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**PLANT GROWTH REGULATORS TO MANIPULATE CEREAL GROWTH IN
NORTHERN GROWING CONDITIONS**

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ABSTRACT

Plant growth regulators (PGRs) are exogenously applied chemical compounds that regulate stem elongation through inhibiting biosynthesis of gibberellins or releasing ethylene. PGRs have been and are still mainly used in modern, high input cereal management to shorten straw and thereby increase lodging resistance. There are indications that PGRs have potential to modify cereal yield formation and plant stand structure additional to stem elongation. Often these changes occur through changes that mimic similar responses to those attributable to daylength.

The principal interest in this thesis was to evaluate the possibilities of applying some commonly used PGRs (CCC, ethephon, trinexapac-ethyl) to modify cereal growth and formation and realisation of yield potential under Finnish, long day growing conditions. This was particularly directed at studying the response of environmentally adapted cultivars of barley, oat and wheat to early (ZGS12-14) and conventionally timed (ZGS 32-39) PGR applications. As PGR response may vary depending on plant height, the response of tall and short cultivars of each cereal species was evaluated to understand better plant height by PGR interactions. PGR effect on assimilate distribution within main shoots and tillers as well as to roots was monitored. Potential PGR induced stress-effect in treated plants was monitored by measuring post-treatment ethylene production rates from the roots and shoots and measuring carbon dioxide change rate (CER) of PGR treated and control plants.

PGRs were generally ineffective in modifying plant stand structure other than stem length. Application of PGRs at recommended times generally reduced stem elongation. When applied during early growth stages, PGRs failed to reduce canopy height measured at maturity. However, when shoot elongation was measured 14 days after early PGR application, main shoot elongation of all species and cultivars was reduced, indicating similar responsiveness to PGRs at early growth stages, independent of PGR or genotype. PGRs did not change markedly photo-assimilate distribution or translocation pattern in studied cultivars. Tillering was slightly increased by early PGR applications, but the effect was only temporary and at maturity no PGR effect on tiller number was recorded. Root growth, in terms of elongation or dry-weight accumulation, was not improved by PGRs. According to results of ethylene evolution and photosynthesis measurements, PGRs do not appear to induce marked stress in treated plants, or at least not a stress associated with elevated ethylene production or markedly reduced CER. Both yield increases and decreases followed PGR applications. Changes in grain yield were associated with changes in single grain weight or in grain number per head. Due to variable yield responses following PGR applications in the absence of lodging pressure, no general recommendations can be given and careful consideration is needed when selecting a PGR for a specific cultivar.

LIST OF ORIGINAL PUBLICATIONS

The thesis consists of the following papers, which are referred to by their Roman numerals in the text.

- I Rajala, A. and Peltonen-Sainio, P. 2001. Plant growth regulator effects on spring cereal root and shoot growth. *Agronomy Journal* 93: 936-943.
- II Rajala, A., Peltonen-Sainio, P., Onnela, M. and 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.
- III Peltonen-Sainio, P., Rajala, A., Simmons, S., Caspers, R. and 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.
- IV Rajala, A. and 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.

LIST OF ABBREVIATIONS

| | |
|-------|--|
| dd °C | degree days (accumulation of temperature above + 5 °C) |
| CCC | chlormequat chloride |
| CER | carbon dioxide exchange rate |
| cv. | cultivar |
| DAT | days after treatment |
| DL | day length |
| ETH | ethephon |
| GA | gibberellic acid |
| HI | harvest index (%) |
| PGR | plant growth regulator |
| SGW | single grain weight |
| TE | trinexapac-ethyl |
| ZGS | Zadoks growth scale |

1 INTRODUCTION

Plant growth regulators (PGRs) comprise a large group of endogenous and exogenous chemical compounds that can regulate plant growth in numerous ways. In this thesis, the term PGR is used in a restricted sense to refer to exogenously applied chemicals, the so-called anti-lodging agents, primarily targeted to shortening stem length.

PGRs have been and are still mainly used in modern, high input cereal management to shorten stems and thereby to increase lodging resistance (Gianfagna, 1995; Rajala and Peltonen-Sainio, 2000). Lodging that occurs at pre-anthesis or during early grain filling can cause considerable yield loss through, for example, interference with light absorption of the canopy, intra-plant water availability and nutrient and photosynthate transport and translocation. In lodged, humid plant canopies saprophytic fungi can grow and pre-harvest sprouting is likely to occur. This is especially so when high temperatures and precipitation occur simultaneously during the grain ripening period. Furthermore, lodging increases time and energy needed for combine harvesting and drying, which causes an increase in production costs. Therefore, preventing, delaying or reducing lodging of cereals promotes quantity, quality and harvestability of the grain and helps ensure a favourable economic outcome (Rajala and Peltonen-Sainio, 2000).

Plant breeders have successfully directed cereal biomass distribution from the straw to the grains, resulting in cultivars with higher harvest index (HI) and from tall cultivars to shorter, more lodging resistant ones (Austin et al., 1989; Peltonen-Sainio, 1990; Evans, 1993). These modern, short stature cultivars evidently require less exogenous lodging protection. Application of high amounts of nitrogen fertilisers increases the risk of lodging, but their use is limited by the terms of the national agri-environmental support, especially the EU-Nitrate directive. Hence, the relevance of PGRs in current cereal production may be questionable. It is legitimate to ask if the principal aim is to shorten the stem, or if PGRs can in other ways be used to modify cereal growth. Numerous references suggest that PGRs have potential to modify cereal growth patterns additional to their primary target of stem elongation. Tillering and spikelet set are often altered through changes that mimic similar responses to those attributable to daylength. Changes in assimilate demand and

distribution within the plant may provide excess resources that stimulate root growth, tiller and spikelet initiation and grain set and growth. However, most studies have been conducted under a shorter photoperiod compared with the prevailing daylength in Finland. Northern growing conditions strongly influence growth, development rate and yield formation in cereals, enabling the earliest cultivars to mature in less than 90 days (Vuorinen and Kangas, 2002). High seeding rates are used in spring cereals to promote main shoot dominance in plant stands and in yield formation in Finnish growing conditions. Therefore, PGR induced effects and the potential to manipulate cereal growth and yield formation may differ markedly according to growing conditions, especially daylength and management practices. The main focus of the research that comprises this thesis was to evaluate the potential of three commonly used PGRs (CCC, ethephon and trinexapac-ethyl) to modify cereal growth and development under the long-day conditions that characterise the northern margin of cereal production.

2 LITERATURE REVIEW

2.1 Anti-lodging PGRs and their mode of action

Anti-gibberellic plant growth regulators used for shortening cereal stems inhibit gibberellin biosynthesis at different stages of the metabolic pathway (Adams et al., 1992; Graebe et al., 1992; Rademacher, 2000). The exception to anti-gibberellic PGRs is ethephon the stem shortening effect of which is based on inter-cellular ethylene release (Luckwill, 1981).

Gibberellins (GA) are a large group of endogenously synthesised phytohormones that stimulate stem lengthening through enhancing cell elongation (Goodwin and Mercer, 1988). The gibberellin biosynthesis pathway comprises four main phases: 1) the pathway from mevalonic acid or D-glyceraldehyde 3-phosphate to geranylgeranyl pyrophosphate (GGPP), 2) cyclization of GGPP to *ent*-kaurene, 3) conversion of *ent*-kaurene to GA₁₂-aldehyde, and 4) conversion of GA₁₂-aldehyde to other gibberellins (Sponsel, 1995; Lichtenthaler, 1999; Rademacher, 2000). Different antigibberellins block the gibberellin biosynthesis pathway at different stages (Figure 1). Onium-type compounds such as *chlormequat chloride* (CCC) and *mepiquat chloride* interfere with the early stages of gibberellin biosynthesis primarily by blocking the A-activity of *ent*-kaurene synthesis (Graebe et al., 1992; Rademacher, 2000). Nitrogen containing heterocycles, including *triazoles* and *imidazoles*, interfere with oxidation of *ent*-kaurene to *ent*-kaurenoic acid (Burden et al., 1987; Rademacher, 2000). More recently developed PGRs such as cyclohexanetriones, including *cimectacarp*s (*trinexapac-ethyl*), interfere with gibberellin biosynthesis in the late stages of the metabolic pathway, by inhibiting 3 β -hydroxylation of GA₂₀ to active GA₁ (Adams et al., 1992; Rademacher, 2000). Ethephon does not interfere in the gibberellin biosynthesis pathway, but releases ethylene when absorbed in the cell. Ethylene is a growth-retarding phytohormone that *inter alia* stimulates fruit ripening and leaf abscission, and inhibits stem elongation and root growth and nodulation in peas, *Pisum sativum* L. (Goodwin and Mercer, 1988; Jackson, 1991; Lee and LaRue, 1992). Decomposition of ethephon is pH dependent; ethephon is stable at less than pH 4, but when absorbed into neutral cytoplasm, its breakdown to ethylene, chloride and phosphate ions begins (Luckwill, 1981).

