Review article

Plant growth regulators to manipulate oat stands

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Plant growth regulators (PGRs) are exogenously applied chemicals that alter plant metabolism, cell division, cell enlargement, growth and development by regulating plant hormones or other biological signals. For example, some PGRs regulate stem elongation by inhibiting biosynthesis of gibberellins or through releasing ethylene. PGR effects are widely studied and reported on barley (Hordeum vulgare L.) and wheat (Triticum aestivum L.), whereas there are only a few reports addressing oat (Avena sativa L.). This is likely to be a result of smaller acreage and lower intensity of oat management and production and hence a reduced need for stem shortening by PGRs. However, this is not the case for all cereal producing regions and there exists a need to understand the potential application of PGRs to oat production. This paper represents a review of the potential of PGRs to regulate stem elongation and other biological traits governing plant stand structure and yield components, with special emphasis on oat and its responses to PGRs. Yield improvement requires more heads per unit land area, more grains per head or heavier grains. Of these yield-determining parameters, the number of head bearing tillers and grain numbers per head, compared with grain weight, are more likely to be improved by PGR application. In the absence of lodging, PGR may reduce grain yield due to potential reduction in mean grain weight and/or grain number. Cultivation systems aiming at extensive yields with intensive use of inputs likely benefit from PGR applications more often compared with low or moderate input cultivation, for which cost effectiveness of PGRs is not frequently reached.

Key words: Avena sativa L., oat, plant growth regulator, plant stand structure, yield potential

Introduction

Plant growth regulators (PGRs) are used in highinput cereal management to shorten the stem and thereby reduce lodging susceptibility. There are many reports that describe the various effects of PGRs on plant stand structure and yield formation of barley and wheat. Oat is generally tall and prone to lodging compared with barley or wheat. However, only very few references deal with oat. This is likely to be due to declining acreage and reduced interest in oat compared with the main cereal crops, barley and wheat. Oat has been grown less intensively, in fields considered less suitable for barley and wheat.

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Therefore, it is likely that the need for stem shortening has not been great. However, this is not the case for all situations. At the northern margins of cereal cultivation oat plays an important role in crop production. As oat grain contains certain health promoting compounds, such as Omega, there might be renewed interest in growing it elsewhere in the world. In Finland, oat typically covers 30 to 40% of the total cereal producing area (http://www.finfood.fi). Therefore, interest in the potential of PGRs to modify stem elongation, plant stand structure and yield formation exists for oat, especially in regions where oat cultivation represents a substantial component of crop production.

As noted above, PGRs are primarily targeted at reduction of stem elongation, but many references suggest that PGRs may have potential to modify additional cereal growth patterns. PGR applications have been shown to alter tiller and spikelet set through changes that resemble daylength responses. Reduced shoot growth and elongation may change assimilate demand and distribution within the plant and thus provide excess resources that in turn may stimulate, for example, root growth, tiller and spikelet initiation and grain set and growth.

Mode of action of plant growth regulators

PGR induced reduction in stem elongation can be linked either with reduction in gibberellic acid (GA) synthesis or increase in ethylene synthesis (Gianfagna 1995). Gibberellins are a diverse group of endogenous phytohormones, which play a role, among others, in cell elongation processes. So-termed anti-gibberellic plant growth regulators inhibit gibberellin biosynthesis at different stages of the metabolic pathway as shown in Figure 1, resulting in reduced amounts of active gibberellins and consequent reduction in stem elongation (Rademacher 2000). Also, some of

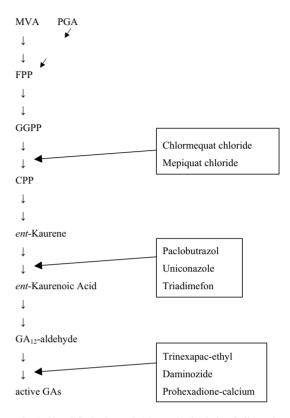


Fig. 1. Simplified schematic biosynthesis chain of gibberellins. Some antibberellic PGRs and their points of inhibition are presented. Adapted from Rademacher (2000). Abbreviations: MVA mevalonic acid, PGA D-glyceraldehyde 3-phosphate, FPP farenosyl pyrophosphate, GGPP geranylgeranyl pyrophosphate, CPP copyl pyrophosphate.

the triazole-type fungicides shorten stems in addition to their primary anti-fungal role (Rademacher 2000).

Tolbert (1960a, b) was the first to describe the effect of chlormequat chloride (CCC, chlormequat (2-chloroethyl)-trimethylammonium chloride) on growth and shoot elongation in wheat. In barley, CCC response was noted to vary and to be more genotype dependent (Clark and Fedak 1977). Other types of antigibberellins, like mepiquat chloride (1,1-Dimethylpiperidinium chloride), paclobutrazol (1-(4-chlorophenyl)-4,4dimethyl-2-(1H1,2,4-triazol-1-yl)pentan-3-ol)), and trinexapac-ethyl (ethyl-(3-oxido-4-cyclopropionyl-5-oxo) oxo-3-cyclohexenecarbox-

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ylate)) (Fig. 1), as well as ethylene releasing ethephon (2-chloroethyl phosphonic acid), were developed to increase the variety of suitable antilodging agents for use on more cultivars and species (Luckwill 1981, Herbert 1982, Rademacher 2000).

Ethephon differs from the anti-gibberellic compounds, as the stem shortening effect is based on inter-cellular ethylene release (Luckwill 1981). Ethylene is a gaseous plant hormone, which at elevated concentrations retards or completely inhibits cell elongation (Goodwin and Mercer 1988).

