlorophyll 'b' and carotenoids contents was more distinct than the chlorophyll 'a' in field grown maize (Amin *et al*., 2013).

The foliar application of thiourea on the abiotically stressed plants is much effective. Improvement in plant growth and development under different stresses due to application of thiourea has been observed in crops like maize (Sahu *et al*., 1993; Perveen *et al*., 2015), wheat (Sahu and Singh, 1995; Sahu *et al*., 2006), pearl millet (Parihar *et al*., 1998) and cluster bean (Garg *et al*., 2006). Previous studies confirm that thiourea increased the plant growth under salt stress condition, which might be due to increase in antioxidant activities that alleviated the stress damage (Francisco *et al.*, 2008; Perveen *et al*., 2015). Kaya *et al.* (2015) reported that salinity stress suppressed the dry matter yield but increased H_2O_2, MDA, membrane permeability and antioxidants activities. Foliar spray with thiourea had a positive impact in reducing the amounts of toxic ions and increasing the essential nutrient contents but at the same time declining the H_2O_2, MDA and membrane permeability (Perveen *et al*., 2013). Salinity caused inhibition in PS-II activity while thiourea application improved this attribute (Calatayud and Barreno, 2004).

As noticed in wheat under salinity and heat stresses, foliar application of thiourea increased flag leaf gas exchange and net rate of photosynthesis in two wheat cultivars (Anjum *et al.*, 2008). Foliar spray of thiourea played a major role in regulation of net photosynthesis and grain yield in wheat cultivars under salinity and heat stresses (Table 2). The negative influences of these stresses on shoot length, root growth, dry weight, leaf area and yield were ameliorated by foliar spray of thiourea at seedling and pre-anthesis stages in bread wheat (Anjum *et al.*, 2008, 2011). Under different environmental conditions like arid and semi-arid environments, foliar application of thiourea improved chlorophyll content in drought stressed clusterbean ultimately leading to significant improvement in plant growth by increased biomass and yield (Burman *et al*., 2004). During drought stress, foliar application of thiourea improved net photosynthesis and chlorophyll content in cluster bean (Garg *et al*., 2006). Thiourea may be a nutrient supplement or may act as scavenger of reactive oxygen species (Pandey *et al.*, 2013; Perveen *et al.*, 2015).

Medium Supplementation

Few past studies show the use of thiourea as a medium supplement in tissue culture studies (Erez, 1978). Although reports are limited on the medium supplementation (*in vivo* and *in vitro*) of thiourea in plants, the available studies provided promising information. In *Cicer arietinum* addition of thiourea initially released the K^+ in the germination medium but reabsorbed later. This reabsorption of K^+ was transported to the embryonic axis of *Cicer arietinum*, which enhanced the carboxylation efficiency of phosphoenol-pyruvate (Hernández-Nistal *et al.,* 1983). Thiourea applied at the rate of 10 kg/ha to the wheat field improved the grain yield and grain yield contributory attributes, although final grain yield was increased by 17.3% (Sahu and Singh, 1995). Medium supplemented thiourea, amongst other chemicals, was the most effective in further augmenting the productivity of clusterbean (Sharma and Singh, 2005). Perveen *et al.* (2013) showed that 0.25 mM thiourea applied to the pot grown composite maize roots was highly effective in improving root growth and health and total dry mass, while higher levels were inhibitory. In a short term experiment, treatment of germinating wheat seedlings with 20 mM thiourea resulted in the enhanced induction of the activities of enzymatic antioxidants like peroxidase and catalase (Hameed *et al.,* 2013). An *in vitro* study showed that out of a range of thiourea levels used, 400 µM concentration was the most effective in the induction of callus, origination of shoot and root from the hybrid maize explant (Sanaullah *et al.*, 2016).

About role of medium supplemental thiourea in abiotic stress tolerance, the available literature shows distinctiveness of thiourea to improve stress tolerance but it is strongly dependent upon the plant species, type of stress applied and growing medium used. Salinity stress, being severer deterrent of plant performance, was successfully mitigated with the medium supplementation of thiourea in different plant species (Table 2). Among the profound changes with medium supplementation of thiouea in the saline medium were improved seed germination rate and velocity of germination in *Allenrolfea occidentalis* (Gul and Weber, 1998) and *Atriplex prostrata* (Khan *et al.*, 2003a), biomass yield in barley (Ikram and Javed, 2014) and maize (Sanaullah *et al.*, 2016). In addition, medium supplementation of thiourea reduced the cadmium toxicity possibly by binding/inactivation thereby resulting in improved photosynthetic pigments and gas exchange properties and improved essential contents of leaves under cadmium intoxication (Perveen *et al.*, 2013, 2015).

