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Review Article

Response of cereals to cycocel application

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ABSTRACT- Growth retardants are natural or synthetic chemical substances which are directly applied to crops to alter some structural processes. It is expected that these alterations modify hormonal balance and growth leading to increased yield, improved crop quality or facilitated harvesting. Cycocel (CCC) or chlormequat chloride (2-chloro ethyl trimethyl ammonium chloride) as a synthetic growth retardant has been recommended for wheat since 1960s. Cycocel inhibits gibberellin biosynthesis via blocking ent-kaurene synthesis in the metabolic pathway of gibberellin production, resulting in reduced amounts of active gibberellins and consequent reduction in stem elongation. The stem shortening effect of cycocel in such cereals as wheat seems to be less important, due to release of many dwarf and semi dwarf wheat cultivars. However, using cycocel in cereal fields would be inevitable if its effect on grain yield is definite and this area needs further investigation. Importance of cycocel is greater under environmental stress conditions, and more research needs to be focused on cycocel-induced stress tolerance. In this paper, the current knowledge and possible applications of cycocel, which can be used to improve the growth and yield of cereals, have been reviewed and discussed. The role of cycocel to mitigate the harmful effects of drought and salt stresses in cereals is also examined. Furthermore, various biochemical and physiological processes leading to improved cereal crop production under the influence of cycocel are discussed.

Using Plant Growth Regulators in Cereals

Plant growth regulators (PGRs) are widely used in contemporary agriculture to promote plant growth, yield, and grain quality. Both beneficial and adverse effects of PGRs on growth and development as well as plant metabolism have been addressed extensively (Ashraf et al., 2011). Environmental stresses have been known to alter the levels and ratios of different endogenous hormones by modifying their signal transduction pathways. Such alterations often cause serious metabolic disorders that lead to general suppression in plant growth and development under stress conditions (Lerner and Amzallag, 1994). Abiotic stresses generally cause reduction in the synthesis of plant hormones in plants, and their degradation is also noticed in some cases. For example, it has been shown that drought stress is associated with greater abscisic acid concentration in most crop plants having a negative impact on gibberellins, indole acetic acid and cytokinin concentrations (Wang et al., 2008; Bano and Yasmeen, 2010; PirastehAnosheh et al., 2013). Under abiotic stresses conditions; however, the application of PGRs, either to the seed before planting (i.e. seed priming) or to the growing plant (i.e. foliar application), may overcome much of the internal PGRs deficiency and may lead to alleviation of the inhibitory effects of abiotic stress (Ashraf and Foolad, 2007).

The question of “whether the application of PGRs overcomes the imbalance of regulatory substances caused by the stress, generates specific defense mechanisms against the stress, or just improves plant vitality” still needs to be answered. Nevertheless, from a practical viewpoint, the application of PGRs offers a potential approach to mitigate the inhibitory effects of stress on plant growth and crop productivity (Ashraf et al., 2008; Ashraf et al., 2011).

The interest in maximizing cereal crop yield has stimulated the adoption of certain practices in these crops such as optimized sowing time, row spacing and orientation, seeding density, increased soil fertility status and diseases, insects and lodging control (Rodrigues et al., 2003). Lodging is one of the most problems in cereals production, which refers to the displacement of the stem from its vertical position and leaning towards the soil (Espindula et al., 2009). Stem lodging is usually caused by the weight of mature ears in low stem resistance cereals and could be attributed to heavy irrigation and fertilization and wind (Emam, 2011; Bahrami et al., 2014b). Harper (1983) proposed that stem diseases or adverse weather conditions, such as wind storms, were the principal agents inducing lodging in cereals. He reported that stem characteristics were crucial in determining lodging incidence. This phenomenon can be controlled by restricting nitrogen fertilizer application using short stature cultivars or PGRs application (Espindula et al., 2009; Bahrami et al., 2014b).

PGRs were used in high-input cereal management to shorten the stem, thereby reducing lodging susceptibility. There are many reports that describe the various effects of PGRs on plants stand structure and yield formation of cereals (Ma and Smith, 1991; Emam and Moaied, 2000; Afzal et al., 2002; Rajala, 2004; PirastehAnosheh et al., 2012; PirastehAnosheh et al., 2014b). Generally, cereals like barley (*Hordeum vulgare* L.) and oat (*Avena sativa* L.) have higher stem height and hence are more prone to lodging compared to semi-dwarf wheat crops (Emam, 2011). Therefore, examining the PGRs ability to modify stem elongation, plant stand structure and yield formation represents a substantial component of research in crop production (Rajala, 2004).

Some physiologists such as Pinthus and Rudich (1967), Bragg et al. (1984) and Emam and Moaied (2000) opined that although the introduction of stiff-strawed semi-dwarf cultivars of cereals such as that for wheat with the reduced height (*Rht*) genes largely solved the problem of lodging, evidence was already accumulating that a timely application of growth retardants such as cycocel can increase yield of both wheat and barley, independently of any control on lodging. Rajala (2004) also indicated that PGRs are primarily targeted at the reduction of stem elongation; however, many researchers suggest that irrespective of the effect on stem height, PGRs can modify cereal growth patterns, leading to a greater grain yield (Ma and Smith, 1991; Ma and Smith, 1992a; Peltonen-Sainio and Rajala, 2001; Shekoofa and Emam, 2008) irrespective of the effect on stem height. PGRs applications have been known to alter tiller and spikelet production as well as survival through changes that resemble day-length responses (Davies, 2010). Reduced shoot growth may change assimilate partitioning within the plant and thus provide excess resources which in turn may stimulate, for example, root growth, tiller and spikelet initiation and grain set and growth (Ma and Smith, 1992a; Emam, 2011).