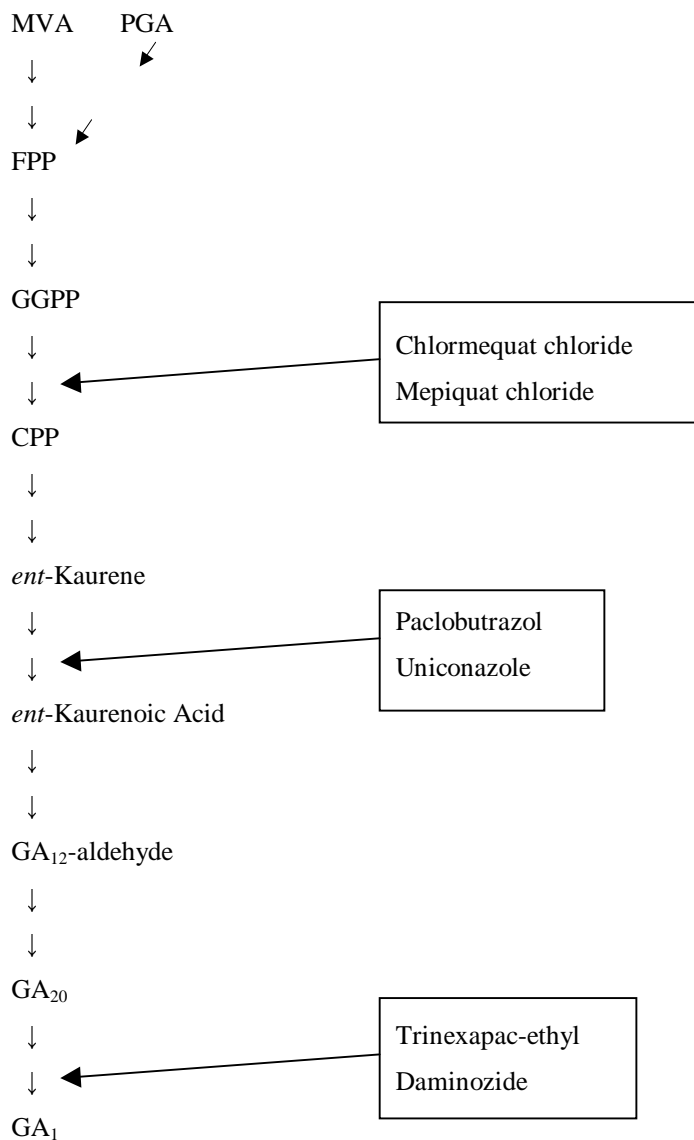


Figure 1. Simplified schematic biosynthesis chain of gibberellins. Some antibberellic PGRs and their points of inhibition are presented. Adapted from Rademacher (2000).

Abbreviations: MVA mevalonic acid, PGA D-glyceraldehyde 3-phosphate, FPP farenosyl pyrophosphate, GGPP geranylgeranyl pyrophosphate, CPP copyl pyrophosphate

Reduction in stem elongation following PGR application can be linked firmly either with reduction in GA synthesis or increase in ethylene synthesis. Though, regulation of plant development and growth in general, seem to be associated with changes in proportional concentrations of different phytohormones, their potential interaction, or changes in sensitivity to phytohormones (Jackson, 1987; Trewavas, 1987; Thomas et al., 1997). This

complexity in hormonal regulation of development and growth does make the issue rather difficult to study and to draw firm conclusions.

2.2 Potential to modify cereal growth through plant growth regulation

Testing PGRs on different cereal species and cultivars began in the late 1950s when Tolbert (1960a, b) described the effect of chlorocholine chloride (CCC) on growth of wheat (*Triticum aestivum* L.) cultivar *Thatcher* (Tolbert, 1960a,b). Since then, numerous papers characterising the effect of CCC, and later other PGRs, on growth, development and yield components of various cereal species and cultivars have been published. The majority of the papers report PGR effects under relatively shorter day conditions compared to daylength in Finland (Humbries et al., 1965; Larter, 1967; Clark and Fedak, 1977; Stanca et al., 1979; Simmons et al., 1988; Naylor, 1989; Ma and Smith, 1991a; Erviö et al., 1995; Sanvicente et al., 1999).

A schematic cereal growth cycle for Finnish growing conditions is presented in Figure 2. Rapid development and a high growth rate characterise spring cereals in northern growing conditions. In oat (*Avena sativa* L.), some 140 growing degree days dd °C are needed for the apex to reach the generative phase, while fertilisation occurs at 470 dd °C (Peltonen-Sainio and Pekkala, 1993). This is considerably less compared, for example, with requirements of spring barley (*Hordeum vulgare* L.) grown in southern Wales (Jones and Allen, 1986). With a longer duration of apical development (till fertilisation), more grains are set (Peltonen-Sainio, 1994). Duration and rate of apical development and number of formed spikelets is strongly controlled by the length of photoperiod (Cottrell et al., 1982; Craufurd and Cartwright, 1989). A long photoperiod combined with a high seeding rate results in plant stands dominated by main shoots (Peltonen-Sainio and Järvinen, 1995). Long day conditions accelerated tiller and spikelet initiation rate, but reduced their number, likely resulting in fewer grains per plant and unit land area (Hutley-Bull and Schwabe, 1982).

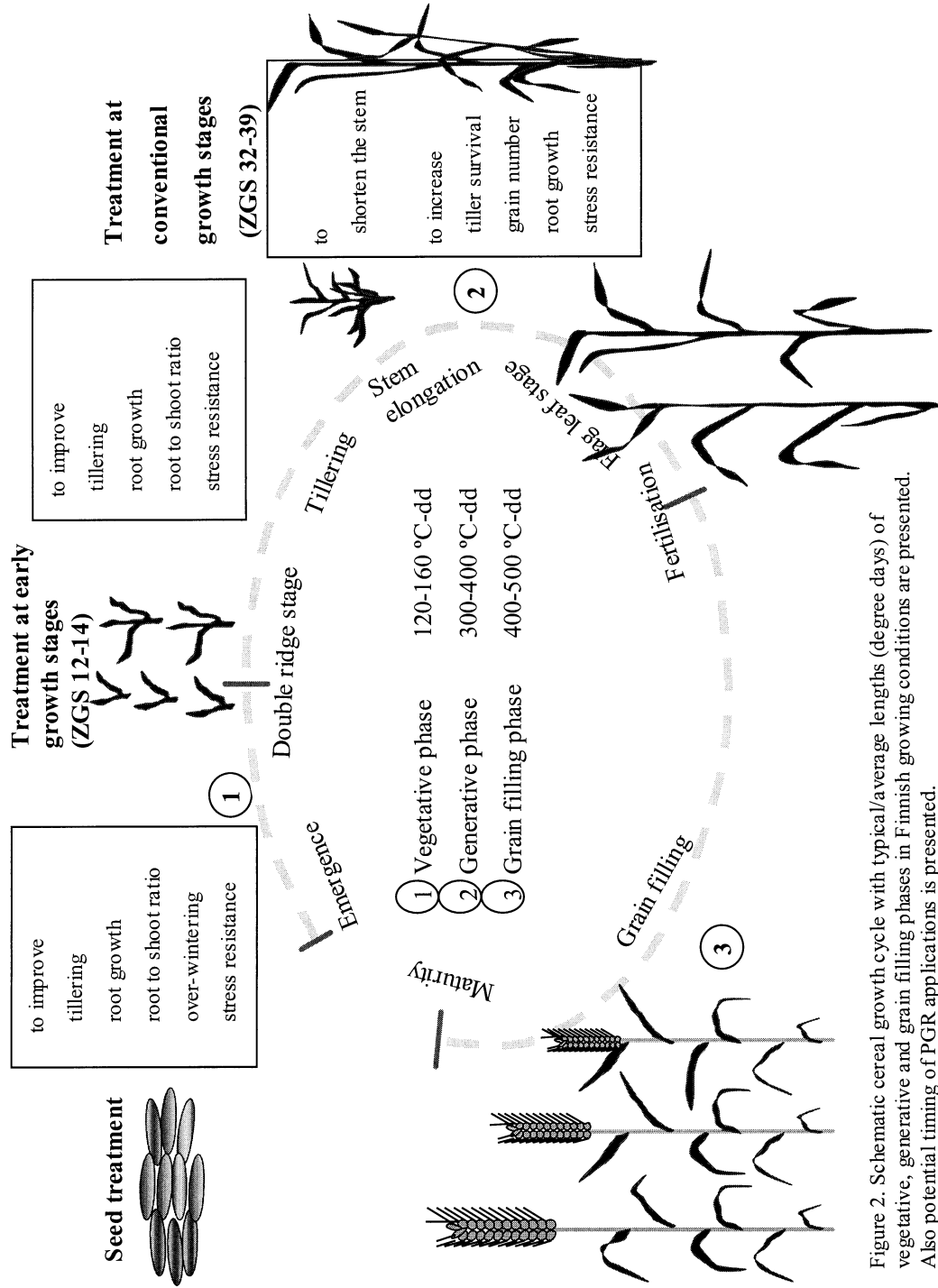


Figure 2. Schematic cereal growth cycle with typical/average lengths (degree days) of vegetative, generative and grain filling phases in Finnish growing conditions are presented. Also potential timing of PGR applications is presented.

According to literature, there are several phases during this growth cycle where PGRs could be applied to modify plant growth and development. For example, application of CCC and triazoles to seed could have potential to improve over-wintering and stress resistance of seedlings (Anderson, 1989; Aufhamer and Federolf, 1992; Webb and Fletcher, 1996; Gilley and Fletcher, 1997). Also, CCC and a mixture of mepiquat chloride and ethephon used as a seed treatment could promote root growth and enhance tillering (De et al., 1982; Woodward and Marshal, 1987; Naylor et al., 1989). Similarly, CCC and ethephon applied prior to tillering have the potential to promote root growth, nutrient uptake and tillering (Cooke et al., 1983; Bragg et al., 1984; Naylor et al., 1986; Woodward and Marshal, 1988; Ma and Smith, 1991b; Peltonen and Peltonen-Sainio, 1997). By applying CCC at the beginning of stem elongation and the other PGRs at later stages, prior to heading, cereal straw can be shortened (Knapp et al., 1987; Simmons et al., 1988; Cox and Otis, 1989; Naylor, 1989; Foster et al., 1991; Ma and Smith, 1992a; Berry et al., 2000; Peltonen-Sainio and Rajala, 2001).