In crux, the foliar spray of thiourea was capable of profoundly modifying many morphological and physiological responses in quite a few plant species both under stress and no stress treatments. The foliar spray of thiourea was more effective under stress condition, as the improvisation ranged from ~4–21% under no stress to ~5–33% under salinity or heat stress conditions. Although studies are lacking but the available evidences suggest that medium supplementation of thiourea was quite effective in promoting the plant growth and physiological attributes more pronouncedly under abiotic stress effects than under no stress applied.

Some Mechanisms of Thiourea Action

In the previous section, we have noticed that thiourea produces a range of morphological, physiological and biochemical changes. These changes are the result of induction of certain molecular mechanisms ranging from the signaling of gene expression to the synthesis of pertinent proteins and accumulation of metabolites, irrespective of the application mode and the plant species investigated (Table 3). Nonetheless, it is important to find that thiourea is more effective under stress than under no stress applied in a great majority of the studies (Table 2). The induction of molecular mechanisms is the first step in the production of biochemical, biochemical and eventually the morphological changes in plants irrespective of the treatment applied. The seed treatment of thiourea led to coordinated regulation of signaling molecule and effector mechanism in salt-grown *Brassica juncea* (Srivastava *et al.*, 2010a). However, medium supplementation of thiourea caused changes in the post-transcriptional gene expression, down-regulation of miRNA and regulation of hormonal synthesis especially auxins under salinity stress in *B. juncea* (Srivastava *et al.*, 2010a, 2017). In addition, medium supplementation of thiourea improved water homeostasis of root under salinity stress with the expression of isoforms of aquaporins (PIPs) in *B. juncea* (Srivastava *et al.*, 2010b).

Among biochemical changes in different plant species, seed treatment of thiourea resulted in the induction of antioxidants and eventually led to the reduced generation of hydrogen peroxide and malondialdehyde in salt-grown *B. juncea* (Pandey *et al.*, 2013) and mungbean (Perveen *et al.*, 2016). Combined application of thiourea and salicylic acid were the most effective among other treatments in the induction of antioxidant enzymes activities, increasing the leaf carotenoids contents and improving the contents of phosphorus, potassium, calcium and magnesium in drought stressed wheat (Abdelkader *et al.*, 2012). Under heat stress the exogenous use of thiourea reduced membrane injury and improved photosynthetic pigment contents in wheat (Asthir *et al.*, 2013) and induction of an array of enzymatic and non-enzymatic antioxidants in sunflower (Akladious *et al.*, 2014). Seed soaking in thiourea solution enhanced the activities of invertases in sugar metabolism both in the shoot and root of high temperature stressed wheat (Asthir *et al.*, 2013). Moreover, seed soaking in 500 ppm solution of thiourea improved mtATPase activity and mitochondria function in salinity stressed brassica plants (Srivastava *et al.*, 2009).

Among the physiological effects, exogenously applied thiourea increased the photosystem-I and II activities in wheat under no stress condition (Nathawat *et al.*, 2007) as well as under reduced water availability in wheat (Hassanein *et al.*, 2012). In Indian mustard, foliar spray of thiourea improved the synthesis of anthocyanins, flavonoids and phenolic compounds leading to a lesser damage to leaf chlorophyll contents under UV-B stress (Pandey *et al.*, 2012). Thiourea spray enhanced the source strength and sucrose export to the developing reproductive organs in *B. juncea* (Pandey *et al*., 2013). Among other physiological impacts of thiourea, leaf gas exchange and improvised photosynthetic pigment contents are amongst the pronounced and favorable changes produced by thiourea in quite a few plant species regardless of the stress applied (Burman *et al*., 2007; Anjum *et al*., 2008; Perveen *et al*., 2013, 2015, 2016).