Growth Retardants and Cereals

Pioneering studies in the 19th century have demonstrated that various plant growth processes are regulated by some substances. These substances move from one part of the plant to another part (Darwin, 1880). It took over a century to realize that growth substances are actually small molecules derived from various essential metabolic pathways. In general, these compounds, as phyto-hormones, are present at very low concentrations and act either locally, at or near the site of synthesis, or in distant tissues (Santner et al., 2009). Their major groups include indole-3-acetic acid (IAA or auxin), cytokinin, gibberellic acid (GA), ethylene, abscisic acid (ABA), brassinosteroids (BRs), jasmonic acid (JA) and salicylic acid (SA). Synthesis as well as the activity of some of these phyto-hormones can be restricted by growth retardants.

Growth retardants are chemical substances which can alter the growth and developmental processes, leading to increased yield, improved grain quality or facilitated harvesting (Espindula et al., 2009). Growth retardants induced reduction in stem elongation in such crops as cereals can be linked with either reduction in gibberellic acid (GA) synthesis or increase in ethylene synthesis (Gianfagna, 1995). Growth retardants could act as chemical signal and regulate plant growth and development. They usually bind to the special receivers in plants and induce a series of cell changes affecting initiation or modification of organ or tissue development. Since plant growth retardants are usually antagonist to gibberellins by modifying their metabolism (Rodrigues et al., 2003), they are frequently called “antigibberellins”. Inhibiting products of gibberellin are commercially used to prevent lodging in some plants. In cereals, studies with trinexapac-ethyl, paclobutrazol, moddus and chlormequat chloride (cycocel) have demonstrated satisfactory results in reducing plant stature and consequently improved grain yield (Emam and Karimi, 1996; Emam and Moaied, 2000; Rajala and Peltonen-Sainio, 2002; Rodrigues et al., 2003; Shekoofa and Emam, 2008; Espindula et al., 2009; PirastehAnosheh and Emam, 2012 a & b; PirastehAnosheh et al, 2012 & 2014b).

Mode of Action of Growth Retardants

Gibberellin biosynthesis inhibitors are divided into three categories, each interrupting one of the three stages of gibberellin synthesis (Srivastava, 2002; Espindula et al., 2009).

The first class includes quaternary ammonium (chlormequat chloride or CCC, mepiquat chloride and AMO-1618) and phosphonium (chlorophenium chloride) salts, which block the ent-kaurene synthesis from geranylgeranyl diphosphate in GA production pathway. AMO-1618 and CCC specifically inhibit the activity of copalyl diphosphate synthase and, in a smaller degree, of ent-kaurene synthase.

The second class consists of heterocyclic compounds containing nitrogen, such as ancymidol (a pyrimidine), tetcyclases (a norbornanodiazetine), and triazole type compounds (paclobutrazol and uniconazole). These compounds inhibit the oxidation of ent-kaurene to ent-kaurenoic acid by the P450 monooxygenases during stage 2 of gibberellin production pathway.

The third class of compounds includes acylcyclohexanediones that inhibit 2-oxoglutarate-dependent dioxygenases at stage 3 of gibberellin production pathway. Acylcyclohexanediones, such as prohexadione- Ca and trinexapac-ethyl (a salt and an ester, respectively), have structures similar to 2-oxoglutarate and therefore, inhibit the dioxygenase activity by competing for the biding site of the co substrate 2-oxoglutarate.

Cycocel

Several growth retardants have been used in cereals, among which 2-chloro ethyl trimethyl ammonium chloride (Fig. 1), known as "cycocel (CCC)" has been recommended for wheat since 1960 (Rodrigues et al., 2003; PirastehAnosheh et al., 2012). Cycocel has been most widely used in wheat to stimulate tillering, re-distribute biomass with increased root growth, reduce plant stature and increase stiffness of straw that limits the risk of lodging (Rodrigues et al., 2003; Emam, 2011). The success of this growth retardant has been reported from its application on wheat crop at commercial scale in many countries, especially under conditions of good moisture and fertility where high grain yields are obtained (Rodrigues et al., 2003; Rajala, 2004; Emam, 2011).

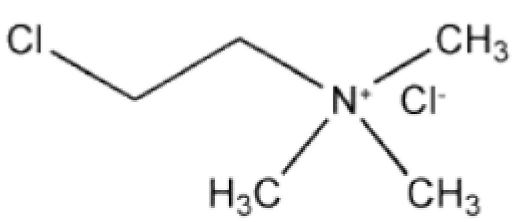

Fig. 1. Chemical structure of cycocel

Gibberellins are a diverse group of endogenous phyto-hormones, which play an important role in cell elongation processes (Rajala, 2004). Anti-gibberellic plant growth regulators inhibit gibberellin biosynthesis at different stages of the metabolic pathway resulting in reduced amounts of active gibberellins and consequent reduction in stem elongation (Rademacher, 2000; PirastehAnosheh and Emam, 2012a). The first report on the effect of cycocel in reducing shoot elongation of wheat dates back to 1960 (Tolbert, 1960a & b). However, in barley, response to CCC was found to be variable and genotype specific (Clark and Fedak, 1977; Bahrami et al., 2014a & 2014b). Recently, PirastehAnosheh et al. (2014b) concluded that the positive effect of cycocel priming on wheat, maize, and rapeseed was observed only at moderate osmotic levels, whereas barley and safflower responded to CCC priming at all levels of osmotic stress.