2.3 Changes in morphology and assimilate distribution

2.3.1 Stem elongation

Culm length is likely to be the major factor, though not the sole one, associated with lodging sensitivity (Pinthus, 1973; Crook and Ennos, 1994; Berry et al., 2000). High precipitation and nitrogen fertilization favour stem elongation and increase risk of lodging (Pinthus, 1973). Furthermore, at high latitudes, long days and a low angle of incident radiation favour stem elongation (Smith, 1982; Salisbury, 1985). Shortening the stem through PGR application reduces the risk of lodging. To achieve this goal, PGRs are applied either at early stem elongation phases (CCC, Rademacher et al., 1992) or at more advanced growth stages; latest at booting stage (ethephon, trinexapac-ethyl, Luckwill, 1981; Rademacher et al., 1992). Reduction in plant height as a consequence of PGR treatment is associated with the reduced elongation of internodes (Stanca et al., 1979; Crook and Ennos, 1995; Sanvicente et al., 1999; Peltonen-Sainio and Rajala, 2001). The, uppermost internodes and peduncle, in particular, are shortened.

Antigibberellin-induced stem shortening is based on the PGR capacity to block gibberellin biosynthesis. Antigibberellic CCC was noted to inhibit stem growth in wheat effectively

(Tolbert, 1960b; Humbries et al., 1965), whereas in barley, response to CCC was variable and more genotype dependent (Clark and Fedak, 1977). Also, wheat and oat cultivars in which *Rht1*, *Rht2*, or *Dw6* dwarfing genes have been incorporated, though not necessarily requiring any chemical lodging protection, have shown weak or no response to CCC (Abbo et al. 1987; Beharav et al., 1994; Evans et al. 1995; Peltonen-Sainio and Rajala 2001). Other types of antigibberellins, as well as ethylene releasing ethephon, were developed to broaden the selection of anti-lodging agents for use on more cultivars and species (Luckwill, 1981; Herbert, 1982).

PGR induced increase in lodging resistance does not solely result from stem shortening. Already in the 1960s, Tolbert (1960a, b) described an increase in stem diameter following CCC treatment. This, however, is not in line with results from experiments carried out some decades later. For example, Stanca et al. (1979), Gendy and Höfner (1989) and Berry et al. (2000) did not record PGR induced changes in culm anatomy, other than in internode length. Furthermore, no marked changes in content of structural compounds, such as cellulose, lignin and hemicelluloses, were documented to follow CCC and ethephon treatments (Clark and Fedak, 1977; Knapp et al., 1987). On the other hand, stem structural compounds and diameter and cell wall thickness in the two basal internodes, expressed no clear relationship with lodging susceptibility in barley cultivars (Stanca et al., 1979). Even successful shortening of the stem with PGRs is not inevitably or necessarily associated with reduced lodging as noted in wheat and barley (Knapp et al., 1987; Ma and Smith, 1992a). Onset of lodging may be delayed however (Clark and Fedak, 1977).

2.3.2 Root growth

Growth and yield capacities of plants are strongly dependent on root growth and functioning. Practical difficulties in accurately monitoring root growth in the field means that the importance of root mass and its vertical distribution in the soil is not fully appreciated (Cannell, 1981; Léon and Schwarz, 1992; Mian et al., 1994). There are indications that breeding has altered cereal growth patterns towards shallower or lighter root systems in modern cultivars (Mac Key, 1988; Siddique et al., 1990), though some disagreement exists with this assumption (Comfort et al., 1988; Feil, 1992). Reduced root growth may lessen yield stability in water and nitrogen deficient soils (Schwarz et al., 1991; Léon and Schwarz, 1992). Root length, density and branching of the root system,

seem not directly to determine water uptake capacity and grain yield 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, PGRs simultaneously enhance root growth (Cooke et al., 1983).

Seed treatment or early application of PGRs to emerged seedlings has been employed with varying results to improve root growth. Seed application of CCC stimulated root growth and improved water uptake in wheat grown under arid conditions (De et al., 1982).

Soaking triticale (*X Triticosecale* Wittmack) seeds in tetcyclacis or CCC increased root to shoot weight ratios by inhibiting shoot growth, when measured one week after treatment and by enhancing root growth when measured 9 weeks after treatment (Yang and Naylor, 1988). Early application of CCC, at ZGS 13-14 (Zadoks et al., 1974), slightly enhanced root length in winter barley (measured in July) and root density in winter wheat (measured in April) in the field (Bragg et al., 1984). Early CCC application at ZGS 11-12 to foliage increased root to shoot ratio in winter wheat seedlings grown hydroponically by reducing dry-matter accumulation in shoots and enhancing its translocation into roots (Cooke et al., 1983). However, in trials, in which the response of root growth and nutrient (N, P, K) uptake of long- and short-strawed wheat cultivars to CCC application at ZGS 11-12 was studied, no CCC induced stimulation was recorded in either of the characters measured (Cooke et al., 1983). When CCC was applied to soil, root to shoot ratios increased in barley temporarily for some 7 to 14 days post-treatment due to reduced dry-matter accumulation in shoots compared with roots. This phenomenon was independent of water availability (Enam and Cartwright, 1990). Treating seeds with triazole-type paclobutrazol markedly improved (visual observation) root length and density in waterlogged wheat seedlings, indicating improved capacity to sustain growth in inundated, hypoxic soil (Webb and Fletcher, 1996). No change in root length was recorded following foliar CCC treatment to barley and wheat grown in the field. Also, root biomass accumulation was unchanged for barley, whereas the root biomass of wheat was higher in plants treated with four times the normal dose of CCC (Steen and Wünsche, 1990).

PGRs have also been shown to suppress root growth. Ethepon mixed with mepiquat chloride and applied to seeds reduced root weight and length in barley when measured 19 DAT (Woodward and Marshall, 1987). No change in root to shoot ratio was recorded, indicating similar reductions in dry-matter accumulation in aerial plant parts as in roots

(Woodward and Marshall, 1987). On the other hand, ethephon applied to barley seeds did not influence root and shoot dry-matter when measured both on 21-day-old seedlings and mature plants (Banowitz, 1993). Foliar application of ethephon to barley seedlings reduced root length and weight when measured 15 DAT (Woodward and Marshall, 1988).

According to available information, antigibberellins seem more often to have a greater stimulatory effect on root performance than ethylene releasing ethephon. If altered root and shoot growth is based on source to sink interaction, i.e. demand and availability of photo-assimilates, PGR induced reduction in growth of aerial plant parts may direct photo-assimilates more to the roots, irrespective of the particular PGR used.

2.3.3 Intra-plant photo-assimilate dynamics

Even though photosynthesising leaves are the principal assimilate source for the grains, the capacity of cereal plants to accumulate and store excess carbohydrates temporarily in stem and leaf reserves, and their mobilisation during grain filling, evidently contributes to grain yield (Borrell et al., 1989; Davidson and Chevalier, 1992). The contribution of stored carbohydrates to grain yield is estimated to be approximately 10% and 20-25% of pre- and post-anthesis stored carbohydrates, respectively (Austin et al., 1977; Borrell et al., 1991; Bonnett and Incoll, 1992; Shakiba et al., 1996). Tall cultivars are reported to have larger assimilate reserve stem capacity than short cultivars (Aggarwal and Sinha, 1984; Shakiba et al., 1996; Blum et al., 1997). This potentially contributes to enhanced stress tolerance during grain filling, resulting in improved yield stability over a range of growing conditions (Ehdaie and Waines, 1989; Mäkelä et al., 1997).

Because cereal stem growth, in terms of elongation and dry mass accumulation continues during the early phase of grain filling (Borrell et al., 1989; Bonnett and Incoll, 1992; Peltonen-Sainio, 1999), it is likely to compete for available resources with grains (Austin et al., 1977). It can be hypothesised that PGR induced inhibition of shoot elongation provides excess photo-assimilates for growth of alternative sinks i.e. for grain filling or growth of tillers, or for accumulation of carbohydrate reserves to be used later for respiration or grain filling (Höfner and Kühn, 1982). Results supporting increased activity in both alternative sinks exist. When CCC was applied at the beginning of stem elongation or, even more evidently when ethephon was applied at the flag leaf stage, water-soluble

carbohydrate content was increased in wheat culms when measured at mid grain filling period (Knapp et al., 1987). Similarly, CCC and ethephon applied at the flag leaf -stage enhanced dry matter accumulation in culms and upper leaves in barley (Ma and Smith, 1992b). This increase was likely to be due to enhanced accumulation of non-structural, i.e. remobilisable carbohydrates, as PGRs have not been found to change the structural carbohydrate composition and content (Clark and Fedak, 1977; Knapp et al., 1987). In contrast, short and tall wheat cultivars, whose source capacity was deliberately restricted by reducing the photosynthesising leaf area, expressed no difference in the contribution of reserve assimilates to the grain yield (Rawson and Evans, 1971). Similarly, in a more recent study, grain filling capacity of wheat genotypes, either with or without dwarfing genes (*Rht1* and *Rht2*), expressed strong limitation in sink capacity (Miralles and Slafer, 1995). These results indicate that reducing the stem competition for photo-assimilates does not necessarily result in improvement in grain filling capacity or increase in single grain weight.