Lodging — stem length

The major factor associated with lodging sensitivity is stem length (Pinthus 1973, Crook and Ennos 1994, Berry et al. 2000). Lodging is often associated with quantity and quality losses in grain yield and evidently increased harvesting and drying expenses (Pinthus 1973). Abundant nitrogen fertilization, in conjunction with high precipitation, favours stem elongation and hence, results in increased risk of lodging (Pinthus 1973, Berry et al. 2000). At high latitudes long days and a low angle of incident radiation further promote stem elongation (Smith 1982, Salisbury 1985). Stem length is also associated with stem leaning, which has less of a detrimental effect on grain yield than lodging (White et al. 2003). Inhibiting stem elongation by PGR application generally reduces the risk of lodging. To shorten the stem, PGRs are applied either at early stem elongation phases (CCC) or at more advanced growth stages, booting stage at latest (ethephon, mepiquat chloride, trinexapacethyl) (Luckwill 1981, Rademacher et al. 1992, Rademacher 2000). Plant height reduction is associated with the reduced elongation of internodes (Stanca et al. 1979, Crook and Ennos 1994, Sanvicente et al. 1999, Peltonen-Sainio and Rajala 2001). The uppermost internodes and peduncle in particular are shortened, resulting in reduced shoot leverage and hence reduced lodging susceptibility (Berry et al. 2000).

Literature dealing with the oat stem elongation responses to PGRs indicates considerable stem shortening following treatment with compounds including chlormequat chloride, 2,3dichloroisobutyric acid (DciB), ethephon and trinexapac-ethyl (Table 1) (Tennenhouse and Lacroix 1972, Clark and Fedak 1977, Gendy and Höfner 1989, Pietola et al. 1999, Gans et al. 2000, Peltonen-Sainio and Rajala 2001, Rajala and Peltonen-Sainio 2002, Peltonen-Sainio et al. 2003, White et al. 2003). CCC and ethephon applied to oat prior to onset of stem elongation resulted in similar short-term reduction in stem elongation of main shoot and T1 and T2 tillers (Peltonen-Sainio et al. 2003). This indicates that even when tillers are not directly exposed to PGR application, the elongation retarding effect may be transferred to the tillers (Peltonen-Sainio et al. 2003).

There are indications in the literature that PGR treatments in some cases enhance shoot elongation. In oat, chlormequat treatments increased stem length, especially in cultivars possessing the Dw6 dwarfing gene, or when applied at early growth stages, prior to the onset of stem elongation (Tennenhouse and Lacroix 1972, Leitch and Hayes 1990, Peltonen-Sainio and Rajala 2001, Rajala and Peltonen-Sainio 2002). Similar stimulation following CCC treatments has been reported to occur in barley (Clark and Fedak 1977, Waddington and Cartwright 1986). The reason for this reversed response is thought to be associated with increased accumulation of gibberellic acid precursors induced by slowing down of GA biosynthesis following CCC application. After the inhibitive effect of CCC declines and the GA synthesis resumes, these excess precursors are used in biosynthesis, resulting in elevated GA levels and enhanced stem elongation (Clark and Fedak 1977, Primost 1977, Peltonen-Sainio and Rajala 2001). In some Dw6 oat genotypes the dwarfing effect is possibly turned off at later growth stages, resulting in normal or increased elongation of the peduncle (Burrows 1986). When this associates with potentially in-

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Table 1. Some oat experiments with special emphasis on plant growth regulator (PGR) effects on yield, stem length and lodging.

Paper	PGR	Time of application	N kg ha ⁻¹	Stem length	Lodging	Yield
Tennhouse and Lacroix 1972	CCC	5 leaf	0 90	-13% -10%	sig. reduced sig. reduced	_9% +3%
Clark and Fedak 1977	CCC	4–5 leaf	0 56	−3% −15%	delayed onset	± 0
Gendy and Höfner 1989	CCC DCiB CCC+DCiB	ZGS 32,	110	-8% ± 0 -20%	sig. reduced ± 0 sig. reduced	+10% +8% +10%
Leitch and Hayes 1990	CCC	ZGS 23 ZGS 30 ZGS 32	125–150	+3% -12% -23%	slightly increased sig. reduced sig. reduced	+1% +5% -7%
Peltonen and Peltonen-Sainio 1997	CCC	ZGS 22–23	100	-	-	+6 to +13%
Pietola et al. 1999	CCC	3–4 leaf	0 30 60 90 120 150	-3 to -7% 0 to -12% -6 to -17% -7 to -16% -11 to -16% -10 to -13% -8 to -11%	0 0 0 -14% -26% -22% -23%	-2 to +11% -2 to +10% 0 to +11% 0 to +11% 0 to +10% 0 to +10% +3 to +24%
Gans et al. 2000	CCC CCC+DCiB	ZGS 31–32 ZGS 45	100	-8% -10%	± 0 reduced	+2 to +10 ± 0
Peltonen-Sainio and Rajala 2001	CCC ETE	ZGS 32 ZGS 39	80	+ 6 to -12% 0 to -11	- -	0 to +13% 0 to -17%
Rajala and Peltonen-Sainio 2002	CCC ETE TE	ZGS 13 and 32 ZGS 13 and 39 ZGS 13 and 39	80		- - -	0 to $+7\%$ ± 0 ± 0
White et al. 2003	CCC	-	140–160	-8%	-4%	± 0

CCC = chlormequat chloride, DCiB = isobyturic acid, ETE = etephon, TE = trinexapac-ethyl.

creased levels of GAs, stem elongation may be enhanced (Peltonen-Sainio and Rajala 2001). However, increase in stem elongation seems not to be characteristic of all antigibberellins, as trinexapac-ethyl, which blocks GA biosynthesis at a very late stage, did not stimulate a similar enhancement in stem elongation (Rajala and Peltonen-Sainio 2002).

When PGR responses of barley, oat and wheat were recorded shortly after the PGR applications at 13-14 of Zadoks Growth Stage (ZGS) (Zadoks

et al. 1974), similar reductions in short-term shoot elongation were recorded irrespective of the genotype and PGR (Rajala and Peltonen-Sainio 2002). This indicates that at early growth stages even genotypes considered to be insensitive to CCC are responsive. Reduced shoot elongation was a short-term effect only, as no general effect on final plant height was recorded (Rajala and Peltonen-Sainio 2002).

In general, there are effective PGR compounds that control stem elongation in oat. How-

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ever, the need for them in less intensive oat production may be lower than for barley and wheat. Also, in some cases CCC may increase shoot elongation rather than depress it, which can be unexpected and unwanted.