It has been suggested that cycocel-treated cereal crops may have a higher optimum population density. This idea is justified in the light of the knowledge that early stem elongation and apex development are promoted in higher plant densities or when GA_3 is applied; however, cycocel has the reverse action, i.e. it decreases the elongation growth and slows down the rate of apical development by reducing the amount of active gibberellin available (Bode and Wild, 1984; Ma and Smith, 1991; Emam and Karimi, 1996; Emam and Moaied, 2000). Timely application of CCC to a crop stand with near-optimum population density has been shown to increase the number of fertile shoots per plant (Waddington and Cartwright, 1986; Ma and Smith, 1991; Emam and Karimi, 1996). The rate of apical development is reported to be hastened by population density. Kirby and Faris (1970) studied apical development across a wide range of planting densities from 50 to 1600 plants m^{-2} in barely and found that increased population density was associated with higher rate of apical development. Contrarily, Ma and Smith (1991) reported that the application of cycocel at the third leaf stage equal to ZGS 13 [Zadoks growth scale (Zadoks et al., 1974)] could slow the rate of apical development in the main shoot of barley, so that barley plants treated with cycocel could have higher optimum population density.

Cycocel Seed Priming

PGRs are applied as foliar spray, through root growing medium, or as pre-sowing seed treatment (Ashraf et al., 2011). The latter is generally called seed priming, a process that tends to modulate pre-germination metabolic activities to make seed perform better under normal and stressful environments (Hamidi et al., 2013b; Khaliq et al., 2013). Seed priming with different PGRs (hormo-priming) such as cycocel has been proposed as an effective approach to improve seed germination and seedling growth under osmotic stress in several plant species (Ashraf et al., 2011; Ozgur, 2011; Hashemi et al., 2012; Hamidi et al., 2013a). Foliar application of cycocel has been well documented in several earlier studies for many crops (Tolbert, 1960; Clark and Fedak, 1977; Cartwright and Waddington, 1981; Bode and Wild, 1984; Bragg et al., 1984; Emam and Karimi, 1996); however, little is known about the ability of cycocel application as seed priming in modulating the harmful effects of osmotic stress in crops at germination and seedling growth stages. In a recent study (PirastehAnosheh et al., 2014b), the effects of cycocel priming at three levels (0, 2.5, and 3.5 g L^{-1}) were evaluated on seed germination, early growth, and vegetative growth of six commercial crops including wheat, barley, maize, sunflower, safflower, and rapeseed under five osmotic stress levels (0, as non-stress, −0.5, −1.0, −1.5, and −2.0 MPa). It was concluded that priming with optimum cycocel concentration mitigated osmotic stress-induced adverse effects on these crops to a great extent. Cycocel priming was found to be effective in diverting a major proportion of assimilates to root, since the root to shoot dry weight ratio was increased upon cycocel application under all osmotic stress levels. Although there were no significant differences among cycocel priming concentrations in terms of germination under varying osmotic stress regimes, 3.5 g L^{-1} cycocel resulted in a better performance at later growth stages. Improvement in crop germination and growth realized under CCC priming was attributed to increased nutrient remobilization through increased physiological activities and also enhanced root proliferation (PirastehAnosheh et al., 2014b).

There are a few studies which have examined the role of cycocel priming on crop performance. For example, Afria et al. (1998) showed that cycocel primed guar (*Cyamopsis tetragonoloba* L.) plants by 1.5 g L^{-1} had higher leaf area, straw and seed yield and reduced transpiration and harvest index under stress conditions. Furthermore, in the study done by Naylor et al. (1989), it was shown that triticale and barley plants primed with cycocel also produced seedlings with significantly more leaves and primary tillers, greater leaf lamina, and a higher shoot dry weight. These altered processes were found to be beneficial for increased crop yield. Kanp et al. (2009) also reported that seed pretreatment with CCC effectively enhanced the storage potential of seeds and field performance of pea (*Pisum sativum* L.) and horse gram (*Dolichos biflorus* L.) plants.

Hashemi et al. (2012) showed that cycocel seed presoaking had a significant effect on germination percentage and germination rate as well as radicle and plumule length of safflower. They concluded that cycocel seed presoaking could improve germination and seedling growth of safflower under drought stress conditions. Under without- or light drought stress, cycocel at 3.5 g L^{-1} and under moderate- or severe drought stress cycocel at 2.5 g L^{-1} were appropriate concentrations.