2.4 Changes in formation of yield potential

Yield potential can be determined as a sum of its principle components; head number per unit land area, grain number per head and single grain weight. Yield potential is depending on genotype and environment and their interaction (Evans and Fischer, 1999; Rajala and Peltonen-Sainio, 2000). According to its association with verifying traits, yield potential fluctuates in varying sets of environments and genotypes and no fixed value for it can be given. In contrast to this, potential yield - a theoretical maximum yield in a particular environment, is a more constant value. Although, in some occasions, the level of hypothesised maximum grain yield have been stretched (Evans, 1993). When looking for the most dominant factor determining the grain yield in cereals, it is largely the grain number per unit land area (Ferris et al., 1998; Smith et al., 1999).

2.4.1 Tiller growth and productivity

Tillering is an adaptive mechanism of cereals that facilitates utilisation of the space and available resources. Tillering improves cereal plasticity, the ability to respond to fluctuations in plant density and environment. Tiller production is largely dependent on species, genotype, seeding rate, photoperiod, temperature, and water and nutrient status

during tillering period (Langer, 1972; Easson et al., 1993; Peltonen-Sainio and Järvinen, 1995; Crooke and Ennos, 1995). At hormonal level, auxins and cytokinins play major role in apical dominance and tillering pattern (Harrison and Kaufmann, 1982; Salisbury and Marinos, 1985). In addition to these factors, several reports indicate that tiller performance may also be modified by PGRs.

Antigibberellins applied at early growth stages changed wheat response to photoperiod and under long-day conditions apical development rate was retarded and more tillers were produced, mimicking growth under shorter day conditions (Hutley-Bull and Schwabe, 1982; Craufurd and Cartwright, 1989). Chlormequat chloride increased tiller number in barley and triticale, when applied as a seed treatment (Naylor et al., 1989), and in winter barley when applied before or during tillering (Naylor et al., 1986). Similarly, CCC sprayed on to foliage (between ZGS 12 to 31) increased tiller number in wheat (Tolbert, 1960b; Humbries et al., 1965; Craufurd and Cartwright, 1989; Peltonen and Peltonen-Sainio, 1997). Not only the antigibberellic PGRs are capable of promoting tillering. Application of a mixture of mepiquat chloride and ethephon to barley grains stimulated tillering (Woodward and Marshall, 1987). Foliar application of ethephon had a similar effect (Woodward and Marshall, 1988). In Finland, long day conditions particularly promote development rate prior to heading. In conjunction with use of high seeding rates this effectively suppresses tiller formation, leading main shoots to dominate plant stands and tillers to contribute little to grain yield (Peltonen-Sainio, 1999).

When PGR induced tillering result in more heads per plant, this may directly improve grain yield (Humbries et al., 1965; Waddington and Cartwright, 1986). If only the number of vegetative tillers is increased, the phenomenon is more complex. Non-head-bearing tillers may be considered purely as a waste of growth resources. On the other hand, they may serve for a temporary storage of photoassimilates, produced excessively for the requirements of the main shoot growth. During early main shoot stem elongation, substantial amounts of photoassimilates were translocated from the non-surviving tillers of spring barley to the main shoot (Lauer and Simmons, 1988). Similarly, non-surviving tillers were recorded to translocate twice the amount of dry matter to the main shoot as was supplied to them by the main shoot (El-Alaoui et al., 1992). These findings indicate, that non-surviving vegetative tillers may be important for the growth and productivity of the spring cereals.

Head-bearing tiller formation and growth was increased in wheat by CCC treatment at ZGS 16 (Humbries et al., 1965), at ZGS 22 (Peltonen and Peltonen-Sainio, 1997) and in barley at ZGS 31 (Naylor and Saleh, 1987). Also, PGRs other than CCC have the potential to increase head bearing tiller number. Ethephon, mepiquat chloride and mixtures of CCC or mepiquat chloride with ethephon, when applied to seeds or foliage prior to heading, enhanced formation, growth and survival of head bearing tillers in barley (Cartwright and Waddington, 1981; Waddington and Cartwright, 1986; Woodward and Marshall, 1987; Ma and Smith, 1991a; Moes and Stobbe, 1991; Ma and Smith, 1992a) and in wheat (Khan and Spilde, 1992).

As noted earlier, grain yield is determined by number of heads per unit land area, number of grains per head and single grain weight (SGW). Change in any one of these traits alters grain yield when the other traits remain unchanged. However, change in one trait is often compensated for by alteration in another trait and by this means the potential effect on yield is diminished (Höfner and Kühn, 1982; Flintham et al., 1997; Whaley et al., 2000). Thus, PGR induced change in one of these yield components does not necessarily result in improved grain yield.

2.4.2 Grain set

Introducing dwarfing genes into wheat has resulted in shorter stem and improved floret and grain set, further resulting in improved HI (Austin et al., 1989; Borrell et al., 1991; Miralles and Slafer, 1995; Gent and Kiyomoto, 1998). Increase in grain number per unit land area is the major yield determining factor (Ferris et al., 1998; Smith et al., 1999). This increase in grain number could be a result of reduced assimilate competition between elongating stems and yield components at both pre- and post-anthesis phases (Austin et al., 1977; Brooking and Kirby, 1981; Borrell et al., 1991; Gent and Kiyomoto, 1998). However, in some studies, association in assimilate distribution between the stem and grains has not been unequivocally confirmed (Rawson and Evans, 1971; Miralles and Slafer, 1995).

Similarly to achievements gained through plant breeding, PGR induced reduction in stem elongation potentially improves yields in cereals by enhancing grain and spikelet set.

Already in the 1960s, wheat treated with CCC at the six-leaf-stage was reported to result in more grains per head (Humbries et al., 1965). Later, CCC applications before or at stem elongation were noted to increase grain number in barley, oat, triticale and wheat (Naylor; 1989; Ma and Smith, 1992a; Börner and Meinel, 1993; Peltonen and Peltonen-Sainio, 1997). More grains per tiller head were reported to follow ethephon treatment at the beginning of stem elongation in barley (Ma and Smith, 1991a). Moreover, late application of CCC and ethephon, administered by peduncle perfusion, starting at anthesis and continuing for 30 days, resulted in more grains per head compared with untreated barley (Ma et al., 1994). In that particular case fewer aborted grains resulted in the difference in grain numbers per head.

Increase in grain number following early PGR application is due to more initiated 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 more likely explanation for increased grain number per head is reduction in spikelet, floret and grain abortion rate (Ma et al., 1994). Spikelets and florets are produced in excess compared with developed and filled grains, especially in oat panicles, but also in wheat spikes. Marked reduction in spikelet and floret number occurred just prior to heading at stigmatic branch differentiation (Peltonen-Sainio and Peltonen, 1995). Accordingly, if the PGRs modify grain number in oat and wheat, it is more likely to be a result of reduced abortion rate prior to and at early grain filling, rather than further increase in numbers of already abundant spikelets and florets (Craufurd and Cartwright, 1989).

2.4.3 Grain filling

The endosperm cells develop during an approximately 14 day post-fertilisation cell division phase. The number of endosperm cells principally determines the potential grain size (Brocklehurst, 1977). A strong association between cell number and grain size has been established for wheat (Brocklehurst, 1977; Radley; 1978). When cell division ceases, the degree to which this potential is realized depends largely on environmental factors during grain filling. These factors include nutrient status of the soil, water availability, temperature, biotic stresses etc. According to results of earlier studies, grain size seems to be either unaffected, or it is rather reduced than increased 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). If lodging occurs prior to or during early grain filling it may considerably reduce the filling capacity of the grain (Pinthus, 1973; Stanca et al., 1979). If the PGR applications successfully delay the onset of lodging, or reduce the degree of lodging, this indirectly results in single grain weight close or equal to that of non-lodged plant stands. This was the case in barley treated at ZGS 37 with mixture of ethephon and mepiquat chloride (Stanca et al., 1979), and in winter wheat and barley treated with ethephon at ZGS 35 to 45 (Cox and Otis, 1989; Moes and Stobbe, 1991).

2.5 Causing stress or improving stress tolerance?

In general, PGR applications are not recommended for plant stands suffering from or expected to be exposed to drought or other abiotic stresses. This is to avoid potential PGR induced stress and consequent disadvantageous effects on yield formation. Physiological disharmony stress in cereals, caused by PGR application, has been little studied (Rademacher, 2000). Increase in ethylene evolution rate following ethephon treatment is documented (Foster et al., 1992), whereas the effect of antigibberellins on ethylene evolution is not so well documented. Studies conducted on plant species other than cereals indicate that antigibberellins tend to lower stress hormone ethylene synthesis (Grossmann, 1992; Rademacher, 2000). Evidently, PGR applications, especially ethephon, may cause yield reduction (Simmons et al., 1988; Taylor et al., 1991; Stobbe et al., 1992). Barley plants have expressed the highest sensitivity to ethephon and drought during pre-anthesis growth stages, resulting in significant yield reductions (Bergner and Teichmann, 1993). On the other hand, foliar CCC application was noted to sustain photosynthetic capacity of wheat under water deficit and in Fe-deficient maize (*Zea mays* L.) (Sairam et al., 1989; Nenova and Stoyanov, 2000) and reduce the damaging effect of elevated ozone on wheat (McKee and Long, 2001).