Possibilities for modifying traits other than stem elongation

Root growth

Appropriate root growth and function are essential for water and nutrient uptake and hence for the growth and yield capacity of plants. However, root characteristics including root length, density and branching, have not been unequivocally associated with water uptake and yielding capacity in cereals (Hamblin and Tennant 1987, Comfort et al. 1988, Mian et al. 1994). There are some indications in the literature that while reducing shoot growth, antigibberellic PGRs may simultaneously improve root growth and performance (De et al. 1982, Cooke et al. 1983, Bragg et al. 1984, Yang and Naylor 1988, Webb and Fletcher 1996), though reports indicating yield improvement with PGR induced change in root growth are rare (De et al. 1982). In some cases PGR applications improved root to shoot ratio by reducing above ground growth (Enam and Cartwright 1990, Rajala and Peltonen-Sainio 2001). When exposed to water shortage, reduction in transpiring plant parts could indicate better drought tolerance (Enam and Cartwright 1990). Moreover, papers indicating negative impact on root growth exist. Short-term retardation in root growth occurred, especially when ethephon containing PGRs were applied to the seeds or seedlings of barley, oat and wheat (Woodward and Marshall, 1987, 1988, Rajala et al. 2002). PGRs can change root growth pattern and biomass distribution to the roots and shoots to some extent, but whether this occurs frequently and the consequences for change in yield and yield stability are uncertain.

Tillering, tiller growth and productivity

Ability of cereals to form tillers allows for efficient utilisation of the space and available resources. Tillering improves cereal plasticity and the ability to respond to fluctuations in plant density and environment. Species, genotype, seeding rate, photoperiod, temperature, and water and nutrient status during the tillering period affect tiller production and head-bearing tillers (Langer 1972, Easson et al. 1993, Peltonen-Sainio and Järvinen 1995, Crook and Ennos 1995). Spring wheat response to photoperiod was changed by antigibberellins applied at early growth stages (Hutley-Bull and Schwabe 1982, Craufurd and Cartwright 1989). Under long-day conditions, apical development rate of wheat was retarded and more tillers were produced, mimicking development and growth under conditions of shorter photoperiod (Hutley-Bull and Schwabe 1982, Craufurd and Cartwright 1989). Chlormequat chloride seed treatment increased tiller number in barley and triticale (Naylor et al. 1989), and in winter barley when applied before or during tillering (Naylor et al. 1986). CCC applied to wheat foliage prior to shoot elongation resulted in more tillers (Tolbert 1960b, Humbries et al. 1965, Craufurd and Cartwright 1989, Peltonen and Peltonen-Sainio 1997). Other types of PGR have been reported to promote tillering. A mixture of mepiquat chloride and ethephon applied to the seeds stimulated tillering in barley (Woodward and Marshall 1987), as well as ethephon applied to foliage (Woodward and Marshall 1988). The literature on tillering responses of oat is limited. Ethephon and trinexapac-ethyl applied at early growth stages improved tillering in the greenhouse only slightly (Rajala and Peltonen-Sainio 2001), likewise CCC applied at shoot elongation phase increased head bearing tiller number in the field (Gendy and Höfner 1989, Peltonen-Sainio and Rajala 2001).

When PGR application initiates more heads per plant, grain yield may be directly improved (Humbries et al. 1965, Waddington and Cartwright 1986, Naylor and Saleh 1987, Ma and

Smith 1992a). Non-head-bearing tillers could be considered as a waste of growth resources, but can also be considered as temporary storage of photoassimilates, produced in excess of current requirements for main shoot growth. Non-surviving tillers of spring barley have been shown to translocate considerable amounts of photo assimilates for the growth of the main shoot during the stem elongation phase (Lauer and Simmons 1988, El-Alaoui et al. 1992). Tillering enables faster canopy closure, which improves interception of radiation, reduces transpiration and hence improves efficient use of soil moisture reservoirs, resulting in improved growth (Peltonen-Sainio 1999). Accordingly, non-surviving vegetative tillers may play an important role in overall growth and productivity of spring cereals.

CCC treatment prior to stem elongation enhanced growth of head-bearing tillers in wheat and barley (Humbries et al. 1965, Naylor and Saleh 1987, Peltonen and Peltonen-Sainio 1997). Various applications of ethephon, mepiquat chloride and mixtures of CCC or mepiquat chloride with ethephon, enhanced formation, growth and survival of head bearing tillers of barley (Cartwright and Waddington 1981, Waddington and Cartwright 1986, Woodward and Marshall 1987, Ma and Smith 1991, Moes and Stobbe 1991, Ma and Smith 1992a) and in wheat (Khan and Spilde 1992).

Similarly, positive responses in head number following PGR applications have been reported for oat (Gendy and Höfner 1989, Peltonen-Sainio and Rajala 2001). On the contrary, PGR did not affect head bearing tiller number (Leitch and Hayes 1990, Peltonen and Peltonen-Sainio 1997, Rajala and Peltonen-Sainio 2002). This seems to be typical in literature dealing with PGRs, where conflicting results are reported. Reasons for varying responses are likely an outcome of changing growing conditions and a cultivar's responsiveness to PGRs, and a combination of these factors. Accordingly, the relevance of PGRs for manipulating tiller and head bearing tiller number and increasing yield potential, for any cereals, and for oat in particular, remains case specific.

Grain set

Dwarfing genes introduced by wheat breeding programmes have resulted in shorter stems and improved floret and grain set, further resulting in improved harvest index (HI) in modern cultivars (Austin et al. 1989, Borrell et al. 1991, Miralles and Slafer 1995, Gent and Kiyomoto 1998). A similar trend is also evident for oat (Peltonen-Sainio 1991, Salman and Brinkman 1992). Grain number per unit land area is the major yield determining factor in cereals (Ferris et al. 1998, Smith et al. 1999). Cultivars with higher grain number per plant could result from reduced assimilate competition between elongating stems and florets and grains at both pre- and post-anthesis phases (Austin et al. 1977, Brooking and Kirby 1981, Borrell et al. 1989, Borrell et al. 1991, Gent and Kiyomoto 1998).