Appearance of morphological changes on the plants are ultimate responses of the treatments applied. Whether applied via seed pretreatment, foliar spray or via medium supplementation, the effective concentrations of thiourea used were helpful in producing profound changes in plants (Table 1). From the available literature, it was known that thiourea was capable of promoting plant growth and yield at whatever the stage it was applied. For example, reduction in the time taken to the emergence of embryonic tissues and improved germination percentage (Germchi *et al*., 2011; Belwal *et al*., 2015; Chattha *et al*., 2017), breaking bud and seed dormancy and improved sprouting and greater biomass and grain yield under stress conditions or otherwise (Kuden *et al*., 1995; Kumar *et al*., 2007; Sardana *et al*., 2008; Germchi *et al*., 2011; Jana and Das, 2014).

To conclude, thiourea produces an array of modifications starting from gene expression to altered morphological responses. However, to accomplish these changes emphatically an effective level should be optimized. From the available data, it is appealing that with the action of thiourea at molecular and physiological levels, the plant growth and productivity can be improved under stressful or otherwise conditions. No concrete reports are available on the histological changes in plants, which could be an important area for the establishment of more roles of thiourea in plant biology. Despite all that, the supporting evident is still insufficient and more research need to be done to establish these reports on firm footings.

Conclusion and Futuristic Outlook

Thiourea is an important compound with biologically important thiol and amino groups. It has been found to be quite effective in relieving the seeds and buds especially from innate physiological or environmentally induced dormancy. Use of thiourea proved of great significance in the alleviation of adverse effects of salinity, high temperature, drought and heavy metal intoxication by various application modes. These changes were attributable to the modulation of gene expression, induction of antioxidative defense system and resulting in improvised content of photosynthetic pigments and leaf gas exchange properties. Even though quite a few aspects of thiourea action have been explored and published, there are still more plant biology avenues that need to be investigated. Major ones of these include histological changes, osmolyestes accumulation, water and nutritional relations and functional genomics under normal or stressful conditions.

References

Abdelkader, A.F., R. Hassanein and H. Ali, 2012. Studies on effect of salicylic acid and thiourea on biochemical activities and yield production in wheat (*Triticum aestivum* var. Gimazaq) plant growth under drought stress. *Afr. J. Biotechnol*., 11: 1728–12739

Akladious, S.A., 2014. Influence of thiourea application on some physiological and molecular criteria of sunflower (*Helianthus annuus* L.) plants under conditions of heat stress. *Protoplasma,* 251: 625–638

Aldasoro, J.J., A. Matilla and G. Nicolás. 1981. Effect of ABA, fusicoccin and thiourea on germination and K^+ and glucose uptake in chick-pea seeds at different temperatures. *Physiol. Plant*., 53: 139–145

Amin, A.A., A.A. Abd El-Kader, M.A.F. Shalaby, F.A.E. Gharib, E.M. Rashad and J.A. Teixeira da Silva, 2013. Physiological effects of salicylic acid and thiourea on growth and productivity of maize plants in sandy soil. *Commun. Soil Sci. Plant Anal*., 44: 1144–1155

Anitha, S., E. Sreenivasan and S.M. Purushothaman. 2004. Effect of thiourea application on cowpea (*Vigna unguiculata* L.) productivity under rainfed conditions. *J. Trop. Agric*., 42: 53–54

Anjum, F., 2008. Use of thiourea for improving wheat (*Triticum aestivum* L.) under contrasting environmental conditions. *Ph.D. Thesis*. Department of Botany, University of Agriculture, Faisalabad, Pakistan

Anjum, F., A. Wahid, F. Javed and M. Arshad. 2008. Influence of foliar applied thiourea on flag leaf gas exchange and yield components of bread wheat (*Triticum aestivum*) cultivars under salinity and heat stresses. *Int. J. Agric. Biol.*, 10: 619–626

Anjum, F., A. Wahid, M. Farooq and F. Javed, 2011. Potential of foliar applied thiourea in improving salt and high temperature tolerance of bread wheat (*Triticum aestivum*). *Int. J. Agric. Biol*., 13: 251–256

Asthir, B., R. Thapar, M. Farooq and N.S. Bains, 2013. Exogenous application of thiourea improves the performance of late sown wheat by inducing terminal heat resistance. *Int. J. Agric. Biol*., 15: 1337–1342