There is some further evidence that PGRs applied as a seed treatment or at early growth stages may improve the tolerance cereals to abiotic stresses. Seed treatment with triazole-type (paclobutrazol) PGR improved drought, heat and waterlogging tolerance of wheat seedlings (Webb and Fletcher, 1996; Gilley and Fletcher, 1997). Also, seed dressing with

CCC improved growth and yield performance of wheat under arid conditions (De et al., 1982).

Autumn sown cereals are exposed to various harsh conditions during over-wintering. Seed dressing of winter wheat with CCC and triazole-type growth retardants reduced tillering and suppressed the growth of sub-crown internodes in the autumn (Anderson, 1989; Aufhammer and Federolf, 1992). Shoot apices situated lower below the ground level were better protected against freezing, which possibly resulted in improved over-wintering. Also, PGRs applied at conventional to late growth stages may improve stress tolerance as noted by McKee and Long (2001). They reported that CCC and ethephon treatment at the flag leaf stage resulted in less ozone-induced inhibition of growth and yield formation in wheat. Accordingly, antigibberellins are not very likely to cause marked stress symptoms or to elevate stress hormone synthesis. In addition, some references quite clearly indicate that in some cases PGRs may protect plants from abiotic stresses, though the mode of action varies from changes in morphology to altered physiology or both.

3 OBJECTIVES OF THIS STUDY

The growing season in Finland is short and crop growth is intensive compared with that in other cereal producing countries. Long day conditions and relatively high temperatures from the very beginning of seedling emergency promote development rate. Therefore, yield components are set in a relatively short period and main shoots dominate plant stands. PGRs evidently have potential to modify plant stand structure and yield formation, though not necessarily consistently. The major reason for this probably lies in very divergent environments, species, cultivars, PGRs, as well as in sensitivity to application time and rate of PGRs. For these reasons it is difficult to draw firm and well-justified conclusions about the potential of different PGRs to modify plant stand structure and yield formation under Finnish long day growing conditions. Therefore, the principal interest in this thesis was to evaluate the potential of three commonly used PGRs to modify cereal growth and development in spring cereals. This was particularly directed at studying the response of environmentally adapted cereals to PGR treatments. Thus, the following hypotheses were put forward:

- 1) *PGRs are able to modify plant stand structure and secure the realisation of yield potential of spring cereals grown under long day conditions.*
- 2) *The mode of action and the impact of PGRs differs among PGR compounds, time of application and genotype.*
- 3) *Plant responses to PGRs are different in contrasting light conditions, because long day conditions promote development rate and growth of the main shoot.*
- 4) *Tall cultivars are more responsive to the PGRs than those with shorter stem.*
- 5) *Antigibberellins (CCC, trinexapac-ethyl) and ethylene-releasing compounds (e.g. ethephon), induce temporary stress in treated plants.*

4 MATERIALS AND METHODS

4.1 Laboratories and experimental sites

The experiments done in a greenhouse reported in paper I, and field experiments reported in paper IV, were both conducted at Viikki Experimental Farm, University of Helsinki, Finland. In 2000, an additional field trial was carried out at Jokioinen, MTT Agrifood Research Finland (Paper IV). The seminal root elongation and ethylene evolution studies reported in paper II were carried out at IACR-Long Ashton Research Station, University of Bristol, UK. Tillering responses of oat cultivars to daylength and application of PGRs reported in paper III were carried out in growth chambers at the University of Minnesota, Department of Agronomy and Plant Genetics, USA.

4.2 Crop cultivars

The same set of six cultivars was used in most of the experiments reported in this thesis. The origin and stem lengths of the cultivars are presented in Table 1. To improve applicability of the results of this study, common cultivars were included. This was one of the primary selection criteria for the cultivars. Another important criterion was stem length. To monitor the possible interaction between stem length and PGR response on growth and yield formation, two cultivars of each species were selected that contrasted in stem length. However, modern cultivars do not vary much in stem length and stem length of barley and wheat cultivars differed only modestly. For oat, a tall landrace and a dwarf cultivar, possessing *Dw6* dwarfing gene, were included in the experiments (Table 1).

Barley cultivars included were *Kymppi* (tall) and *Saana* (short), oat included *Veli* (tall) and *Pal* (short), and *Mahti* (tall) and *Tjalve* (short) were the wheat cultivars. Oat cv. *Pal* is a Minnesota-adapted dwarf cultivar, whereas the other cultivars were bred for and adapted to northern, long day conditions. These cultivars were included in the experiments reported in papers I, II and IV.

Table 1. Cultivars, their origin and stem lengths involved in this study

| Species | Cultivar | Origin | Stem length* | Paper |
|---------|---------------|-------------|--------------|----------------|
| Barley | Kymppi | Swalöv | 76 | I, II, IV |
| | Saana | Boreal | 66 | I, II, IV |
| Oat | Bred landrace | Hankkija | 114** | I |
| | Milton | Univ. of MN | | III |
| | Pal | Univ. of MN | 84*** | I, II, III, IV |
| | Salo | Swalöv | 83 | I |
| | Veli | Boreal | 102 | I, II, IV |
| | Virma | Boreal | 95 | III |
| Wheat | Mahti | Boreal | 85 | I, II, IV |
| | Tjalve | Swalöv | 75 | I, II, IV |

* Source: Maatalouskalenteri 1999

** Peltonen-Sainio, 1992

*** average height in three-year field study

To include greater variation in stem length, three oat cultivars, dwarf *Pal*, intermediate *Salo* and old and very tall *Bred Landrace* were involved in root to shoot ratio experiments reported in paper I. Moreover, three oat cultivars were included in experiments with response to daylength and PGR effect. To study the potential interaction between daylength and PGR treatment on leaf and tiller production and stem elongation, oat cultivars adapted to longer and shorter day conditions were selected. *Virma* is a Finnish cultivar adapted to long day growing conditions, whereas *Milton* and *Pal* were bred for the shorter day conditions of Minnesota. These cultivars were included in the experiments reported in paper III.

4.3 Plant growth regulators, their application, timing and application rates

The plant growth regulators used in the experiments reported in papers I, II and IV were chlormequat chloride [CCC, chlormequat (2-chloroethyl)-trimethylammonium chloride a.i. 750 g l⁻¹, Kemira Agro, Finland], trinexapac-ethyl [Moddus, ethyl-(3-oxido-4-cyclopropionyl-5-oxo) oxo-3-cyclohexenecarboxylate 250 g l⁻¹, Kemira Agro, Finland] and ethephon [Cerone, (2-chloroethyl)-phosphonic acid, 480 g l⁻¹, Kemira Agro, Finland]. In experiments carried out in Minnesota (paper III) chlormequat chloride [Cycocel, a.i. chlormequat (2-chloroethyl)-trimethylammonium chloride, Olympic Horticultural Products

Co., PA, USA] and ethephon [Floral, a.i. ethephon (2-chloroethyl), Southern Agricultural Insecticides Inc., NC, USA] were included (Table 2).

Plant growth regulators were applied in the field (University of Helsinki and MTT Agrifood Research Finland, Paper IV) using either a tractor-mounted sprayer or a hand-held plot sprayer at a rate of 300 l ha⁻¹. Treatment rates were those recommended for spring cereals: 1 l CCC ha⁻¹ for oat and 0.5 l CCC ha⁻¹ for barley and wheat, 0.5 l ethephon ha⁻¹ for all species, and 0.3 l trinexapac-ethyl ha⁻¹ for all species. All PGRs were applied either at early growth stages (ZGS 13-14, Zadoks et al., 1974) or at recommended times [CCC at ZGS 31-32 and trinexapac-ethyl and ethephon at flag leaf stage (ZGS 39-40)].

In the experiments carried out in the greenhouse at the University of Helsinki and University of Minnesota, PGRs were applied with a battery or hand-operated small-scale atomizer at 4 to 8 ml per pot or at 1 ml per plant (see Papers I and III). Application concentrations were 0.5% CCC, 0.25% ethephon (Paper I and III) and 0.15% trinexapac-ethyl (Paper I) for all species and cultivars. All applications were conducted at early growth stages (ZGS 12-14) (Table 2).

In experiments carried out at IACR-Long Ashton (Paper II), an automated moving-arm spray applicator (Research Engineers Ltd., London, UK) set at 200 l h a⁻¹ was employed to apply PGRs. PGR treatment concentrations varied from 0.1 to 50 times the recommended treatment rate (see paper II).

As the main interest in this thesis was to study the potential of commonly used PGRs to modify plant stand structure other than stem length, the three PGRs were not applied to the three species according to common practice: Ethephon is not applied to oat in commercial farming, and also, due to inconsistent effect, CCC is not recommended for controlling stem growth in barley.