PGR induced reduction in stem elongation resembles achievements gained through plant breeding, potentially enhancing assimilate availability and distribution to grain and spikelet set. Wheat treated with CCC at the six-leaf-stage resulted in more grains per head (Humbries et al. 1965). CCC applications before or at stem elongation increased grain number in barley, triticale and wheat (Naylor 1989, Ma and Smith 1991, 1992a, Börner and Meinel 1993). Similar increase in grain number was noted in oat (Gendy and Höfner 1989, Peltonen and Peltonen-Sainio 1997).

The reported boost in grain number following early PGR application could be due to enhanced initiation of spikelets and florets per head (Höfner and Kühn 1982, Hutley-Bull and Schwabe 1982, Waddington and Cartwright 1986, Peltonen and Peltonen-Sainio 1997). When PGRs are applied close to anthesis a likely explanation for increased grain number per head is the decline in abortion of spikelets, florets and grains (Ma et al. 1994). Oat and wheat produce spikelets and florets in excess compared with the numbers that are eventually filled (Peltonen-Sainio and Peltonen 1995). Spikelet and floret numbers are strongly reduced just prior to heading at stigmatic branch differentiation (Peltonen-

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Sainio and Peltonen 1995). When synthetic cytokinin was applied to oat prior to onset of floret abortion more spikelets per panicle were evident, but they were mostly sterile and hence, cytokinin was ineffective in improving grain yield (Peltonen-Sainio 1997).

Hence, the potential to modify grain number in oat and wheat 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 would be achieved by ensuring adequate assimilate flow and avoidance of external stresses, such as high temperature, water shortage and pathogens prior to heading and anthesis. Naturally, plants should remain upright for successful grain filling. Short stature plant stands, either produced by breeding or by PGR application, reduce the risk for lodging and hence, facilitate undisturbed assimilate flow from vegetative plant parts to the grains till the very end of the grain filling process (El-Alaoui et al. 1992, Ma and Smith 1992b, Peltonen-Sainio 1999).

Grain filling

As the grain number per unit land area is strongly associated with grain yield, increase in number of head bearing tillers and/or grains per head directly enhances yield potential. To which degree this potential enhancement is realized as improved grain yield, depends strongly on growing conditions prior to pollination and during grain filling. Unfavorable conditions during this critical period likely result in increased abortion and incompletely filled grains and hence, reduction in potential yield enhancement. The indications that the number of endosperm cells formed during the post-fertilisation cell division phase determine potential grain size (Brocklehurst 1977, Radley 1978), further emphasises the significance of growing conditions for the realization of the yield potential.

According to the literature, single grain weight seems to be either unaffected, or it is slightly reduced by PGR treatments (Humbries et al. 1965, Höfner and Kühn 1982, Naylor 1987, Simmons et al. 1988, Naylor and Stephen 1993, Ma et al. 1994, Pietola et al. 1999). Also, similar responses of single grain weight to PGRs have been reported for oat (Gendy and Höfner 1989, Leitch and Hayes 1990, Peltonen and Peltonen-Sainio 1997, Pietola et al. 1999, Peltonen-Sainio and Rajala 2001, White et al. 2003). When lodging occurs prior to or during grain filling it may considerably reduce the grain filling capacity (Pinthus 1973, Stanca et al. 1979). If PGR applications reduce the degree of lodging or delay the onset of lodging, the result is undisturbed grain filling and single grain weights close or equal to those of non-lodged plant stands (Stanca et al. 1979, Cox and Otis 1989, Moes and Stobbe 1991).

Stress following PGR treatments — sensitivity of the species and cultivars

When plant stands suffer from or are expected to be exposed to drought or other abiotic stresses, PGR applications are not recommended. This is to avoid potential PGR induced stress and consequent negative effects on yield formation. This phenomenon has not been studied extensively (Rademacher 2000). Ethephon treatment has a marked effect on ethylene evolution rate (Foster et al. 1992, Rajala et al. 2002). The effect of antigibberellins on ethylene evolution is not well documented (Rajala et al. 2002), but some evidence indicates that antigibberellins tend to reduce stress hormone synthesis (Grossmann 1992, Rademacher 2000). Rajala et al. (2002), found no CCC and trinexapac-ethyl response on ethylene production of roots and shoots in barley, oat and wheat. When carbon dioxide exchange rate

was measured after the CCC, ethephon and trinexapac-ethyl treatments, no clear or long lasting change was recorded in wheat (Rajala and Peltonen-Sainio 2001). Furthermore, foliar CCC application sustained photosynthetic capacity of wheat under water deficit (Sairam et al. 1989) and CCC and ethephon applied at flag leaf stage reduced the damaging effect of elevated ozone on wheat (McKee and Long 2001). These findings indicate that PGRs are not likely to cause marked stress in treated plants, or not stresses involving increased ethylene or reduced photosynthesis. PGRs may in some cases reduce the stress effects.

Despite lack of direct evidence of PGR induced stress and some evidence suggesting stress protecting capacity, PGR applications may cause considerable yield reduction, especially when there is no lodging (Simmons et al. 1988, Cox and Otis 1989, Leitch and Hayes 1990, Taylor et al. 1991, Ma and Smith 1992b, Stobbe et al. 1992, Bergner and Teichmann 1993, Peltonen-Sainio and Rajala 2001, Rajala and Peltonen-Sainio 2002). Reasons for yield reduction could be the timing of applications and interaction between PGR and cultivar. PGR applications at the flag leaf stage coincide with onset of floret abortion prior to fertilisation (Peltonen-Sainio and Peltonen 1995, Peltonen-Sainio 1997). On some occasions PGR applications at this stage may increase the abortion rate and consequently reduce grain number per head. There are reports of reduced grain number following PGR applications, mainly of ethephon at flag leaf stage. This supports the reports of increased abortion of spikelets and grains (Simmons et al. 1988, Gendy and Höfner 1989, Ma and Smith 1992b, Stobbe et al. 1992, Peltonen-Sainio and Rajala 2001, Rajala and Peltonen-Sainio 2002). Not only do PGR applications at the flag leaf stage have potential to cause yield reductions: CCC applied at the beginning of stem elongation reduced grain yield in wheat. This was not associated with fewer grains, rather with reduced grain filling (Rajala and Peltonen-Sainio 2002).