Foliar Application of Cycocel

Although cycocel could be absorbed by stems or even roots (Emam, 2011), to achieve higher efficiency, it should be applied to the leaves. Furthermore, cycocel is compatible with most herbicides such as 2,4-D and MCPA and its joint use represents a reduction of application cost. Furthermore, foliar application of cycocel has been shown to be more effective than seed priming application in promoting plant growth, or modulating different physiological processes for better adaptation under changing environments. Cycocel foliar application has been reported to improve growth and yield in numerous crops, including wheat (Pinthus and Rudich, 1967; Clark and Fedak, 1977; Bode and Wild, 1984; Bragg et al., 1984; Shekoofa and Emam, 2008; Espindula et al., 2009; PirastehAnosheh et al., 2012a & b; PirastehAnosheh et al., 2012& 2014b), barley (Clark and Fedak, 1977; Bragg et al., 1984; Waddington and Cartwright, 1986; Ma and Smith, 1991; Emam and Karimi, 1996, Emam and Moaied, 2000, PirastehAnosheh et al., 2014b; Bahrami et al., 2014a; ; Bahrami et al., 2014b; Latifkar et al., 2014), maize (PirastehAnosheh et al., 2014b), sunflower (Hashemi et al., 2012; PirastehAnosheh et al., 2014b), safflower (PirastehAnosheh et al., 2014b), rapeseed (PirastehAnosheh et al., 2014b), oat (Clark and Fedak, 1977) and cucumber (Ozgur, 2011).

Cycocel Induced Responses in Plants

Morphological Responses

Cycocel is used in high input cereal management to shorten the stem, thereby reducing the risk of lodging. There are numerous reports describing the various effects of cycocel on plant morphology of cereals. For example, Emam and Moaied (2000) indicated that CCC application at the lemma primordium stage affected certain morphological aspects like true stem length, pseudo stem length, apex length, and spike length of winter barley. They also found that the onset of rapid stem elongation was delayed by the early application (i.e., at the lemma primordium stage) of cycocel. This is consistent with the "anti-GA" mode of action of cycocel. Indeed, such antagonistic effects of cycocel treatment on stem elongation provided indirect evidence in favor of "cycocel hindered" GA activity (Ma and Smith, 1992a). Leitch and Hayes (1990) found that cycocel applied at ZGS 32 shortened stems of oat plants to the tune of 24% in 1985-86 and 31% in 1986-87. Earlier applications were significantly less effective in this regard.

Reduction in plant height is considered as the most important morphological outcome of cycocel application. According to Shekoofa and Emam (2008), it was associated with reduced elongation of the internodes, rather than lowering the number of internodes. The uppermost internodes as well as peduncle, in particular, are found to be shortened under cycocel application. Curtailed stem elongation by cycocel application generally reduces the risk of lodging. To shorten the stem, cycocel is applied either towards the end of tillering or at early stem elongation (Rademacher, 2000; Rajala, 2003). Cycocel applied prior to the onset of stem elongation resulted in a similar short-term reduction in stem elongation of main shoot and T_1 and T_2 tillers (Peltonen-Sainio et al., 2003). Rajala (2003) indicated that even when tillers are not directly exposed to cycocel application, the elongation retarding effect may be transferred to the tillers. Emam and Moaied (2000) and Bahrami et al. (2014a) noticed that although cycocel foliar applied barley plants had lower plant height at the early stages, this reduction was compensated for by the flowering stage so that there has been no significant difference between treated and non-treated plant heights by the end of the growing season. This might be related to the accumulation of precursors of GA at early growing season due to the anti-gibberellic feature of cycocel. Ma and Smith (1991) reported similar results too. Bahrami et al. (2014a) also found that height reduction at tillering led to higher tiller survival and enhanced fertile tillers, which resulted in greater yield in barley.

Leaf area index (LAI) is another morphological trait that is strongly influenced by cycocel application. Results of the study conducted by Miranzadeh et al. (2011) revealed that wheat crop treated with cycocel exhibited higher LAI. These researchers attributed the increase in LAI to increased tiller survival. Adding further, PirastehAnosheh et al. (2012) indicated that lowered developmental rate or delayed plant maturity and senescence contributed indirectly to greater LAI under cycocel application. Enhanced LAI in cycocel treated plants consequently led to enhanced growth and yield. Indeed, the increase in assimilatory surface (i.e., leaf area) or photosynthesis rate was the most obvious factor responsible for such a response (Ma and Smith, 1991; Miranzadeh et al., 2011). On the other hand, PirastehAnosheh et al. (2014b) reported that cycocel application at varying levels (2.5 and 3.5 g L^{-1}) had no significant effect on leaf number of three cereal crops including wheat, barley and maize.

Miranzadeh et al. (2012) indicated that although cycocel foliar application increased LAI and dry matter of all tested wheat cultivars, significant differences were observed regarding the response of different wheat cultivars to cycocel foliar application (Table 1). Nicknejad and Azar-found that wheat cultivars showed a greater response to cycocel application than the rest of cultivars. In this study, plants treated with cycocel and receiving supplemental nitrogen, in the form of urea, had higher LAI. Bahrami et al. (2014a) also showed that LAI of five barley cultivars (Viktoria, Reyhane, Jonoub, Gorgan and Valfajr) responded positively to cycocel application; however, Reyhane and Gorgan cultivars had the highest and the lowest responses, respectively.

Physiological and Biochemical Responses

There are various reports on the effect of cycocel application on physiological and biochemical traits of cereals. Treatment with cycocel enhanced relative water content that improved plant drought tolerance (Imbamba, 1973). Imbamba (1973) also observed that stomatal opening was suppressed by cycocel; however, the number of stomata per unit leaf area was increased resulting in increased relative water content. Canopy temperature has been shown to be a sensitive trait to cycocel application and was decreased by foliar spray of cycocel at 2.5 g L^{-1} concentration (PirastehAnosheh et al., 2012) which may be due to the role of cycocel in greater stay-green duration. Cycocel is also reported to be involved in osmoregulation (Rademacher, 2000).