Table 2. Species, cultivars, plant growth regulators, treatment time, and traits measured in experiments presented in the original papers.

| ZGS | | | | | | | |
|-------|-----------------|--------|-------------------------------|--|--|--|----------------------------|
| I | 1 | Oat | Bred landrace Salo Veli | CCC ETH | 12, 14, 32, 39 " " | Root to shoot ratio | |
| | 2 | Barley | Kymppi Saana | CCC ETH TE | 13 " " | Root to shoot ratio | |
| | | Oat | Veli Pal | " " | " " | | |
| | | Wheat | Mahti Tjalve | " " | " " | | |
| | 3 | Wheat | Mahti | CCC ETH TE | 13 " " | Yield formation Root to shoot ratio | |
| 4 | Wheat | Mahti | CCC | 12 | Root growth Pattern | | |
| II | 5 | Wheat | Mahti | CCC ETH TE | 13 " " | CER | |
| | | Barley | Kymppi Saana | CCC ETH TE | 12 " " | | Seminal root Elongation |
| | | Oat | Veli Pal | " " | " " | | |
| Wheat | Mahti Tjalve | " " | " " | Root and shoot ethylene production | | | |
| III | | Oat | Milton Pal Virma | CCC ETH | 14 " | Tiller and leaf Production Stem elongation | |
| IV | 1 | Barley | Kymppi Saana | CCC ETH TE | 13-14, 31-32 13-14, 39-40 13-14, 39-40 | Plant stand structure | |
| | | Oat | Veli Pal | " " | " " | | |
| | | Wheat | Mahti Tjalve | " " | " " | | Yield formation |
| | 2 | Barley | Saana | CCC | 14, 32 | Plant stand Structure Yield formation | |

4.4 Measurements

PGR effects on main shoot growth and tiller initiation as well as general growth and performance were measured in experiments done for papers I, III, and IV. Yield and yield components were gauged for papers I and IV. PGR induced change in carbon dioxide exchange rate (CER) and biomass accumulation in roots and shoots were measured for paper I. Root and shoot ethylene evolution and seminal root elongation were measured post PGR treatment for paper II (Table 2).

4.5 Statistics

All statistical analyses throughout the thesis were carried out with Statistical Analyses System (SAS Institute Inc. NC, USA). PROC MIXED was employed to analyse the data in all papers, except in experiments 1, 2, and 3 in paper I for which PROC GLM was used. A repeated measures method in PROC MIXED (Littell et al., 1996) was employed when analysing data with repeated measurements, including carbon dioxide exchange rate (CER) paper I), seminal root elongation (paper II), stem elongation (paper III) and above-ground biomass production (paper IV).

5 RESULTS AND DISCUSSION

The question arises as to whether there is still a role for PGRs in modern, sustainable cereal production. This is emphasised because modern short, lodging resistant cultivars require less chemical stem shortening, especially when moderate nitrogen fertilisation is used. Furthermore, consumers' concerns for agrochemical residues in food products and leaching of nutrients and plant protection chemicals into the environment are likely to favour production systems that are less reliant on chemical inputs. On the other hand, when growing conditions are characterised by risk of lodging and subsequent reduction in yield quantity and quality, use of PGRs to ensure economic returns is evidently reasonable. Accordingly, the results presented in the four papers included to this thesis, indicate that early applications of PGRs have often minimal, if any effect, on plant stand structure. Therefore, PGR applications at early growth stages to promote tillering, grain set or root growth are not reasonable. When PGRs are applied at recommended growth stages it allows more time to assess the need to shorten the straw and choose an effective chemical. This strategy results in reduced straw length and lodging reasonably consistently.

5.1 PGR effects on growth dynamics of main shoot and tillers

Use of PGR applications to increase tiller or head bearing tiller number and thereby to improve formation of yield potential is likely to be ineffective in spring cereals grown under long day conditions. High seeding rates of 500 to 600 viable seeds per square meter are commonly used in Finland. Along with long day conditions, this suppresses tiller initiation and growth and may diminish the potential PGR effect compared with more southerly conditions where considerably lower seeding rates are used. In the field, CCC, ETH and TE treatments applied at ZGS 13-14 increased tiller number by 10 to 15 % in wheat when recorded 14 DAT, whereas in barley and oat such increases were not recorded (Paper IV). Despite the increased tiller number, only ETH treatment boosted tiller weight significantly in wheat. This boost in tiller number and growth was only temporary. When plant stand structure was studied from the mature plant samples, no marked PGR effects on tiller number or weight were recorded (Paper IV). It was not determined whether PGRs applied at more conventional times increased tiller number temporarily, but the outcome was evident: none of the treatments resulted in more tillers per main shoot at maturity in the species studied (Paper IV). These results are not in strict agreement with those

published previously. Improved tillering was reported to follow CCC and mepiquat chloride treatment (Humbries et al., 1965; Waddington and Cartwright, 1986; Naylor et al., 1986; Khan and Spilde, 1992), and specifically under northern growing conditions (Peltonen and Peltonen-Sainio, 1997; Peltonen-Sainio and Rajala, 2001). Similarly to the antigibberellins, ethephon treatments have been shown to improve tillering (Woodward and Marshall, 1987; Ma and Smith, 1991b; Moes and Stobbe, 1991). High seeding rates were used in the field trials, but employing lower seeding rates does not necessarily make the cereal plant more responsive to PGRs under long day conditions. This was studied in an additional experiment, in which seeding rates as low as 200 and 300 seeds per square meter for barley cv. *Saana*, did not result in better response of tillering to CCC over conventional rates of 400 and 500 seeds per square meter (Paper IV).

When studied in a controlled environment, early application of (ZGS 12-14) PGRs showed limited potential in increasing tiller initiation in cereals. Tiller production in barley, oat and wheat was enhanced (5 - 90 %) by ETH and TE treatment when recorded 14 DAT in the greenhouse (Paper 1). This boost in tiller number was not reflected in the total weight of the tillers per plant. At maturity, no marked differences in tiller number and tiller weight per plant were noted in wheat cv. *Mahti* (Paper I). The increase in tiller number is in accordance with the results obtained from studies done in the growth chamber with wheat treated with antigibberellins (Hutley-Bull and Schwabe, 1982; Craufurd and Cartwright 1989) and barley treated with ethephon or with a mixture of ethephon and mepiquat chloride (Woodward and Marshall, 1988). Daylength influences development rate and affects tiller number. Contrary to the tillering response of wheat (Hutley-Bull and Schwabe, 1982; Craufurd and Cartwright 1989), no apparent daylength nor PGR effect was recorded for tiller initiation in oat cultivars grown at 14 and 18 h DL (Paper III). PGRs inhibited main shoot elongation and dry-weight accumulation of oat cultivars, but the reduction in main shoot growth was not associated with enhanced growth of T1 and T2 tillers. Tiller elongation and dry weight accumulation was either reduced or unaffected by PGRs (Paper III).

These results from the field and greenhouse trials indicate that PGRs applied before or during tillering have only limited potential to enhance tiller emergence and early growth. Furthermore, it seems evident that either growth of PGR induced tillers ceases at later development stages or untreated control plants make up for the difference in tiller number,

as no marked PGR effect on tiller number or tiller weight was recorded at maturity for any of the cultivars included in this study. Also, PGR treatments did not alter dry-matter translocation from the tillers to main shoot, as no increase in main shoot weights was recorded (Paper I, IV). Altogether, these data do not provide support for marked or long-lasting PGR effects on photo-assimilate distribution and translocation in the studied spring cereal cultivars grown in the northern growing conditions, and do not support postulated hypothesis 1 and 4. Long day conditions promoted development and growth in oat cultivars, but not tillering. There was no daylength or PGR effect on tiller growth pattern.

5.2 Grain yield and plant stand structure

PGR treatments had negative, positive or no effect on yield in the field (Paper IV). This seems to be a common result in PGR experiments (Simmons et al., 1988; Moes and Stobbe, 1991; Taylor et al., 1991; Ma and Smith, 1992a,b; Erviö et al., 1995; Pietola et al., 1999; Peltonen-Sainio and Rajala, 2001). Application of CCC at ZGS 13-14 increased grain yield in oat by 7% and ETH applied at ZGS 39-40 decreased it by 5%. In wheat, an 8% decrease in grain yield followed CCC application at ZGS 31-32 (Paper IV). No statistically significant PGR by cultivar or PGR by year interactions were recorded for grain yield or yield components in oat and wheat. This indicates similar PGR responses independent of cultivar, stem length and growing season (Paper IV).

No main PGR effect was recorded on barley yield. Barley cultivars responded differently to PGR treatments as evidenced by an apparent PGR x cultivar interaction. Yield increases followed ETH and TE applications to cv. *Kymppi* and yield reduction following TE application at ZGS 39-40 to cv. *Saana* (Paper IV). A minor increase (100 to 150 g m⁻²) in grain yield was noted to follow CCC application at ZGS 13-14 and ZGS 31-32 to barley cv. *Saana* in the second experiment of Paper IV.

Yield reduction in CCC treated wheat was associated with reduced main head weight and single grain weight in conjunction with reduced main shoot vegetative growth (Paper IV). This result contrasts with that of an earlier study, in which more head bearing tillers and higher grain yield followed CCC treatment under long day conditions (Peltonen and Peltonen-Sainio, 1997). As there was no change in tiller number or tiller produced grain yield following CCC treatment, increased competition by the tillers can be ruled out as a

source for the reduced main shoot head weight and single grain weight. Neither was it associated with grain number in the main shoot head, as it was unchanged by PGRs. CO₂ exchange rate was not measured, but according to the results of an experiment carried out in the greenhouse, CCC application had no effect on CER, whereas ETH and TE, especially at highest treatment rate, tended to slightly reduce CER in wheat cv. *Mahti* (Paper I). It has been reported that CCC can be without effect or can sustain photosynthesis under stress conditions (Höfner and Kühn, 1982; Sairam et al., 1989; McKee and Long, 2001). Whether CCC application induced stress in treated plants is not known, but indirect evidence does not support such hypothesis as no increase in ethylene production of wheat was recorded following CCC application (Paper II). Furthermore, treatment at four times the recommended application rate of CCC did not reduce wheat yield according to results of a Swedish field study (Steen and Wünche, 1990). It has not been established whether CCC applied at the initiation of stem elongation reduces potential grain size by hindering the cell division phase following anthesis and hence reduces the number of formed endosperm cells. Reduction in cell number is unlikely. It takes two to three weeks to reach anthesis after CCC application at ZGS 32. The subsequent cell division phase lasts approximately another two weeks or less (Brocklehurst, 1977). Reducing the cell division of the developing grain after such a long period of time is not very likely, particularly because the principle mode of action of CCC is to reduce cell elongation, not cell division (Grossmann, 1992). It is likely that effectively reducing stem elongation, CCC may in some cases simultaneously hinder dry-mass accumulation into vegetative and generative plant parts. According to the literature this phenomenon is not unexpected (Humbries et al., 1965; Höfner and Kühn, 1982; Bragg et al., 1984; Steen and Wünche, 1990).