Asthir, B., R. Kaur and N.S. Bains, 2015. Variation of invertase activities in four wheat cultivars as influenced by thiourea and high temperature. *Acta Physiol. Plant.*, 37: 1711–1719

Atia, A., A. Debez, M. Rabhi, H.R. Athar and C. Abdelly, 2006. Alleviation of salt induced seed dormancy in the perennial halophyte *Crithmum maritimum* L. (Apiaceae). *Pak. J. Bot*., 38: 1367–1372

Ayari, O., 2014. Effect of hydrogen peroxide and thiourea to the composition biochemical potato tubers (*Solanum tuberosum* L.). *Agric. Biol. Sci*., 11: 2–7

Balai, L.R. and G.L. Keshwa, 2011. Effect of thiourea on yield and nutrient uptake of coriander (*Coriandrum sativum* L.) varieties under normal and late sown conditions. *J. Spices Arom. Crops*, 20: 34–37

Buchanan, B., W. Gruissem and R. Jones, 2015. *Biochemistry and Molecular Biology of Plants*, 2nd edition. Wiley-Blackwell, Oxford, UK

Burman, U., B.K. Garg and S. Kathju. 2004. Interactive effects of thiourea and phosphorus on clusterbean under water stress. *Biol. Plant*., 48: 61–65

Burman, U., B.K. Garg and S. Kathju. 2007. Interactive effects of phosphorus, nitrogen, and thiourea on clusterbean (*Cyamopsis tetragonoloba* L.) under rainfed conditions of the Indian arid zone. *J. Plant Nutr. Soil Sci*., 170: 803–810

Belwal, T., A. Bisht, I.D. Bhatt and R.S. Rawal. 2015. Influence of seed priming and storage time on germination and enzymatic activity of selected *Berberis* species. *Plant Growth Regul*., 77: 189–199

Baskin, C.C. and J.M. Baskin, 1998. *SEEDS – Ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press, New York, USA

Calatayud A. and E. Barreno, 2004. Response to ozone in two lettuce varieties on chlorophyll a fluorescence, photosynthetic pigments and lipid peroxidation. *Plant Physiol. Biochem.*, 42: 549–555

Chang, Y.S. and F.H. Sung, 2000. Effects of gibberellic acid and dormancy-breaking chemicals on flower development of *Rhododendron pulchrum* sweet and *Rhododendron scabrum Don. Sci. Hort.*, 83: 331–337

Chao, W.S., M.E. Foley, D.P. Horvath and J.V. Anderson, 2007. Signals regulating dormancy in vegetative buds. *Int. J. Plant Dev. Biol.*, 1: 49–56

Chattha, M.B., I. Khan, A. Mahmood, M.U. Chattha, S.A. Anjum, U. Ashraf, M. Zain and U. Bilal, 2017. Seed priming with thiourea improves the performance of late sown wheat. *J. Agric. Res.*, 55: 29–39

El-Keblawy, A. and S. Gairola, 2017. Dormancy regulating chemicals alleviate innate seed dormancy and promote germination of desert annuals. *J. Plant Growth Regul.*, 36: 300–311

El-Keblawy, A., 2013. Impacts of dormancy-regulating chemicals on innate and salinity-induced dormancy of four forage grasses native to Arabian deserts. *Grass Forage Sci.*, 68: 288–296

Erez, A., 1978. Thiourea-A plant growth promoter in callus tissues. *J. Exp. Bot.*, 29: 159–165

Esashi, Y. and H. Katoh, 1977. Dormancy and impotency of cocklebur seeds. IV. effects of gibberellic acid, benzyladenine, thiourea, and potassium nitrate on the growth of embryonic axis and cotyledon segments. *Plant Physiol.,* 59: 117–121

Farooq, M., A. Wahid, N. Kobayashi and S.M.A. Basra, 2009. Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev.*, 29: 185–212

Francisco, A.A., A.R. Tavares, S. Kanashiro, P.R.R. Ramos and G.P.P. Lima, 2008. Plant growth regulators in polyamines endogenous levels during the development of taro cultivated *in vitro*. *Ciencia Rural*, 38: 1251–1257

Garg, B.K., U. Burman and S. Kathju, 2006. Influence of thiourea on photosynthesis, nitrogen metabolism and yield of cluster bean (*Cyamopsis tetragonoloba* (L.) Taub.) under rainfed conditions of Indian arid zone. *Plant Growth Regul.*, 48: 237–245