Cycocel application increased proline, protein, sugar and chlorophyll content. Ibrahim et al. (2001) found that the protein and amino acid contents were higher in cycocel treated maize seedlings. In another research, cycocel increased free proline content, but did not change total soluble protein in wheat (PirastehAnosheh et al., 2012). However, PirastehAnosheh et al. (2014b) reported that free proline remained almost unchanged in wheat, barley, maize, sunflower, safflower and rapeseed subjected to cycocel priming. The results of Wang et al.'s study (2010) showed that 1.5 and 2.0 g L^{-1} cycocel treatments significantly increased the activity of enzymatic antioxidants such as superoxide dismutase, peroxidases and catalase in potato leaves. They further argued that enhanced superoxide activity in cycocel-treated leaves may help protect the photosynthetic apparatus against damage of reactive oxygen species (ROS) in crops exposed to low temperature stress or other abiotic stresses. Nevertheless, PirastehAnosheh et al. (2012) observed that the activity of superoxide dismutase remained unchanged in wheat, whereas peroxidase and catalase activity was increased in response to cycocel foliar application. It was found that cycocel improved the root growth in response to a slight increase in IAA content. Decrease in GA concentration under cycocel application may be due to the fact that CCC interferes with the early stages of gibberellin biosynthesis primarily by blocking the activity of *ent*-kaurene synthesis (Rademacher, 2000).

Influence of Cycocel on Grain Yield and its Components

The positive role of cycocel on yield components such as greater fertile tillers, spike number, fertile spikelets, grain number and in some cases mean grain weight has been shown in studies evaluating the production potential of cereals; however, numerous studies have revealed that the grain number has been the main important component significantly associated with enhanced grain yield in response to cycocel application. The major impact of cycocel on grain yield is mediated via initiation of more fertile tillers per plant resulting in a greater number of grains. The work of Emam and Moaied (2000) on winter barley as well as that of Shekoofa and Emam (2008) on winter wheat confirmed that the increased grain yield was the result of higher grain number. Various applications of cycocel enhanced formation, growth and survival of head bearing tillers of barley (Cartwright and Waddington, 1981; Waddington and Cartwright, 1986; Ma and Smith, 1991; Ma and Smith 1992a), wheat (Khan and Spilde, 1992; Latifkar et al., 2014) and oat (Peltonen-Sainio and Rajala, 2001). However, Leitch and Hayes (1990) reported that oat grain yields were unaffected by single and repeated early applications of cycocel.

When cycocel is applied close to anthesis, a likely explanation for increased grain number is the decline in spikelet, floret and grain abortion (Ma et al., 1994; Rajala, 2003). This implies that the potential to modify grain number in cereals is more likely to result from reduced abortion rate prior to and at early grain filling, rather than from further increase in the number of already abundant spikelets and florets (Craufurd and Cartwright, 1989, Peltonen-Sainio, 1997). This suggested that adequate assimilate would be supplied by enhanced photosynthesis.

Table 1. The effect of cycocel on LAI and production on four wheat cultivars (Tukey's test 5%)

Cultivars	Cycocel	LAI		Dry matter at anthesis (g m^{-2})		Total biomass (g m^{-2})	
		2006-07	2007-08	2006-2007	2007-2008	2006-07	2007-08
Agosta	Cycocel	1.53d	1.07d	200.6bc	182.3c	272.3de	246.1c
	Control	1.49e	1.02e	197.3c	174.5d	264.7e	235.5d
Nicknejad	Cycocel	1.79a	1.21b	241.3a	166.0e	326.8a	225.8e
	Control	1.64c	1.06de	233.7a	155.1f	314.3b	209.3f
Azar-2	Cycocel	1.73b	1.32a	208.6b	198.8a	283.5c	268.3a
	Control	1.68c	1.14c	206.5b	188.8bc	276.2cd	254.8bc
Fin-15	Cycocel	1.65c	1.24b	201.5bc	192.1b	271.9de	259.3ab
	Control	1.49e	1.21b	196.2c	182.7c	264.8e	246.6c

Miranzadeh et al., 2012

Many researchers opined that grain weight either remained unaffected, or was slightly reduced by cycocel treatments (Ma et al. 1994; Pietola et al., 1999; Rajala, 2003). This might be due to *individual sink-limitation*, suggesting that mean grain weight of cereals is an almost stable yield component. Lodging occurrence during grain filling considerably reduces grain filling capacity. Cycocel application reduces the lodging intensity or delays the onset of lodging whose result is undisturbed grain filling and single grain weight close or equal to those of non-lodged plant stands (Stanca et al., 1979; Cox and Otis, 1989; Rajala, 2003). Reduced stem elongation in response to cycocel application potentially enhances assimilate availability and distribution to spikelet set and grains (Rajala, 2003). Thus, according to the above discussion, the increased assimilate availability could not increase grain size; however, it could fill more grains per plant.