No PGR (main or interaction) effect was recorded on any of the determined yield components in oat (Paper IV). Despite significant yield increase (370 kg ha⁻¹) and decrease (270 kg ha⁻¹) following PGR treatments, no associated response was noted in yield components. Yield increases associated with CCC treatment in oat under long day conditions, have followed either recorded increase in main shoot grain number (Peltonen and Peltonen-Sainio, 1997) or increase in tiller produced grain yield (Peltonen-Sainio and Rajala, 2001). In this study no such changes were noted. Grain yield difference of 200 to 300 kg per hectare reaches the level of statistical significance, but the association of grain yield difference with determined yield components (of 40 plants) is lacking. This is not (totally) implausible when the yield difference of this magnitude is examined at the level of

yield components of individual plants. One to two kernels per plant produce 200 to 300 kg grains per hectare, or similarly, 20 to 30 heads per square meter, when assuming the typical plant density of 400 - 500 plants per square meter. These rather small differences in yield components may not be (constantly) detectable or statistically significant. This remark is applicable for all species, not just for oat.

Some of the PGR induced changes in grain yield of barley were associated with changes in yield components (Paper IV). Head weight and grain number of main shoots were unchanged, whereas changes did occur in yield components of tillers. This was evident for TE applied at flag leaf stage to cv. *Saana*, when there was a 400 kg grain yield reduction associated with lower grain number (-2) in tiller heads. Early application of CCC resulted in a 200 kg increase in grain yield and increased grain number (+2) in tiller heads for cv. *Kymppi* (Paper IV). In contrast, slightly enhanced grain yield in CCC treated barley cv. *Saana* was associated with reduced single grain weight (exp. 2, Paper IV).

To be cost-effective and useful PGR treatments need to increase yield, improve yield quality or facilitate the harvesting. In non-lodged plant stands benefit from the yield increase needs to cover at least the management costs. To reach this threshold level, 150 to 300 kg yield improvement per hectare, depending on the species and PGR, is the minimum requirement. This was reached in early CCC treated oat and in barley cv. *Kymppi* treated with ETH and TE. PGR treatments that stimulate yield effects below the threshold level or which have negative effects are evidently not beneficial. Grain yield and yield component data support, to some extent, the hypothesis 1 and 2, although the responses were not consistently positive. Conventional time applied PGRs were more prone to cause yield reductions than the early applications. No PGR x cultivar interaction existed for grain yield and yield components of oat and wheat, which do not support hypothesis of genotype and stem length dependent PGR response in these species. On the other hand, barley cultivars differed in their responses, but these data alone are not adequate to support the postulated hypothesis 4.

5.3 Stem and root elongation and growth

In general, conventional timing of CCC, ETH and TE application reduced stem height (Paper IV). An exception to this was barley, which did not respond to CCC, and dwarf oat

cv. *Pal*, which did not markedly respond to any of the treatments. In addition, some seasonal variation in PGR responses occurred, as a significant year x PGR interaction was noted for all species. Wheat did not respond to ETH and TE treatments in 1996 and oat cv. *Veli* responded poorly to all PGR treatments in 1998 (Paper IV). PGR effect varied between growing seasons and among cultivars as recorded previously (Clark and Fedak, 1977; Stanca et al., 1979; Waddington and Cartwright, 1986; Cox and Otis, 1989; Ma and Smith, 1991a; Erviö et al., 1995).

On some occasions CCC treatment increased stem elongation in oat. Also, some variation in the response of dwarf oat cultivar *Pal* was recorded to early and later applications of CCC. CCC applied at the usual time tended to enhance stem elongation slightly more than the early application, though the most marked increase in stem elongation (+ 5 c m) was recorded for cv. *Veli* after early CCC treatment in 1997 (Paper IV). As CCC was noted to reduce stem elongation 14 to 19 DAT (Paper III, IV), the elongation of the highest internodes must have been enhanced to result in same height or taller plants compared with untreated controls. This phenomenon was noted previously in other studies (Clark and Fedak, 1977; Waddington and Cartwright, 1986; Abbo et al., 1987; Leitch and Hayes, 1990; Peltonen-Sainio and Rajala, 2001). The reason for the increase in stem elongation is not thoroughly understood, but it is thought to be associated with increased accumulation of GA precursors induced by slowdown of gibberellic acid (GA) biosynthesis. Later, when the inhibition effect diminishes and GA synthesis resumes, there are excess precursors for use in synthesis, resulting in elevated GA levels and enhanced stem elongation (Clark and Fedak, 1977; Primost, 1977; Peltonen-Sainio and Rajala, 2001). However, why this enhancement seems to occur more frequently in species or cultivars insensitive to CCC and cultivars with dwarfing genes, is not thoroughly understood, although Burrows (1986) suggested that dwarfing effect may be turned off at later growth stages in some *Dw6* oat genotypes, resulting in normal or enhanced elongation of the peduncle. It is also noteworthy that TE, which blocks GA biosynthesis at a very late stage, apparently does not have a similar, stem elongation enhancing effect.

Lodging occurred only once during the four years of field trials. Weather conditions and moderate fertilization rates, in conjunction with modern, relatively lodging resistant cultivars, resulted in low lodging pressure during trials. This provided an excellent opportunity to study the potential of PGRs to modify plant stand structure and yield

formation in the field, without interference from lodging. When lodging occurred (1998), PGR treatments reduced its extent in barley cv. *Kymppi*, whereas for oat cv. *Veli* no PGR response was recorded. Stem elongation in all species was favored in 1998, likely due to abundant rainfall (app. 1), resulting in an approximately 10 to 15% increase in stem length over the average for the cultivars in these studies. Height of oat cv. *Veli* reached 135 cm and while PGR treatments did not reduce the stem height, it was prone to lodging. In 1998, species responded very differently to PGR treatments. Oat did not respond to PGRs, only a slight reduction in CCC treatment at ZGS 32 was recorded, whereas wheat responded strongly to all PGRs at both times of application. The reason for this exceptional and marked reduction in plant height of wheat following early application of PGRs in 1998 is not known. Variation in PGR effects to control stem elongation and lodging in the field is quite common however (Clark and Fedak, 1977; Waddington and Cartwright, 1986; Steen and Wünche, 1990; Erviö et al. 1995).

When plant height from soil surface to uppermost leaf ligule was measured 14 days after early-application (ZGS 13-14) of CCC, ETH and TE, there was reduced main shoot elongation (-3.5 to -8.2%) in barley and oat. In wheat, statistically significant reduction occurred only in 1998, when early shoot elongation was reduced by up to 21% by CCC (Paper IV). Short and tall cultivars responded similarly to early PGR treatments in the field and no PGR x cultivar interaction occurred for shoot elongation at 14 DAT for any of the studied species (Paper IV). Even barley and dwarf oat, which often show lack of response to antigibberellins (Clark and Fedak, 1977; Abbo et al., 1987; Peltonen-Sainio and Rajala, 2001), responded significantly to early application of CCC and TE. Similarly, stem elongation of dwarf cv. *Pal* was reduced by CCC at 14 to 19 DAT, though the response was not so evident as in tall cultivars *Virma* and *Milton* (Paper III).

Reductions in early stem elongation indicate that all species and cultivars, irrespective of height, were equally responsive to CCC, ETH and TE applications at early growth stages. If PGR capacity to modify cereal growth - boost root growth, tiller initiation and growth or grain set and filling - is based on availability of photo-assimilates (Cooke et al., 1983; Knapp et al., 1987; Ma and Smith, 1992b), the observed reduction in main shoot elongation provides supporting evidence for the first hypothesis that all PGRs used in these studies had equal potential to modify cereal growth, at least in the short term. Similarly, PGRs retarded main shoot dry matter accumulation in all species in the greenhouse (Paper

I) and in conventional oat cultivars in growth chambers (Paper III). This reduction in main shoot growth was, however, mainly a short-term effect. At later growth stages the effects were no longer noted (Paper I, III, IV). PGR induced reduction in dry matter accumulation to the main shoot was not associated with increased dry matter allocation to tillers in oat. T1 and T2 tiller growth was retarded similarly as for the main shoot and as noted for conventional oat cultivars (Paper III). On the other hand, data from the experiments carried out in the greenhouse (Paper I) showed that ETH and TE treatments increased tiller weight, though the increase was modest and less than the PGR induced reduction in the main shoot weight (Paper I). PGR induced reductions in growth of aerial plant parts were not associated with increased root growth (Paper I). Neither was root elongation enhanced (Paper II).