Germchi, S., F.G. Behroozi and S. Badri, 2011. Effect of thiourea on dormancy breaking and yield of potato (*Solanum Tuberosum* L.) minitubers Marfona cv. in greenhouse. *In*: *Proceedings of the International Conference on Environmental and Agriculture Engineering (IPCBEE)*, Vol. 15. IACSIT Press, Singapore

Germchi, S., M. KhorshidiBenam, D. HassanPanah, M. Yarnia and A. Faramarzi. 2010. Effect of Thiourea on dormancy breaking and performance of *Agria minitubers* in green house and laboratory. *J. New Agric. Sci.*, 18: 65–72

Gianfagna T.J., 1987. Natural and Synthetic Growth Regulators and Their Use in Horticultural and Agronomic Crops. *In*: *Plant Hormones and their Role in Plant Growth and Development*, pp: 614-635. Davies, P.J. (ed.). Springer, Dordrecht, The Netherlands

Gul, B. and D. Weber, 1998. Effect of dormancy relieving compounds on seed germination of non-dormant *Allenrolfea occidentalis* under salinity stress. *Ann. Bot.*, 82: 555–560

Gupta, R.C., 2012. *Veterinary Toxicology*, 2nd edition. Academic Press, London

Häkkinen, R., T. Linkosalo and P. Hari, 1998. Effects of dormancy and environmental factors on timing of bud burst in *Betula pendula*. *Tree Physiol.*, 18: 707–712

Hameed, A., L. Jafri and M.A. Sheikh, 2013. Effect of thiourea on proteins, catalase, guaiacol peroxidase and protease activities in wheat leaves under H_2O_2 induced oxidative stress. *Iran. J. Plant Physiol.,* 4: 857–864

Hassanein, R.A., A.F. Abdelkader, H. Ali, A.A. El-Said Amin and E.M. Rashad, 2012. Grain-priming and foliar pretreatment enhanced stress defense in wheat (*Triticum aestivum* var. Gimaza 9) plants cultivated in drought land. *Aust. J. Crop. Sci.*, 6: 121–129

Hassanein, R.A., A.A. El-Said Amin, E.M. Rashad and H. Ali, 2015. Effect of thiourea and salicylic acid on antioxidant defense of wheat plants under drought stress. *Int. J. Chem. Tech. Res.*, 7: 346–354

Hernández-Nistal, J., J. Aldasoro, D. Rodriguez, A. Matilla and G. Nicolás, 1983. Effect of thiourea on the ionic content and dark fixation of CO_2 in embryonic axes of *Cicer arietinum* seeds. *Physiol. Plant.*, 57: 273–278

Hopping, M.E., 1977. Effect of growth regulators and dormancy-breaking chemicals on bud break and yield of ‘Palomino’ grape vines. *N.Z. J. Exp. Agric.*, 5: 339–343

Ikram, S. and F. Javed, 2015. Cadmium stress alleviation by thiourea in barley. *Int. J. Innov. Appl. Stud.*, 12: 384–389

Ikram, S., F. Javed, A. Wahid and R. Ahmad, 2014. *In vitro* relationship between cadmium stress and thiourea in two barley genotypes. *Pak. J. Agric. Sci.*, 5: 673–678

Jagetiya, B.L. and M.J. Kaur, 2006. Role of thiourea in improving productivity of soybean. *Int. J. Plant Sci.*, 1: 308–310

Jana, B.R. and B. Das, 2015. Effect of dormancy breaking chemicals on flowering, fruit set and quality in Asian pear (*Pyrus pyrifolia* L.). *Afr. J Agric. Sci.*, 9: 56–60

Jocelyn, P.C., 1972. *Biochemistry of –SH group: The Occurrence, Chemical Properties, Metabolism and Biological Function of Thiols and Di-sulphides*, pp: 42-44. Academic Press, London

Kaya, C., M. Ashraf and O. Sönmez, 2015. Promotive effect of exogenously applied thiourea on key physiological parameters and oxidative defense mechanism in salt-stressed *Zea mays* L. plants. *Turk. J. Bot.*, 39: 786–795

Khan, M.A., I.A. Ungar and G. Bilques, 2003a. Alleviation of salinity enforced seed dormancy in *Atriplex prostrata*. *Pak. J. Bot.*, 35: 906–912