Due to apparent cultivar by PGR interaction, there is likely to be variation in stem elongation

and yield response. Therefore, knowledge on suitable chemicals for particular cultivars would be ideal when selecting a PGR to avoid the unwanted negative stem elongation and yield responses.

Future of PGRs in cereal production

When PGR treatments prevent lodging or reduce its magnitude, the advantageous effects on yield quality and quantity and easier harvesting are likely to make the treatments profitable. When there is no lodging PGR treatments should increase the yield to cover at least the management expenses to be cost-effective. To reach this threshold level, 150 to 300 kg per hectare yield improvement is likely to be the minimum requirement, depending on the crop and PGR. According to the literature, such improvements are not always possible. Predicting the lodging pressure accurately is difficult, therefore applying PGR just in case is understandable, especially when the farmer aims at high grain yield through high input management. In such cases, PGRs may be considered as insurance on the inputs invested. Therefore the cost of PGR application is (perhaps) acceptable to the farmer, even when not actually profitable.

In production systems in which moderate levels of external inputs are used on modern relatively short-strawed, lodging resistant cultivars, the need for stem shortening by PGR application is small. In addition, consumers' concerns about agrochemical residues in food products and leaching of nutrients and plant protection chemicals into the environment favours production systems that are less reliant on chemical inputs such as PGRs.

In the future, plant protection agents that are effective while being environmental safe are likely to dominate a highly competitive and tightly regulated agrochemical market. This is will also

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be the case for plant growth regulating agents. For the new PGRs to realize their potential and gain market shares they will have to be competitively priced. Even with the relatively low cost of current PGRs, such as chlormequat chloride and ethephon, a positive economic outcome is unlikely given low grain prices. Perhaps dual function compounds, stem-shortening fungicides or insecticides, will become more in demand in the future.

References

- Austin, R.B., Edrich, J.A., Ford, M.A. & Blackwell, R.D. 1977. The fate of dry matter, carbohydrates and 14C lost from leaves and stems of wheat during grain filling. *Annals of Botany* 41: 1309–1321.
- Austin, R.B., Ford, M.A. & Morgan, C.L. 1989. Genetic improvement in the yield of winter wheat: a further evaluation. *Journal of Agricultural Science, Cambridge* 112: 295–301.
- Bergner, C. & Teichmann, C. 1993. A role for ethylene in barley plants responding to water shortage. *Journal of Plant Growth Regulation* 12: 67–72.
- Berry, P.M., Griffin, J.M., Sylvester-Bradley, R.E., Scott, R.K., Spink, J.H., Baker, C.J. & Clare, R.W. 2000. Controlling plant form through husbandry to minimise lodging in wheat. *Field Crops Research* 67: 59–81.
- Börner, A. & Meinel, A. 1993. The effects of the growth retardant chlormequat (CCC) on plant height and yield in GA insensitive wheats. *Plant Breeding* 110: 255–258.
- Borrell, A.K., Incoll, L.D., Simpson, R.J. & Dalling, M.J. 1989. Partitioning of dry matter and the deposition and use of stem reserves in a semi-dwarf wheat crop. *Annals of Botany* 63: 527–539.
- Borrell, A.K., Incoll, L.D. & Dalling, M.J. 1991. The influence of the *Rht*₂ alleles on the growth of wheat stems and ears. *Annals of Botany* 67: 103–110.
- Brocklehurst, P.A. 1977. Factors controlling grain weight in wheat. *Nature* 266: 348–349.
- Bragg, P.L., Rubino, P., Henderson, F.K.G., Fielding, W.J. & Cannel, R.Q. 1984. A comparison of the root and shoot growth of winter barley and winter wheat, and the effect of an early application of chlormequat. *Journal of Agricultural Science, Cambridge* 103: 257–264
- Brooking, I.R. & Kirby, E.J.M. 1981. Interrelationships between stem and ear development in winter wheat: the effects of a Norin 10 dwarfing gene, *Gai/Rht₂*.

 Journal of Agricultural Science Cambridge 97: 373—381
- Burrows, V.D. 1986. Breeding oats for food and feed: Conventional and new techniques and materials. In:

- Webster, F.H. (ed.). *Oats: Chemistry and technology*. AACC, St. Paul, Minnesota. p. 13–46.
- Cartwright, P.M. & Waddington, S.R. 1981. Growth regulators and grain yield in spring cereals. In: Hawkins, A.F. & Jeffcoat, B. (eds.). *Opportunities for manipulation of cereal productivity*. Monograph 7. British Plant Growth Regulator Group, Wantage. p. 61–70.
- Clark, R.V. & Fedak, G. 1977. Effects of chlormequat on plant height, disease development and chemical constituents of cultivars of barley, oats and wheat. *Canadian Journal of Plant Science* 57: 31–36.
- Comfort, S.D., Maizer, G.I. & Bush, R.H. 1988. Nitrogen fertilization of spring wheat genotypes: Influence on root growth and soil water depletion. *Agronomy Jour*nal 80: 114–120.
- Cooke, D.T., Hoad, G.V. & Child, R.D. 1983. Some effects of plant growth regulators on root and shoot development and mineral nutrient-ion uptake in winter wheat. In: Jackson, M.B. (ed.). Growth regulators on root and shoot development. British Plant Growth Regulator Group, Monograph 10, Wantage. p. 87–101
- Cox, W.J. & Otis, D.J. 1989. Growth and yield of winter wheat as influenced by chlormequat chloride and ethephon. *Agronomy Journal* 81: 264–270.
- Craufurd, P.Q. & Cartwright, P.M. 1989. Effect of photoperiod and chlormequat on apical development and growth in a spring wheat (*Triticum aestivum*) cultivar. *Annals of Botany* 63: 515–525.
- Crook, M.J. & Ennos, A.R. 1994. Stem and root characteristics associated with lodging resistance in four winter wheat cultivars. *Journal of Agricultural Science, Cambridge* 123: 167–174.
- Crook, M.J. & Ennos, A.R. 1995. The effect of nitrogen and growth regulators on stem and root characteristics associated with lodging in two cultivars of winter wheat. *Journal of Experimental Botany* 289: 931–938.
- De, R., Giri, G., Saran, G., Singh, R.K. & Chaturvedi, G.S. 1982. Modification of water balance of dryland wheat through the use of chlormequat chloride. *Journal of Agricultural Science* 98: 593–597.
- Easson, D.L., White, E.M. & Pickles, S.J. 1993. The effects of weather, seed rate and cultivar on lodging and yield in winter wheat. *Journal of Agricultural Science*. Cambridge 121: 145–156.
- El-Alaoui, A.C., Simmons, S.R. & Crookston, R.K. 1992. Allocation of photoassimilate by main shoots and nonsurviving tillers in barley. *Crop Science* 32: 1233– 1237.
- Enam, Y. & Cartwright, P.M. 1990. Effects of drying soil and CC on root:shoot growth and water use in barley plants. In: *Importance of root to shoot communica*tion in the response to environmental stress. British Plant Growth Regulator Group, Monograph 21. p. 389–392.
- Ferris, R., Ellis, R.H., Wheeler, T.R. & Hadley, P. 1998. Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. *An*nals of Botany 82: 631–639.
- Foster, K.R., Reid, D.M. & Pharis, R.P. 1992. Ethylene biosynthesis and ethephon metabolism and transport in barley. *Crop Science* 32: 1345–1352.