There was a temporary effect of early PGR application inducing reduction in stem elongation. At maturity no significant early PGR effect was recorded (except in wheat in 1998). A similar phenomenon has been recorded for dwarf oat and barley, in which antigibberellins reduced elongation of lower internodes, whereas accelerated elongation was noted in upper internodes, resulting in an increase in final plant height (Waddington and Cartwright, 1986; Peltonen-Sainio and Rajala, 2001). This stem shortening recorded in the field somewhat contradicts the results obtained from the growth chamber experiment, in which CCC and ETH applied at ZGS 14, reduced pre-anthesis main shoot and tiller stem elongation of conventional oat cultivars, whereas the response was less evident in dwarf cv. *Pal* (Paper III). Stem elongation responses to PGRs at early growth stages do not support the postulated hypothesis of genotype and PGR dependent responses (hypothesis 2). Tall and shorter cultivars (of all species) responded similarly to PGRs applied at early growth stages. When stem lengths were measured at maturity, barley cultivars expressed insensitivity to CCC, likewise the dwarf oat cultivar to all PGRs. Thus, these results of final stem lengths support the postulated hypothesis 2.

Root growth

Dry matter accumulation to the roots was mainly unaffected or slightly reduced by PGR applications to plants grown in the greenhouse. While dry matter accumulation to the aerial plant parts was reduced, this resulted in an increase in root to shoot ratio, particularly for TE treated plants (Paper I). Increase in relative root proportion of the total biomass may improve water use efficiency (Cooke et al., 1983; Enam and Cartwright, 1990). Early

application of CCC in a mixture with herbicides has been recommended in some production manuals in Finland. This is claimed to have a positive effect on cereal root growth and tillering, although the evidence is not particularly compelling. There are some indications that root growth may be stimulated by CCC or other types of antigibberellin (De et al., 1982; Cooke et al., 1983; Bragg et al., 1984; Naylor et al., 1986; Enam and Cartwright, 1990; Steen and Wünche, 1990; Webb and Fletcher, 1996), but actual data indicating improved yield performance following PGR induced root growth stimulation are scarce (De et al., 1982). No root growth measurements were carried out in the field, and although the association between root growth in a pot or in a paper roll and root growth in the field may not be most definite, the results obtained from the greenhouse and growth chambers, indicate that root growth was not likely to be markedly enhanced by PGRs. If there was a PGR effect on root growth in the field, it did not result in improved aerial biomass production in any of the studied cultivars (Paper IV).

Dry weight accumulation in roots, root length and root area at different vertical sections was not changed by CCC applications at ZGS 12 in wheat cv. *Mahti* (Paper I). Short-term seminal root elongation rate (mm d^{-1}) of barley, oat and wheat did not markedly respond to any of the PGRs applied over the range of the recommended treatment rates (Paper II). Only when ETH and TE application rates far exceeded the recommended rate, apparent retardation in root elongation was recorded in barley and oat. When response of root elongation to ethylene gas was studied, a similar sensitivity pattern was noted as for ETH. Barley was the most and wheat the least sensitive species to ethylene gas present in the rhizosphere (Paper II). The capacity of cereal roots to elongate in temporarily water logged, poorly aerated soils, which are prone to accumulation of ethylene, may determine productivity. Differences in sensitivity of roots to ethylene have been noted to occur among species and cultivars (Smith and Robertson, 1971; Crosset and Campbell, 1975; Huang et al., 1997).

Vertical root penetration facilitates water absorption from deeper soil water resources in conditions when upper soil layers contain no available water for the plant. Fast and deep root penetration may therefore characterise water uptake capacity under drought conditions (Hamblin and Tennant, 1987; Comfort et al., 1988). No clear PGR effect was noted on seminal root elongation during 10 days post treatment (Paper II). This and unchanged root

weight do not support the postulated claims that PGR treatments enhance root growth and hence, potentially improve water and nutrient uptake (Paper I, II).

According to the root growth data, stem length was not associated with root elongation rate, at least not during early growth stages of the barley, oat and wheat cultivars included in this study (Paper II). Neither did it have impact on root growth in terms of dry mass accumulation (Paper I). The only exception was for the old, long-strawed, oat cultivar, which had higher root weight compared with the dwarf and conventional cultivars. The root to shoot ratios were the same however irrespective of cultivar and stem length, indicating that some sort of equilibrium exists in root growth, regarding water and nutrient absorption, and in photosynthesising shoots in those oat cultivars included in this study (Paper I).

According to the results of field and greenhouse experiments, PGRs had no significant effect on biomass allocation to tillers or roots. Stem shortening or reduction of the biomass accumulation to the main shoot did not markedly direct photoassimilates for growth to alternative sinks. In some cases when tillering or tiller growth was boosted (Paper I, IV) it lasted only a short period and at maturity no marked change in biomass partitioning within the plant was recorded.

5.4 Ethylene responses

Species sensitivity to ethephon and ethylene

While studying the response of wheat seminal root elongation to increasing ethephon concentration, it was noted that it was hardly affected despite high ethylene evolution in both roots and shoots, whereas root development in barley and oat was more or less stunted at similar ethylene evolution rates. Exposing the roots directly to varying ethylene gas concentration confirmed the assumption of differences in sensitivity to ethylene between species (Paper II). Elongation of barley roots has been noted to be sensitive to ethylene also by others (Smith and Robertson, 1971; Crosset and Campbell, 1975). Wheat was unexpectedly insensitive even to extreme concentrations of ethylene. There is some evidence that wheat root elongation may tolerate relatively high ethylene concentrations (5 ppm) and that root elongation is enhanced at lower (1 ppm) ethylene concentration (Huang et al., 1997). A wheat cultivar tolerant of ethylene was also noted to tolerate hypoxia,

indicating that these two characters may be associated with each other (Huang et al., 1997). In general, barley is known to be among the most sensitive of spring-sown cereals to waterlogging and poor soil aeration. Further studies are however needed to evaluate the possible relationship between ethylene insensitivity and hypoxia tolerance in cereal species.

Stress ethylene formation

Antigibberellins (CCC and TE) applied at various concentrations did not result in significant change in ethylene production rates for any of the studied cultivars. Increasing ethephon treatment rate associated with elevated ethylene production (Paper II). Accordingly, PGR applications at recommended rates should not cause retarded growth or reduced yield due to enhanced stress ethylene evolution. Therefore, results of ethylene evolution do not support the postulated hypothesis of PGR application induced stress. However, CCC applied at stem elongation significantly reduced grain yield and total phytomass in wheat in all three years. Also, TE applied at flag leaf stage reduced grain yield in barley cultivar *Saana* (Paper IV). TE applied at three leaf stage, reduced growth and grain yield of main shoot in wheat cv. *Mahti* (Paper I). Ethylene production was measured from the plants grown in hydroponics, in non-stressed growing conditions, whereas plants in the field were exposed to various abiotic and biotic stress factors simultaneously. Whether these change the response of cereals to antigibberellic PGRs is uncertain. According to ethylene evolution and root elongation data it seems that CCC and TE treatments are unlikely to cause any growth retardations due to elevated ethylene production (Paper II). This is in agreement with the literature (Grossmann, 1992; Rademacher, 2000). Also some results from experiments undertaken in growing conditions of restricted water supply or high ozone, indicate that CCC application does not enhance the stress effect, rather the opposite (De et al., 1982; Sairam et al., 1989; Enam and Cartwright, 1990; McKee and Long, 2001).

6 CONCLUSIONS

Application of PGRs at recommended times generally reduced stem elongation in the three species studied, whereas when applied during early growth stages they failed to reduce canopy height measured at maturity. However, all species and cultivars responded similarly to PGRs when shoot elongation was measured 14 days after early PGR application, indicating similar responsiveness at early growth stages, independent of PGR or genotype.

Antigibberellins applied according to recommendations did not induce significant change in root and shoot ethylene production rate or in seminal root elongation rate in any of the studied cultivars. Increasing ethephon treatment rate above that recommended, raised the root and shoot ethylene production rate in studied species. CCC treatment did not markedly affect photosynthetic capacity of wheat, whereas ETH and TE treatments tended to slightly reduce CER when measured shortly after treatment. According to these results, PGRs are unlikely to induce marked stress in treated plants, or at least not a stress associated with elevated ethylene production or markedly reduced photosynthesis (CER). When root elongation was studied, species were noted to vary according to ethylene sensitivity. Barley was most sensitive to ethylene and wheat least.

PGRs were generally ineffective when applied to modify plant stand structure other than stem length. PGRs did not change markedly photo-assimilate distribution or translocation pattern. Tillering was slightly increased by early PGR applications, but the effect was only temporary and at maturity no PGR effect on tiller number was recorded. Root growth, in terms of elongation or dry-weight accumulation, was not improved by PGRs.

Both yield increases and decreases followed PGR applications. Changes in grain yield were associated with changes in single grain weight or in grain number per head. Due to variable yield responses following PGR applications in the absence of lodging pressure, no general recommendations can be given and careful consideration is needed when selecting a PGR for a specific cultivar.

According to these results, the most favourable economic outcome will probably result

from using suitable PGRs to prevent lodging, and only then under conditions where it represents a substantial risk.

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Appendix 1. Monthly mean temperature and precipitation for growing seasons 1996, 1997, 1998 and the long term means (1961-1990) at Kaisaniemi Meteorological Station, Helsinki.

| | 1996 | 1997 | 1998 | 1961-1990 |
|--------------------|------|------|------|-----------|
| Mean temperature | | | | |
| May | 8.6 | 8.5 | 9.9 | 9.7 |
| June | 13.3 | 16.5 | 14 | 15.0 |
| July | 15 | 19.2 | 16.4 | 17.0 |
| August | 18.1 | 18.9 | 14.1 | 15.7 |
| Mean precipitation | | | | |
| May | 68 | 17 | 38 | 31 |
| June | 58 | 44 | 102 | 41 |
| July | 122 | 12 | 93 | 60 |
| August | 1 | 25 | 122 | 74 |