Shekoofa and Emam (2008) reported that although both cycocel and ethephon application increased the grain yield of winter wheat plants, the highest grain yield was obtained from plots treated with cycocel. They indicated that the yield increase was the result of an increase in grain number per plant which, in turn, was due to a greater number of fertile tillers. Such higher grain yield was also associated with higher biological yields. Besides, Emam and Moaied (2000) showed that early cycocel application slowed down the rate of apical development of the main shoot of barley plants without any significant effect on its spikelet initiation rate. However, the peak spikelet number in cycocel-treated plants was found to be higher. Latifkar et al. (2014) also reported that the application of chlormequat chloride increased the number of spikes per square meter, thousand grain weight and grain yield significantly; however, the number of grains per spike was decreased.

Enhancement of Stress Tolerance

Since early migration from aquatic to terrestrial environments, plants have had to cope with periodic and unpredictable environmental stresses, such as drought and salinity. Cereal crop production in arid or semi-arid regions is usually restricted by soil moisture deficit as well as soil salinity. Water deficit coupled with salinity in irrigation water is the major limiting factor in most regions where cereals are subjected to extreme water deficit during dry seasons. Enhanced stress tolerance in cereals can be achieved by exogenous application of some PGRs, including cycocel. Exogenous application of cycocel can reduce some of the harmful effects of drought and salt stress and in some cases, compensate losses or damages caused by these stresses (Ashraf et al., 2008).

It has been reported that the application of cycocel partially compensated the reduction in growth, yield and some biochemical traits. Such compensatory effects of cycocel could be due to various reasons such as stomatal closure, increased chlorophyll content and intercellular CO_2 concentration, and stimulatory changes in other physiological and biochemical attributes (PirastehAnosheh et al., 2012). Cycocel can also stimulate root growth, reduce transpiration, increase water use efficiency, and prevent chlorophyll destruction (Rajala, 2003; Wang et al., 2010). Increased levels of soluble protein, free proline and antioxidant enzyme activities in plants under stress conditions are natural responses, which can help plants better tolerate the stress. Exogenous application of cycocel increased these traits and improved stress tolerance in plants. Furthermore, the enhanced antioxidant enzyme activities in response to cycocel application may also protect their photosynthetic machineries against damages caused by ROS during water-deficit conditions (Rajala, 2003; Ashraf, 2010; Wang et al., 2010; PirastehAnosheh et al., 2012).

The role of cycocel in improving leaf area has been well-documented (Ma and Smith, 1991; Leitch and Hayes, 1990; PirastehAnosheh and Emam, 2012a); so, by improving leaf area, cycocel application can result in increased photosynthetic rate, leading to a higher grain yield. The positive effect of cycocel under drought stress in improving the “stay green” trait in wheat and the role of stay green in reducing canopy temperature are also well documented (Shekoofa and Emam, 2008; PirastehAnosheh and Emam, 2012b). Thus, the application of cycocel may improve plant performance under drought via lowering canopy temperature. In another study, Pourmohammad et al. (2013) reported that cycocel application enhanced seed germination and growth under both normal and stressful conditions. This was attributed to higher photosynthesis via increased leaf number and leaf area. They indicated that the increase in respiration potential and ATP generation, as well as protein synthesis have been reported as the main reasons for improved germination of primed-seeds.

In an earlier study, Gill and Singh (1978) found that cycocel treated wheat plants showed higher relative water content, protein and chlorophyll during soil moisture stress. After re-watering, a quicker recovery was also observed in chemical composition in cycocel treated plants. Cycocel sprayed plants produced more yield under optimal as well as moisture stress conditions. Cycocel treated plants also maintained a higher level of nucleic acids, proteins and chlorophyll at all levels of tissue dehydration, suggesting that they were less prone to degradative processes under soil moisture stress conditions.

It appeared that less research has been conducted on possible beneficial effects of cycocel application on cereals grown under saline conditions. Nevertheless, it has been reported that cycocel could regulate plant adaptation to salt stress. Gabr et al. (1977a) found that the wheat grain yield and dry matter accumulation were increased by the application of cycocel under saline conditions. Furthermore, cycocel seed priming consistently increased cotton yield, especially in salinity treatments (Gabr et al., 1977b). Gurmani et al. (2011) found that the application of cycocel on rice crop had a significant role in reducing salinity stress effects (Table 2). They reported that cycocel was an effective PGR in reducing Na^+ and Cl^- concentrations and also Na^+/K^+ ratio, increasing K^+ and Ca^{2+} concentrations, proline accumulation as well as soluble sugar content. Cycocel

Table 2. The effects of cycocel on ion concentrations (± SE) in rice shoot at different salinity treatments

	Na^+ (mmol g^{-1} DW)		K^+ (mmol g^{-1} DW)		Na^+/K^+	
	Control	Cycocel	Control	Cycocel	Control	Cycocel
0 mM	0.060±0.005	0.053±0.01	0.93±0.14	1.05±0.11	0.06±0.02	0.05±0.02
50 mM	1.22±0.08	0.98±0.09	0.63±0.07	0.76±0.17	1.97±0.21	1.32±0.23
75 mM	1.84±0.02	1.60±0.10	0.61±0.03	0.65±0.08	3.07±0.27	2.53±0.39
NaCl	Cl^- (mmol g^{-1} DW)		Ca^{2+} (mmol g^{-1} DW)		Na^+/Cl^-	
	Control	Cycocel	Control	Cycocel	Control	Cycocel
0 mM	0.080±0.02	0.073±0.01	0.035±0.010	0.047±0.005	1.98±0.48	1.20±0.29
50 mM	0.76±0.04	0.65±0.05	0.023±0.013	0.032±0.004	56.6±10.0	32.2±5.6
75 mM	1.11±0.04	0.93±0.02	0.020±0.010	0.024±0.002	95.5±5.0	69.30±4.9

Gurmani et al., 2011

treatments increased rice grain yield by 12% compared to control. Pakar et al. (2015) showed that salinity stress negatively affected growth, yield, antioxidant enzymes and ions accumulation in barley plants; however, some of these changes could be compensated by cycocel foliar application at double ridges stage. They concluded that enhanced antioxidant enzymes and K^+/Na^+ accumulation were some probable mechanisms for cycocel induced salt tolerance in barley plants.