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- Gans, W., Beschow, H. & Merbach, W. 2000. Growth regulators for cereal and oil crops on the basis of 2,3-dichloroisobutyric acid and chlormequat chloride and residue analysis of both agents in the grain of oat. Journal of Plant Nutrition and Soil Science 163: 405–410.
- Gendy, A. & Höfner, W. 1989. Stalk shortening of oat (*Avena sativa* L.) by combined application of CCC, DCiB and ethephon. *Vereinigung für Angewandte Botanik* 63: 103–110.
- Gent, M.P.N. & Kiyomoto, R.K. 1998. Physiological and agronomic consequences of *Rht* genes in wheat. *Journal of Crop Production* 1: 27–46.
- Gianfagna, T. 1995. Natural and synthetic growth regulators and their use in horticultural and agronomic crops. In: Davies, P. (ed.). *Plant hormones: physiology, biochemistry and molecular biology*. 2nd edition. Dordrecht, Kluwer Academic Publishers. p. 751–774.
- Goodwin, T.W. & Mercer, E.I. 1988. *Introduction to plant biochemistry*. Oxford: Pergamon Press. 677 p.
- Grossmann, K. 1992. Plant growth retardants: their mode of action and benefit for physiological research. In: Karssen, C. et al. (eds.). Progress in plant growth regulation. Proceedings of the 14th international conference on plant growth substances. Kluwer, Academic Publishers, Dordrecht. p. 788–797.
- Hamblin, A. & Tennant T. 1987. Root length density and water uptake in cereals and grain legumes: How well are they correlated? *Australian Journal of Agricultural Research* 38: 513–527.
- Herbert, C.D. 1982. Growth regulation in cereals chance or design? In: McLaren, J.S. (ed.). *Chemical manipulation of crop growth and development*. London: Butterworth Scientific. p. 315–327.
- Höfner, W. & Kühn, H. 1992. Effect of growth regulator combinations on ear development, assimilate translocation and yield in cereal crops. In: McLaren, J.S. (ed.). Chemical manipulation of crop growth and development. Butterworth Scientific, London. p. 375–390.
- Humbries, E.C., Welbank, P.J. & Witts, K.J. 1965. Effect of CCC (chlorocholine chloride) on growth and yield of spring wheat in the field. *Annals of Applied Biolo*gy 56: 351–361.
- Hutley-Bull, P.D. & Schwabe, W.W. 1982. Some effects of low-concentration gibberellic acid and retardant application during early growth on morphogenesis in wheat. In: McLaren, J.S. (ed.). Chemical manipulation of crop growth and development. Butterworth Scientific, London. p. 329–342.
- Khan, A. & Spilde, L. 1992. Agronomic and economic response of spring wheat cultivars to ethephon. Agronomy Journal 84: 399–402.
- Langer, R.H. 1972. *How grasses grow.* Edward Arnold, London. 60 p.
- Lauer, J.G. & Simmons, S.R. 1988. Photoassimilate partitioning by tillers and individual tiller leaves in field-grown spring barley. Crop Science 28: 279–282.
- Leitch, M.H. & Hayes, J.D. 1990. Effects of single and repeated applications of chlormequat on early crop development, lodging resistance and yield of winter oats. *Journal of Agricultural Science, Cambridge* 115: 11–14.