Khan, M.A., B. Gul and D.J. Weber, 2003b. Improving seed germination of *Salicorania rubra* (Chenopodiaceae) under saline conditions using germination-regulating chemicals. *Western North Amer. Nat.*, 62: 101–105

Kuden, A.B., A. Kuden and N. Kaska, 1995. The effects of thiourea and potassium nitrate + thiourea treatments on the release from dormancy of peaches and nectarines. *Acta Hort. (ISHS)*, 409: 133–136

Kumar, S., V. Awasthi and J.K. Kanwar, 2007. Influence of growth regulators and nitrogenous compounds on *in vitro* bulblet formation and growth in oriental lily. *Hort. Sci. (Prague)*, 34: 77–83

Liacos, L.G. and E.C. Nord, 1961. Curlleaf Cercocarpus seed dormancy yields to acid and thiourea. *J. Range Manage.*, 14: 317–320

Mani, F., T. Bettaieb, K. Zheni, N. Doudech and C. Hannachi, 2012. Effect of hydrogen peroxide and thiourea on fluorescence and tuberization of potato (*Solanum tuberosum* L.). *J. Stress Physiol. Biochem.*, 8: 62–71

Mayer, A.M., 1956. The action of thiourea as a germination stimulator. *J. Exp. Bot.*, 7: 93–96

Meena, H. and R.S. Meena, 2017. Assessment of sowing environments and bio-regulators as adaptation choice for clusterbean productivity in response to current climatic scenario. *Bangl. J. Bot.*, 46: 41–44

Nadeem, M., F., F. AL-Qurainy, S. Khan, M. Tarroum and M. Ashraf, 2012. Effect of some chemical treatments on seed germination and dormancy breaking in an important medicinal plant Ochradenus arabicus Chaudhary, Hill C. & A.G. Mill. *Pak. J. Bot.*, 44: 1037–1040

Naruka, S.I.S., P.P. Singh, R.P.S. Shaktawat and K.S. Verma, 2013. Effect of seed treatment and foliar spray of thiourea on growth, yield and quality of coriander (*Coriandrum sativum* L.) under different irrigation levels. *Int. J. Seed Spices*, 3: 20–25

Nathawat, N.S., J.S. Nair, S.M. Kumawat, N.S. Yadav, G. Singh, N.K. Ramaswamy, M.P. Sahu and S.F. D’Souza, 2007. Effect of seed soaking with thiols on the antioxidant enzymes and photosystem activities in wheat subjected to water stress. *Biol. Plant.*, 51: 93–97

Nelson, D.L. and M.M. Cox, 2012. *Lehninger Principles of Biochemistry* 6th edition. Freeman, W.H. & Company, New York, USA

Pandey, M., A.K. Srivastava, S. Penna and S.F. D'Souza, 2012. Thiourea mediates alleviation of UV-B stress-induced damage in the Indian mustard (*Brassica juncea* L.). *J. Plant Interact.*, 7: 143-150

Pandey, M., A.K. Srivastava, S.F. D'Souza and S. Penna. 2013. Thiourea, a ROS scavenger, regulates source-to-sink relationship to enhance crop yield and oil content in *Brassica juncea* (L.). *PLOS One*, 8: Article Number: e73921

Parihar, G.N., M.P. Sahu and N.L. Joshi, 1997. Nitrogen, sulphur and thiourea nutrition of pearl millet [*Pennisetum glaucum* (L) R. Br.] - I. Effect on growth and dry matter production. *Ann. Arid Zone*, 36: 353–362

Parihar, G.N., M.P. Sahu and N.L. Joshi, 1998. Nitrogen, sulphur and thiourea nutrition of pearl millet [*Pennisetum glaucum* (L) R. Br.] - II. Effect on yield and yield components. *Ann. Arid Zone,* 37: 59–67

Perveen A., A. Wahid, S. Mahmood, I. Hussain and R. Rasheed, 2015. Possible mechanism of root-applied thiourea in improving growth, gas exchange and photosynthetic pigments in cadmium stressed maize (*Zea mays*). *Braz. J. Bot.*, 38: 71–79