Time of Application and Concentration

The effectiveness of cycocel depends upon several factors, such as concentration, time of application, sowing time, environmental conditions and nutritional status of the crop. Concentration and application timing effects of cycocel have been addressed in a number of published studies; some of which are summarized in Table 3. To achieve the best efficiency of cycocel application, time and concentration of exogenous foliar application should be carefully chosen. For different cereals and even among cultivars of a cereal crop sown at different times, the ideal application time may vary over time. Time of cycocel application must be selected in order to enhance its action in improving plant performance. Application time is considerably related to the objectives of use; for example, if cycocel is applied for reducing the risk of lodging, its application at earlier growth stages is recommended since the lodging resistance is a direct function of the level of thickening of the stem tissues (Rodrigues et al., 2003); or if cycocel is applied for increasing salt stress tolerance, priming and/or application at seedling stage is recommended because germination and establishment are the most sensitive stages to salt stress (PirastehAnosheh et al., 2014a). Kurepin et al. (2013) believed that cycocel is used on cereal grain crops at early vegetative growth stages to achieve higher grain yield. They concluded that cycocel could improve grain yield primarily by reducing lodging caused by heavy rain or hail.

On the other hand, too late application may, depending on conditions, have adverse effects on grain yield since at this time cycocel could shorten uppermost internodes which are usually the longest. This effect is attributed to anti-gibberellic feature of cycocel so that it has been known that gibberellins are important for maximal shoot growth and also for the development of the seed in cereal grain species (Kurepin et al., 2013). Rajala and Peltonen-Sainio (2002), while evaluating the application timings of cycocel to alter spring cereal development, reported that application at ZGS 13-14 (i.e. 3-4 fully expanded leaves) increased grain yield of oat by 370 kg ha^{-1}. In wheat, application at ZGS 31-32 (i.e. 1-2 nodes detectable) reduced grain yield by 480 kg ha^{-1}. They concluded that this yield reduction was associated with less grain yield in the main head and particularly lower single grain weight. In this study, it was shown that early application reduced height at 14 days after treatment in all cereals; however, at maturity, no constant effect was noted. Results found by Leitch and Hayes (1990) reported greater grain yield was obtained under cycocel application at ZGS 32. In this study, it was shown that at maturity, reduction in stem length was best achieved by chlormequat applied at ZGS 32; this treatment shortened stems by an average of 24% and 31% in two years. Earlier applications were significantly less effective. Four-leaf stage was the best time for cycocel application in wheat field based on the findings of Latifkar et al. (2014).

Bahrami et al. (2014a & 2014b) applied cycocel at two concentrations (2 and 4 g L^{-1}) on five barley cultivars, and found that the application of cycocel at 4 g L^{-1} had greater effects on growth and yield of all five barley cultivars. For different cereals and even among cultivars of a cereal sown at different times, the ideal application time may vary over time. Overall, to achieve a more efficient application, it is essential to correctly identify the developmental stage of the target plant. Contrarily, Espindula et al. (2007) reported that the application times had no effect on plant height for any concentration of cycocel.

Table 3. Some studies on cycocel application in cereals

Species	Time	Concentration	Location	Reference
Barley	ZGS* 13-14 or 31-32	0.5 kg ha^{-1}	Helsinki, Finland	Rajala, 2003
	ZGS 30	1.5, 3.0 g L^{-1}	Kerman, Iran	Sharif et al., 2006
	Lemma primordium	1.37 kg ha^{-1}	Shiraz, Iran	Emam and Moaied, 2000
	Mid-tillering	2, 4 g L^{-1}	Shiraz, Iran	Bahrami et al., 2014b
Oat	ZGS 31-32	UN**	UN	Gans et al., 2000
	ZGS 32	UN	UN	Gendy and Hofner, 1989
	ZGS 13-14 or 31-32	1.0 kg ha^{-1}	Helsinki, Finland	Rajala, 2003
	ZGS 13-14	1.125 kg ha^{-1}	Jokioinen, Finland	Pietola et al., 1999
	ZGS 23 or 30 or 32	UN	Tenby, UK	Leitch and Hayes, 1990
Oat and triticale	ZGS 13 & 15	6 kg ha^{-1}	Winnipeg, Canada	Tennhouse and Lacroix, 1972
Wheat	ZGS 30	0.75 kg L^{-1}	Lithuania	Auskalniene and Auskalnis, 2007
	ZGS 31 & 32	0.5, 1.0, 1.5 kg ha^{-1}	Vicosa, Brazil	Espindula et al., 2009
	ZGS 13-14 or 31-32	0.5 kg ha^{-1}	Helsinki, Finland	Rajala, 2003
	ZGS 13-14	0.375 kg ha^{-1}	Jokioinen, Finland	Pietola et al., 1999
	Tillering stage	0.5 g L^{-1}	Ludhiana, India	Gill and Singh, 1978
	Double ridges	2.5 g L^{-1}	Shiraz, Iran	PirastehAnosheh et al., 2012
	Double ridges	2.5 g L^{-1}	Shiraz, Iran	PirastehAnosheh and Emam, 2012a
	Double ridges	2.5 g L^{-1}	Shiraz, Iran	PirastehAnosheh and Emam, 2012b
	ZGS 25	2.20 kg ha^{-1}	Shiraz, Iran	Shekoofa and Emam, 2008
	End of tillering	2.5 kg ha^{-1}	Shiraz, Iran	Miranzadeh et al., 2011
Wheat, barley, maize	Priming	2.5, 3.5 g L^{-1}	Shiraz, Iran	PirastehAnosheh et al., 2014b
Wheat, barley, oat	ZGS 12-14	5 g L^{-1}	Minnesota, US	Rajala, 2003
	ZGS 14	10^{-1} M	Ottawa, Canada	Clark and Fedak, 1977
	ZGS 22-23	6.7 mg L^{-1}	Helsinki, Finland	Peltonen and Peltonen-Sainio, 1997