- Luckwill, L.C. 1981. Growth regulators in crop production. *Studies in Biology* no. 129. Southampton: The Camelot Press Ltd. 59 p.
- Ma, B.L., Dwyer, L.M. & Smith, D.L. 1994. Evaluation of peduncle perfusion for *in vivo* studies of carbon and nitrogen distribution in cereal crops. *Crop Science* 34: 1584–1588.
- Ma, B.L. & Smith, D.L. 1991. The effects of ethephon, chlormequat chloride and mixtures of ethephon and chlormequat chloride applied at the beginning of stem elongation on spike-bearing shoots and other yield components of spring barley (Hordeum vulgare L.). Journal of Agronomy and Crop Science 166: 127– 135.
- Ma, B.L. & Smith, D.L. 1992a. Chlormequat and ethephon timing and grain production of spring barley. *Agronomy Journal* 84: 934–939.
- Ma, B.L. & Smith, D.L. 1992b. Growth regulator effects on aboveground dry matter partitioning during grain fill of spring barley. *Crop Science* 32: 741–746.
- McKee, I.F. & Long, S.P. 2001. Plant growth regulators control ozone damage to wheat yield. *New Phytologist* 152: 41–51.
- Mian, M.A.R., Nafziger, E.D., Kolb, F.L. & Teyker, R.H. 1994. Root size and distribution of field-grown wheat genotypes. *Crop Science* 34: 810–812.
- Miralles, D.J. & Slafer, G.A. 1995. Individual grain weight responses to genetic reduction in culm length in wheat as affected by source-sink manipulations. *Field Crops Research* 43: 55–66.
- Moes, J. & Stobbe, E.H. 1991. Barley treated with ethephon: I. Yield components and net grain yield. Agronomy Journal 83: 86–90.
- Naylor, R.E.L. 1987. The weight and nitrogen content of triticale grains as influenced by nitrogen fertilizer and chlormequat. Aspects of Applied Biology 15: 297– 301
- Naylor, R.E.L. 1989. Effects of plant growth regulator chlormequat on plant form and yield of triticale. *Annals of Applied Biology* 114: 533–544.
- Naylor, R.E.L. & Saleh, M.E. 1987. Effects of plant spacing and chlormequat on the plant stand structure, growth and yield of winter barley. *Crop Research* 27: 97–109.
- Naylor, R.E.L., Saleh, M.E. & Farquharson, J.M. 1986. The response to chlormequat of winter barley growing at different temperatures. *Crop Research* 26: 17–31.
- Naylor, R.E.L. & Stephen, N.H. 1993. Effects of nitrogen and the plant growth regulator chlormequat on grain size, nitrogen content and amino acid composition of triticale. *Journal of Agricultural Sciences, Cam*bridge 120: 159–169.
- Naylor, R.E.L., Brereton, P.S. & Munro, L.1989. Modification of seedling growth of triticale and barley by seed-applied chlormequat. *Plant Growth Regulation* 8: 117–125.
- Peltonen, J. & Peltonen-Sainio, P. 1997. Breaking uniculm growth habit of spring cereals at high latitudes by crop management. II. Tillering, grain yield and yield components. *Journal of Agronomy and Crop Science* 178: 87–95.

Rajala, A. Plant growth regulators to manipulate oat stands

- Peltonen-Sainio, P. 1991. High phytomass producing oats for cultivation in northern growing conditions. *Journal of Agronomy and Crop Science* 166: 90–95.
- Peltonen-Sainio, P. 1997. Nitrogen fertilizer and foliar application of cytokinin affect spikelet and floret set and survival in oat. *Field Crops Research* 49: 169–176.
- Peltonen-Sainio, P. 1999. Growth and development of oat with special reference to source-sink interaction and productivity. In: Smith, D.L. & Hamel, C. (eds.). *Crop yield, physiology and processes*. Springer-Verlag, Berlin, Germany. p. 39–66.
- Peltonen-Sainio, P. & Järvinen, P. 1995. Seeding rate effects on tillering, grain yield, and yield components of oat at high latitude. *Field Crops Research* 40: 49–56
- Peltonen-Sainio, P. & Peltonen, J. 1995. Floret set and abortion in oat and wheat under high and low nitrogen regimes. *European Journal of Agronomy* 4: 253–262.
- Peltonen-Sainio, P. & Rajala, A. 2001. Chlormequat and ethephon effects on growth and yield formation of conventional, naked, and dwarf oat. *Agricultural and Food Science in Finland* 10: 175–184.
- Peltonen-Sainio, P., Rajala, A., Simmons, S., Caspers, R. & Stuthman, D. 2003. Plant growth regulator and day length effects on pre-anthesis main shoot and tiller growth in conventional and dwarf oat. *Crop Science* 43: 227–233.
- Pietola, L., Tanni, R. & Elonen, P. 1999. Responses of yield and N use of spring sown crops to N fertilization, with special reference to the use of plant growth regulators. *Agricultural and Food Science in Finland* 8: 423–440.
- Pinthus, M.J. 1973. Lodging in wheat, barley, and oats: the phenomenon, its causes, and preventive measures. *Advances in Agronomy* 25: 209–256.
- Primost, E. 1977. Effect of Stabilan (CCC) on the internode length of winter barley in field experiments. Zeitschrift für Pflanzenernahrung und Bodenkunde 140: 387–396.
- Rademacher, W. 2000. Growth retardants: Effects on gibberellin biosynthesis and other metabolic pathways. Annual Review of Plant Physiology and Molecular Biology 51: 501–531.
- Rademacher, W., Temple-Smith, K.E., Griggs, D.L. & Hedden, P. 1992. The mode of action of acyclohexanediones a new type of growth retardant. In: Karssen C. et al. (eds.). *Progress in plant growth regulation*. Proceedings of the 14th international conference on plant growth substances. Dordrecht: Kluwer Academic Publishers. p. 571–577.
- Radley, M. 1978. Factors affecting grain enlargement in wheat. *Journal of Experimental Botany* 29: 919–934.
- Rajala, A. & Peltonen-Sainio, P. 2001. Plant growth regulator effects on spring cereal root and shoot growth. Agronomy Journal 93: 936–943.
- Rajala, A. & Peltonen-Sainio, P. 2002. Timing applications of growth regulators to alter spring cereal development at high latitudes. Agricultural and Food Science in Finland 11: 233–244.
- Rajala, A., Peltonen-Sainio, P., Onnela, M. & Jackson, M. 2002. Effects of applying stem-shortening plant