Perveen, A., A. Wahid, I. Hussain, R. Rasheed and S. Mahmood, 2013. Growth bioregulatory role of root-applied thiourea: changes in growth, toxicity symptoms and photosynthetic pigments of maize. *Pak. J. Agric. Sci.*, 50: 455–462

Perveen, S., R. Farooq and M. Shahbaz, 2016. Thiourea-induced metabolic changes in two mung bean [*Vigna radiata* (L.) Wilczek] (Fabaceae) varieties under salt stress. *Braz. J. Bot.*, 39: 41–54

Ratnakumar, P., M.I.R. Khan, P.S. Minhas, M.A. Farooq, R. Sultana, T.S. Per, P.P. Deokate, N.A. Khan and J. Rane, 2016. Can plant bio-regulators minimize crop productivity losses caused by drought, heat and salinity stress? An integrated review. *J. Appl. Bot. Food Qual.*, 89: 113–125

Robak, J. and E. Marcinkiewicz, 1995. Scavenging of reactive oxygen species as the mechanism of drug action. *Pol. J. Pharmacol.*, 47: 89–98

Sahu M.P. and D. Singh, 1995. Role of thiourea in improving productivity of wheat (*Triticum aestivum* L.). *J. Plant Growth Regul.*, 14: 169–173

Sahu, M.P. and N.S. Solanki, 1991. Role of sulphydryl compounds in improving dry matter partitioning and grain production of maize (*Zea mays* L.). *J. Agron. Crop Sci.*, 167: 356–359

Sahu, M.P., N.S. Solanki and N.L. Dashora, 1993. Effect of thiourea, thiamine and ascorbic acid on growth and yield of maize (*Zea mays* L.). *J. Agron. Crop Sci.*, 171: 65–69

Sahu, M.P., S.M. Kumawat, N.K. Ramaswamy and S.F. D'souza. 2006. *Sulphydryl Bioregulator Technology for Increasing Wheat Productivity*, pp: 1-56. Research Bulletin, RAU-BARC

Sahu, M.P., S.M. Kumawat, S.F. D'Souza, N.K. Ramaswamy and G. Singh, 2005. *Sulphydryl Bioregulatory Technology for Increasing Mustard Production*, pp: 1–52. Research Bulletin, RAU-BARC

Saini, L.R., 1991. Effect of thiourea treatments, foliar applied chemicals and elemental sulphur on mitigation of chilling injury and productivity of opium poppy (*Papaver somniferum* L.). *M.Sc. (Agric.) Thesis*, Rajasthan Agricultural University, Bikaner, India

Sanaullah, T., A. Wahid, F. Javed and B. Sadia, 2016. Optimization of thiourea level at cellular and whole plant level for maize hybrids (*Zea mays* L.). *Appl. Ecol. Environ. Res.*, 14: 1–18

Sardana, V., A.K. Atwal, M.K. Sangha, 2008. Effect of foliar application of sulphur on yield, quality and economics of Indian mustard, *Brassica juncea* (L.) Czern & Coss. *Res. Crops*, 9: 728–730

Seif El-Yazal, M.A. and M.M. Rady, 2013. Foliar-applied Dormex™ or thiourea-enhanced proline and biogenic amine contents and hastened breaking bud dormancy in "Ain Shemer" apple trees. *Trees*, 27: 161–169

Shanu, I.S. Naruka, P.P. Singh, R.P.S. Shaktawat and K.S. Verma, 2013. Effect of seed treatment and foliar spray of thiourea on growth, yield and quality of coriander (*Coriandrum sativum* L.) under different irrigation levels. *Int. J. Seed Spices*, 3: 20–25

Sharma, O.P. and G.D. Singh, 2005. Effect of sulphur in conjunction with growth substances on productivity of clusterbean (*Cyamopsis tetragonoloba*) and their residual effect on barley (*Hordeum vulgare*). *Ind. J. Agron.*, 15: 16–18

Siddiqui, E.H. and M. Ashraf, 2008. Can leaf water relation parameters be used as selection criteria for salt tolerance in safflower (*Carthamus tinctorius* L.)? *Pak. J. Bot.*, 40: 221–228

Singh, R.P. and D. Singh, 2017. Response of lentil to thiourea application under rain fed conditions of Central India. *Int. J. Curr. Microbiol. Appl. Sci.*, 6: 2556–2560