*. ZGS: Zadoks growth scale (see Zadoks et al., 1974)
**. UN: Unknown

Future Perspectives

The first use of plant growth retardants such as cycocel was for reduction in plant height to prevent stem lodging. However, nowadays, the effect of cycocel on stem length reduction seems to be less important, due to the release of dwarf and semi dwarf cereal cultivars. Regardless of reduced lodging, the use of cycocel in cereals with the aim of chemical regulation of growth and development to achieve higher grain yield needs further research. It seems that the importance of cycocel will be greater under stressful conditions, which draws the attention of researchers to cycocel-induced stress tolerance.

Based on the available literature, it appeared that more studies are needed to better understand the relationship between cycocel effects and other chemical inputs, cycocel and weed growth, root growth, grain quality, and human health. Since a weed, as a crop's neighbor, grows with the crop and consumes what the crop uses and competes with it, thus as cycocel improves cereals growth may simultaneously simulates weeds growth; however, all studies on cycocel have been conducted in weed-free conditions. Concurrent use of cycocel with herbicides, pesticides and fungicides or even liquid fertilizers could comfort its application in the field. Root distribution and architecture could affect plant ability for resource acquirement and so have a crucial role, especially in regions with limited water resources, so if the positive role of cycocel in root growth improvement could be well-documented, then, cycocel can improve resource use efficiency. The effect of cycocel on cereal grain quality, such as bread quality may be worth further research. Furthermore, studies on genes involved in cycocel signaling pathways in cereals are highly appreciated.

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کلرمکوات‌کلراید
کندکننده‌رشد

چکیده– کندکننده‌های رشد مواد شیمیایی ساخته شده یا طبیعی هستند که به طور مستقیم با هدف تغییر برخی فرآیندهای ساختاری گیاه زراعی به‌کار می‌روند. انتظار می‌رود که این مواد تعادل هورمون‌ها و رشد را در گیاه بهبود بخشیده منجر به افزایش عملکرد بهبود کیفیت محصول و یا تسهیل در برداشت گیاه زراعی شوند. سایکوسل (CCC) یا کلرمکوات کلراید (۲-کلرو اتیل تریمیتیل آمونیم کلرید) به عنوان یک کندکننده رشد ساخته شده از دهه ۱۹۶۰ میلادی برای کاربرد در مزارع گندم پیشنهاد شده است. سایکوسل از راه متوقف کردن ساخت انت-کائرن در مسیر متابولیکی تولید جیبرلین از بیوسنتر جیبرلین جلوگیری می‌کند؛ این امر باعث کاهش مقدار جیبرلین فعال و در نتیجه کاهش رشد طولی ساقه می‌گردد. به نظر می‌رسد هم اکنون با معرفی ارقام متعدد پاکوتاه و نیمه پاکوتاه در برخی غلات مانند گندم، کاربرد سایکوسل با هدف کاهش ارتفاع ساقه از اهمیت کمتری برخوردارباشد. بااین وجود، اگر تاثیر مثبت سایکوسل بر عملکرد دانه قطعیت بیشتری یابد، استفاده از آن در مزارع غلات اجتناب ناپذیر خواهد بود؛ که این موضوع نیازمند انجام پژوهش‌های بیشتری است. اهمیت سایکوسل درشرایط تنش های محیطی بیشتر است و چگونگی درک تحمل به تنش القا شده توسط سایکوسل نیاز به پژوهش‌های تکمیلی دارد. در این مقاله، دانش حاضر و کاربردهای ممکن سایکوسل را که بتواند برای بهبود رشد و عملکرد غلات استفاده شود، مرور شده و مورد بحث قرار گرفته است. همچنین، نقش سایکوسل در کاهش اثرات زیان بارتنش‌های خشکی و شوری در غلات بررسی شده است. علاوه بر این، تنظیم فرآیندهای بیوشیمیایی و فیزیولوژیک ،تحت تاثیر سایکوسل، که منجر به بهبود تولید غلات می شود مورد بحث قرار گرفته است.