- growth regulators to leaves on root elongation by seedlings of wheat, oat and barley: mediation by ethylene. *Plant Growth Regulation* 38: 51–59.
- Sairam, R.K., Deshmukh, P.S. & Shukla, D.S. 1989. Effect of ABA and CCC on water stress induced carbon dioxide and nitrate assimilation processes in tolerant and susceptible wheat genotypes. *Annals of Plant Physiology* 3: 98–107.
- Salisbury, F.B. 1985. Adaptations to the light environment. In: Kaurin, Å. et al. (eds.). *Plant production in the North*. Norwegian University Press. p. 43–61.
- Salman, A.A. & Brinkman, M.A. 1992. Association pf preand post-heading growth traits with grain-yield in oats. *Field Crops Research* 28: 211–221.
- Sanvicente, P., Lazarevitch, S., Blouet, A. & Guckert, A. 1999. Morphological and anatomical modifications in winter barley culm after late plant growth regulator treatment. *European Journal of Agronomy* 11: 45– 51.
- Simmons, S.R., Oeike, O.E., Wiersma, J.V., Lueschen, W.E. & Warnes, D.D. 1988. Spring wheat and barley responses to ethephon. *Agronomy Journal* 80: 829– 834.
- Smith, D.L., Dijak, M., Bulman, P., Ma, B.L. & Hamel, C. 1999. Barley: Physiology of yield. In: Smith, D.L. & Hamel, C. (eds.). Crop yield, physiology and processes. Springer-Verlag, Berlin, Germany. p. 67–107.
- Smith, H. 1982. Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology* 33: 481– 518.
- Stanca, A.M., Jenkins, G. & Hanson, P.R. 1979. Varietal responses in spring barley to natural and artificial lodging and to growth regulator. *Journal of Agricultural Science, Cambridge* 93: 449–456.
- Stobbe, E.H., Moes, J., Bahry, R.W., Visser, R. & Iverson, A. 1992. Environment, cultivar, and ethephon rate interactions in barley. *Agronomy Journal* 84: 789–794.
- Taylor, J.S., Foster, K.R. & Caldwell, C.D. 1991. Ethephon effects on barley in central Alberta. *Canadian Journal of Plant Science* 71: 983–995.
- Tennenhouse, A.N. & Lacroix, L.J. 1972. Effects of (2-chloroethyl) trimethyl ammonium chloride (CCC) on certain agronomic traits of oats and triticale. *Canadian Journal of Plant Science* 52: 559–567.
- Tolbert, N.E. 1960a. (2-Chloroethyl) trimethylammonium chloride and related compounds as plant growth substances. I. Chemical structure and bioassay. *The Journal of Biological Chemistry* 235: 475–479.
- Tolbert, N.E. 1960b. (2-chloroethyl) trimethylammonium chloride and related compounds as plant growth substances. II. Effect on growth of wheat. *Plant Physiology* 35: 380–385.
- Yang, W. & Naylor, R.E.L. 1988. Effect of tetcyclacis and chlormequat applied to seed on seedling growth of triticale cv. Lasko. *Plant Growth Regulation* 7: 289– 301.
- Waddington, S.R. & Cartwright, P. 1986. Modification of yield components and stem length in spring barley by the application of growth retardants prior to main shoot stem elongation. *Journal of Agricultural Science Cambridge* 107: 367–375.

Vol. 13 (2004): 186-197.

White, E.M., McGarel, A.S.L. & Ruddle, O. 2003. The influence of variety, year, disease control and plant growth regulator application on crop damage, yield and quality of winter oats (*Avena sativa*). *Journal of Agricultural Science* 140: 31–42.

Woodward, E.J. & Marshall, C. 1987. Effects of seed treatment with plant growth regulator on growth and tillering in spring barley (*Hordeum distichum*) cv. Triumph.

Annals of Applied Biology 110: 629-638.

Woodward, E.J. & Marshall, C. 1988. Effects of plant growth regulators and nutrient supply on tiller bud outgrowth in barley (Hordeum distichum L.). Annals of Botany 61: 347–354.

Zadoks, J.C., Chang, T.T. & Konzak, C.F. 1974. A decimal code for the growth stages of cereals. Weed Research 14: 415–421.

SELOSTUS

Kasvunsääteet vaikuttavat kauran kasvuston rakenteeseen ja satoon

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Kasvunsääteitä käytetään perinteisesti viljojen korren pituuskasvun hidastamiseen ja lakoutumisen vähentämiseen. Kasvunsääteiden kortta lyhentävä vaikutus perustuu korren pituuskasvua säätelevän gibberelliini-hormonin tuotannon vähenemiseen tai solun pituuskasvua hidastavan etyleeni-hormonin vapautumiseen. Kasvunsääteiden vaikutuksia korren pituuskasvuun ja kasvuston rakenteeseen on tutkittu paljon ohralla ja vehnällä, mutta kauralla tutkimuksia on tehty vähän. Syitä pieneen määrään alan kauratutkimuksia lienevät kauran vähäinen merkitys viljantuotannossa monissa viljantuottajamaissa ja tuotantopanosten vähäisempi käyttö kauranviljelyssä, mikä saattaa osaltaan vähentää myös laontorjunnan tarvetta.

Tässä kirjallisuuskatsauksessa kartoitetaan kasvunsääteiden mahdollisuuksia muokata korren pituuskasvun lisäksi muita kasvusto-ominaisuuksia ja satokomponenttien muodostumista. Sato suurenee lisäämällä röyhyjen lukumäärää neliöllä, jyvien lukumää-

rää röyhyssä tai vaihtoehtoisesti lisäämällä yksittäisen jyvän painoa. Kirjallisuuden mukaan kasvunsääteillä voidaan vaikuttaa röyhyjä tuottavien sivuversojen määrään ja jyvälukumäärään röyhyssä helpommin kuin yksittäisen jyvän painoon. Nämä muutokset vaikuttavat satoa suurentavasti tai pienentävästi.

Onnistunut laon torjunta kasvunsääteiden avulla helpottaa sadonkorjuuta ja saattaa estää huomattavat määrälliset ja laadulliset menetykset. Joissakin tapauksissa kasvunsäädekäsittely pienentää satoa tai sadonlisä ei kata käsittelyn kustannuksia. Korkeita tuotantopanoksia käyttävässä viljelyssä kasvunsääteiden käyttöä pidetään eräänlaisena sadon vakuutuksena, joka turvaa tuotantopanosten kotiuttamisen puintiaikana. Vaikka vilja ei lakoontuisikaan, kasvunsääteet hyväksytään tuotantopanoksiksi. Kun käytetään kohtuullisia tuotantopanoksia, lakoriski on pieni nykyisillä suhteellisen lujakortisilla lajikkeilla, ja siten kasvunsääteiden tarve vähäinen.