Solanki, N.S., 2002. Effect of thiourea and demethyl sulphoxide on phosphorus use efficiency, dry matter partitioning and productivity of cluster bean [*Cyamopsis tetragonoloba* (L.) Taub.]. *Ph.D. Thesis*, Maharana Pratap University of Agriculture and Technology, Udaipur, India

Srivastava, L.M., 2002. *Plant Growth and Development, Hormones and Environment*. Academic Press, California, USA

Srivastava, A.K., N.K. Ramaswamy, P. Suprasanna and S.F. D'Souza, 2010a. Genome-wide analysis of thiourea-modulated salinity stress-responsive transcripts in seeds of *Brassica juncea*: identification of signalling and effector components of stress tolerance. *Ann. Bot.*, 106: 663–674

Srivastava, A.K., N.K. Ramaswamy, R. Mukopadhyaya, M.G. Chiramal Jincy and S.F. D'Souza, 2009. Thiourea modulates the expression and activity profile of mtATPase under salinity stress in seeds of *Brassica juncea*. *Ann. Bot.*, 103: 403–410

Srivastava, A.K., P. Suprasanna, S. Srivastava and S.F. D'Souza, 2010b. Thiourea mediated regulation in the expression profile of aquaporins and its impact on water homeostasis under salinity stress in *Brassica juncea* roots. *Plant Sci.*, 178: 517–522

Srivastava, A.K., G. Sablok, M. Hackenberg, U. Deshpande and P. Suprasanna, 2017. Thiourea priming enhances salt tolerance through co-ordinated regulation of microRNAs and hormones in *Brassica juncea*. *Sci. Rep.*, 7: 45490

Sud, K.C., R.S. Sharma, S.P. Trehan and B.S. Bist, 1991. Effect of thiourea on phosphorus use efficiency by potato (*Solanum tuberosum*) in Shimla hills. *Ind. J. Agric. Sci.*, 61: 731–735

Syrett, P.J. and I.A. Bekheet, 1977. The uptake of thiourea by *Chlorella*. *New Phytol.*, 77: 291–297

Taiz, L., E. Zeiger, I.M. Møller and A. Murphy, 2015. *Plant Physiology and Development*, 6th edition. Sinauer Associates Inc., Sunderland, Massachusetts, USA

Torchinskii, Y.M., 1974. The chemical properties of SH groups sulfhydryl reagents. *In*: *Sulfhydryl and Disulfide Groups of Proteins*. Studies in Soviet Science (Life Sciences). Springer, Boston, Massachusetts, USA

Turnbull, C.G.N. and D.E. Hanke, 1985. The control of bud dormancy in potato tubers. Evidence for the primary role of cytokinins and a seasonal pattern of changing sensitivity to cytokinin. *Planta*, 165: 359–365

Verma, V., P. Ravindran and P.P. Kumar, 2016. Plant hormone-mediated regulation of stress responses. *BMC Plant Biol.*, 16: 86

Wahid, A., A. Noreen, S.M.A. Basra, S. Gelani and M. Farooq, 2008. Priming-induced metabolic changes in sunflower (*Helianthus annuus*) achenes improve germination and seedling growth. *Bot. Stud.*, 49: 343–350

Wahid, A., M. Parveen, S. Gelani and S.M.A. Basra, 2007. Pretreatment of seeds with H_2O_2 improves salt tolerance of wheat seedling by alleviation of oxidative damage and expression of stress proteins. *J. Plant Physiol.*, 164: 283–294

Wang, C.C., J.J. Hu, W.W. Jia, K.X. Wang, X.Y. Wang, M.X. Tang, X.L. Huang and W. He, 2017. Effects of gibberellin and thiourea on dormancy and bud morphogenesis of pre-basic potato under different temperatures. *Southwest Chin. J. Agric. Sci.*, 30: 1035–1040

Yadav, P.V., M. Kumari and Z. Ahmed, 2011. Seed priming mediated germination improvement and tolerance to subsequent exposure to cold and salt stress in capsicum. *Res. J. Seed Sci.*, 4: 125–136

Yamane, H., 2014. Regulation of Bud Dormancy and Bud Break in Japanese Apricot (*Prunus mume* Siebold & Zucc.) and Peach [*Prunus persica* (L.) Batsch]: A summary of recent studies. *J. Japan. Soc. Hort. Sci.*, 83: 187–202

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